When your nose knows what you see : multisensory development of visual categorization : evidence from odor-driven face categorization in the human brain

Diane Rekow

To cite this version:

Diane Rekow. When your nose knows what you see : multisensory development of visual categorization : evidence from odor-driven face categorization in the human brain. Psychology. Université Bourgogne Franche-Comté, 2020. English. NNT : 2020UBFCH028 . tel-03112997

HAL Id: tel-03112997
https://hal.inrae.fr/tel-03112997
Submitted on 18 Jan 2021

THESE DE DOCTORAT DE L'UNIVERSITE BOURGOGNE FRANCHE-COMTE

PREPAREE AU CENTRE DES SCIENCES DU GOUT ET DE L'ALIMENTATION

Ecole doctorale n°554 – Environnements-Santé

Doctorat de Psychologie

Par
Madame Diane REKOW

When your nose knows what you see.

Multisensory development of visual categorization:
Evidence from odor-driven face categorization in the human brain

Quand notre nez connait ce que l'on voit.

Développement multisensoriel de la catégorisation visuelle :
Démonstration au niveau cérébral par la catégorisation des visages induite par l'odeur

Thèse présentée et soutenue à Dijon, le 18 Décembre 2020

Composition du Jury :

Monsieur Rossion, Bruno	Directeur de recherche CNRS, Université de Lorraine	Président du jury
Madame Höhl, Stefanie	Professeure des Universités, Université de Vienne	Rapporteuse
Monsieur Collignon, Olivier	Professeur, Université Catholique de Louvain	Rapporteur
Madame Durand, Karine	Maître de Conférences, Université de Bourgogne	Examinatrice
Monsieur Baudouin, Jean-Yves	Professeur des Universités, Université Lyon 2	Directeur de thèse
Monsieur Leleu, Arnaud	Maître de Conférences, Université de Bourgogne	Co-directeur de thèse

ÉCOLE DOCTORALE
Environnements - Santé
Bourgogne I Franche-Comté

Title: When your nose knows what you see. Multisensory development of visual categorization: evidence from odor-driven face categorization in the human brain

Keywords: odor, cognitive development, face categorization, FPVS-EEG

Abstract: This thesis examines whether and how odors contribute to the development of visual categorization in the human brain using fast periodic visual stimulation coupled with scalp electroencephalography (FPVS-EEG). Specifically, we sought to characterize if a neural visual response selective to the face category is modulated by the presence of a body odor in both infants (Study 1, 2, 3) and adults (Study 4).

In infants, the selectivity of the odor effect on visual categorization was addressed by testing separately three categories in three groups of 4-month-old infants presented with a control odor or their mother's odor. We observed that a face-selective response is largely enhanced by maternal odor over the right occipito-temporal cortex (**Study 1**). By contrast, a car-selective response, observed over the right occipital region, is insensitive to the presence of maternal odor (**Study 2**). Finally, when using nonface objects configured as faces (i.e., facelike objects), a facelike-selective response is amplified over the right hemisphere when infants are exposed to maternal odor, and even initiated in some infants who do not selectivly respond to facelike objects in the absence of maternal odor (**Study 3**). In adults, the selective responses to human faces, cars and facelike objects were recorded in a body, gasoline, or control odor context (**Study 4**). While the categorization of human faces or cars is immune to the presence of odors, the body odor enhances the facelike-selective response, suggesting a facilitating effect of a congruent odor when the visual categroy is ambiguous. For these four studies, the general visual response elicited by all stimuli in the rapid visual sequence remains stable across odor contexts, excluding any general effect of odors in terms of arousal/attention.

Altogether, these findings demonstrate a strong facilitative effect of body odors on congruent visual categorizations (i.e., human or illusory faces). We thus illustrate through olfactory-visual associations that information from different senses are integrated to facilitate visual categorization, especially early in life when the visual system is still immature, and that these intersensory congruent associations are maintained until adulthood in the case of ambiguous visual stimuli.

Titre : Quand notre nez connait ce que l'on voit. Développement multisensoriel de la catégorisation visuelle : démonstration au niveau cérébral par la catégorisation des visages induite par l'odeur

Mots clés : odeur, développement cognitif, catégorisation des visages, FPVS-EEG

Résumé : Cette thèse examine dans quelle mesure les odeurs contribuent au développement de la catégorisation visuelle dans le cerveau humain à l'aide d'une stimulation visuelle périodique rapide couplée à l'électroencéphalographie de surface (FPVS-EEG). Nous avons en particulier cherché à caractériser si une réponse cérébrale sélective à la catégorie visuelle des visages est modulées par la présence d'une odeur corporelle chez le nourrisson (Etudes 1 à 3) et l'adulte (Etude 4).

Chez le nourrisson, la sélectivité de l'effet de l'odeur sur la categorisation visuelle a été testée à l'aide de trois catégories étudiées séparément chez trois groupes de nourrissons de 4 mois exposés à une odeur contrôle ou à l'odeur de leur mère. Nous avons observé qu'une réponse sélective aux visages est largement amplifiée par l'odeur maternelle en regard du cortex occipito-temporal droit (**Etude 1**). En revanche, une réponse sélective aux voitures, mesurée au niveau de la région occipitale droite, ne présente aucun effet de l'odeur (**Etude 2**). Enfin, en utilisant des objets non faciaux configurés comme des visages (visages illusoires), une réponse sélective à ces visages illusoires est amplifiée au niveau de l'hémisphère droit en présence de l'odeur maternelle, et même intiée chez certains nourrissons qui ne répondent pas à ces visages illusoires en l'absence de l'odeur maternelle (**Etude 3**). Chez l'adulte, les réponses sélectives aux visages humains, voitures et visages illusoires ont été mesurées en présence d'odeurs corporelles, de gasoil ou d'une odeur contrôle (**Etude 4**). Tandis que la categorisation des visages humains ou des voitures n'est pas affectée par la présence des odeurs, l'odeur corporelle amplifie la réponse sélective aux visages illusoires, suggérant un effet facilitateur d'une odeur congruente quand la catégorie visuelle est ambigüe. Dans ces quatre études, la réponse visuelle générale élicitée par l'ensemble des stimuli de la séquence visuelle rapide reste stable entre les contextes olfactifs testés, excluant un effet général des odeurs en termes d'éveil/d'attention.

Dans l'ensemble, ces résultats démontrent un effet facilitateur important des odeurs corporelles sur la catégorisation d'informations visuelles congruentes (visages humains ou illusoires). Nous illustrons ainsi par ces associations olfacto-visuelles que les informations provenant de différents sens sont intégrées pour favoriser la catégorisation visuelle, particulièrement en début de vie lorsque le système visuel est encore immature, et que ces associations intersensorielles congruentes se maintiennent jusqu'à l'âge adulte dans le cas de stimuli visuels ambigus.

UBFC
UNIVERSITE
BOURGOGNE FRANCHE-COMTE

Université Bourgogne Franche-Comté
32, avenue de l'Observatoire
25000 Besançon

When your nose knows what you see

Multisensory development of visual categorization: evidence for odor-driven face categorization in the human brain

To Yanna,

who made me question how we perceive our world since I was a child

Forewords

The present PhD thesis was directed by Prof. Jean-Yves Baudouin and co-directed by Dr. Arnaud Leleu. My PhD scholarship was fully funded by the French "Investissements d'Avenir" program, project ISITE-BFC (contract ANR-15-IDEX-03) and delivered by the University of Burgundy, France, from the Doctoral School "Environments-Health"[1]. The research described was conducted in the Center for Smell, Taste and Feeding Behavior, in Dijon, France[2] in the Developmental Ethology and Cognitive Psychology lab, with approval of the French ethics committee (Comité de protection des personnes Sud-Est III - 2016-A02056-45) and in accordance to the Declaration of Helsinki.

This research project received financial support from the French "Investissements d'Avenir" program, project ISITE-BFC (contract ANR-15-IDEX-03), the Centre National de la Recherche Scientifique (CNRS), the "Conseil Régional Bourgogne Franche-Comté" (PARI grant), the FEDER (European Funding for Regional Economic Development), and the French National Research Agency (contract ANR-19-CE28-0009).

Realization of this work was of course permitted by the kind contribution of voluntary body odor donors, infants and parents who accepted to participate and comply with experimental instructions. Recruitment was made by Mrs Sylviane Martin and Veronique Boulanger. Technical assistance was provided by Vincent Gigot for EEG preprocessing. The Biosemi EEG system was previously acquired from funding from the Institut Universitaire de France to Renaud Brochard and the ANT EEG system was funded by the "Conseil Régional Bourgogne Franche-Comté" (PARI grant). I am particularly grateful to the CSGA staff for maintenance of the facilities, helping out and solving any material and logistic issue or helping improving it.

Finally, this work would have not become what it is now if not for reviewers and editors who greatly improved the present research and nourished our reflection throughout the process. The anonymity of the peer-review process and the fact that this service is provided benevolently should not cast shadow on their irreplaceable role in the progress science makes every day. On the same note, I would like to thank my jury for the evaluation of this work in this entirety and for providing valuable inputs for the continuity of this project.

---

[1] Ecole doctorale Environnements-Santé of the University of Burgundy, FR

[2] Centre des Sciences du Goût et de l'Alimentation (CSGA), Université Bourgogne Franche-Comté, UMR 6265 CNRS, UMR 1324 INRAE, Agropsup Dijon, 9^{E} Boulevard Jeanne d'Arc, 21000 Dijon, FR.

Curriculum vitae

Publications

** corresponds to a study of this thesis

- Leleu, A.*, **Rekow, D.***, Poncet, F.*, Schaal, B., Durand, K., Rossion, B., & Baudouin, J.-Y. (2020) Maternal odor shapes rapid face categorization in the infant brain. *Developmental Science,* 23(2), e12877. doi:10.1111/desc.12877 **equal contributions* **
- **Rekow, D.**, Leleu, A., Poncet, F., Damon, F., Rossion, B, Durand, K., Schaal, B., & Baudouin, J.-Y. (2020) Categorization of objects and faces in the infant brain and its sensitivity to maternal odor: further evidence for the role of intersensory congruency in perceptual development. *Cognitive Development,* 55, 100930. doi: 10.1016/j.cogdev.2020.100930 **
- **Rekow, D.**, Baudouin, J.-Y., Rossion, B. & Leleu, A. (2020) An ecological measure of rapid and automatic face-sex categorization. *Cortex,* 127, 150-161. doi: 10.1016/j.cortex.2020.02.007
- Damon, F., Leleu, A., **Rekow, D.**, Poncet, F. & Baudouin, J.-Y. (2020) Expertise for conspecific face individuation in the human brain. *NeuroImage,* 204, 116218. doi: 10.1016/j.neuroimage.2019.116218
- Poncet, F., Leleu, A., **Rekow, D.**, Damon, F., Durand, K., Schaal, B., & Baudouin, J.-Y. (2021) Odor-evoked hedonic contexts influence the discrimination of facial expressions in the human brain. *Biological Psychology*, 158, 0301-0511. doi: 10.1016/j.biopsycho.2020.108005

To come…

- **Rekow, D.**, Baudouin, J.-Y., Poncet, F., Damon, F., Durand, K., Schaal, B., Rossion, B. & Leleu, A. Smells like real faces: Odor-driven categorization of illusory faces in the infant brain. *In revision.* **
- Poncet, F., Leleu, A., **Rekow, D.**, Damon, F., Dzhelyova, M. P., Schaal, B., Durand, K. Faivre, L., Rossion, B. & Baudouin, J.-Y. A neural marker of rapid discrimination of facial expression in 3.5 and 7-month-old infants. *In revision.*
- **Rekow, D.**, Baudouin, J.-Y., Durand, K. & Leleu, A. Smell what you hardly see: odors assist categorization in the human visual cortex. *In preparation*. **
- **Rekow, D.**, Baudouin, J.-Y., Brochard, R., Rossion, B, & Leleu, A. Did you spot the face in the clouds? Conscious categorization of illusory faces (face pareidolia) in the human brain. *In preparation*.

Communications

Posters

- **2020: Rekow, D.**, Leleu, A., Poncet, F., Damon, F., Rossion, B., Durand, K., Schaal, B., & Baudouin, J.-Y. Maternal odor selectively enhances the categorization of face(like) stimuli in the 4-month-old infant brain. *International Conference of Infant Studies: virtual ICIS 2020.*
- **2020: Rekow, D.**, Leleu, A., Poncet, F., Damon, F., Rossion, B., Durand, K., Schaal, B., & Baudouin, J.-Y. Maternal odor selectively enhances the categorization of face(like) stimuli in the 4-month-old infant brain. *Federation of European Neuroscience Societies: 2020 FENS Virtual Forum.*
- **2020:** Leleu, A., **Rekow, D.**, Brochard, R., Rossion, B. & Baudouin, J.-Y. Perceptual awareness of illusory faces in the human brain. *Federation of European Neuroscience Societies: 2020 FENS Virtual Forum.*
- **2020:** Damon, F., **Rekow, D.**, Poncet, F., Leleu, A., Magnier, L. & Baudouin, J.-Y. Development of face pareidolia in objects in 3- to 6-month-old infants. *International Conference of Infant Studies: virtual ICIS 2020*
- **2020:** Poncet, F., Leleu, A., **Rekow, D.**, Damon, F., Dzhelyova, M. P., Schaal, B., Durand, K., Faivre, L., Rossion, B. & Baudouin, J.-Y. A neural marker of rapid discrimination of facial expression in 3.5 and 7-month-old infants. *International Conference of Infant Studies: virtual ICIS 2020*

- **2018: Rekow, D.**, Baudouin, J.-Y., Rossion, B. & Leleu, A. Categorization of face-sex in the human brain. *24th edition of the Young Researcher Forum in Besançon, FR.*
- **2018: Rekow, D.**, Baudouin, J.-Y., Rossion, B. & Leleu, A. Rapid categorization of gender from natural face images in the human brain. *18th Annual Meeting of the Vision Science Society, St. Pete Beach, FL, USA. Abstract published in Journal of Vision, 18 (10), 1339, doi: 10.1167/18.10.1339*
- **2018:** Leleu, A., **Rekow, D.**, Poncet, F., Rossion, B., Durand, K., Schaal, B., & Baudouin, J.-Y. Maternal odor shapes rapid face categorization in the 4-month-old infant brain. *18th Annual Meeting of the Vision Sciences Society, St. Pete Beach, FL, USA. Abstract published in Journal of Vision, 18 (10), 787, doi: 10.1167/18.10.787.*

Talks

- **2020: Rekow D**. Maternal odor selectively enhances the categorization of face(like) stimuli in the 4 month-old infant brain. *European Chemoreception Research Organization: ECRO2020, virtual conference.*
- **2020: Rekow D**. How odors assist the developing visual system in human infants. *15th International Conference on Chemical Signals in Vertebrate, Dijon, FR.* (cancelled due to COVID19)
- **2020: Rekow D.**, Leleu, A. & Baudouin, J.-Y. Selective enhancement of neural face categorization by maternal odor at 4 months. *Annual meeting of the groupement de Recherche Neurosciences Cognitives du Développement in Paris, FR.* (cancelled due to COVID19)
- **2019: Rekow, D.**, Leleu, A., Poncet, F., Damon, F., Schaal, B., Durand, K., Rossion, B., & Baudouin, J.-Y. Maternal odor selectively enhances rapid face categorization from natural images in the 4-month-old infant brain. *25th edition of the Young Researcher Forum in Dijon, FR.*
- **2017:** Leleu, A., **Rekow, D.,** Poncet, F., Schaal, B., Durand, K., Rossion, B., & Baudouin, J.-Y. Maternal odor shapes face categorization in the 4-month-old infant brain. *Annual meeting of the groupement de Recherche Neurosciences Cognitives du Développement in Paris, FR.*

Teaching activities and tutoring

- **2019-2020: Tutoring undergraduate students** (BSc 2nd & 3rd year) for an introduction to experimental research and neuroscience in humans (15 hours / student, over 30 students), under the supervision of Dr. A. Leleu
- **2018: Teaching assistant** – Psychology Department – Université de Bourgogne. Over 100 hours in Developmental Psychology (BSc 1st year) and Statistics (BSc 3rd year)
- **2017: Tutoring a Master student** (2 months) under the supervision of Prof. J.-Y. Baudouin Dissertation: *Cross-modal association between face gender and male and female body odors in 3- and 6-month-old infants*

Grants and awards

- **2020: FENS Forum Award**, awarded by the French Neuroscience Society, to participate in the 2020 FENS Virtual Forum (130€).
- **2019: Travel grant** for an in-doctoral internship, awarded by Ecole Doctorale ES-Université de Bourgogne, 1000 €, at the Institut des Sciences Cognitives (Bron, FR). Supervisor: Dr. J.-R. Hochmann
- **2017-2020: PhD scholarship.** Funded from an interdisciplinary research grant, I-Site BFC (French “Investissements d’Avenir” program), 140 k€ (PI: Prof. J.-Y. Baudouin).

Special thanks

It all started in September 2015, when I didn't really picture what research looked like: I had just enrolled in an Ethology Master's program and I was contemplating lab's research on insects' (chemical) behavior. What were the odds for adding a simple keyword in my Google search that would make me find the team's webpage? Intrigued by the transdisciplinarity echoing my forever quest for knowledge, I sent my application. Little did I know, that was the tiny flap of a butterfly's wings that would revolutionize my entire life? Luck and curiosity are the first recipients of this cosmic gratitude.

Along this path, I met so many people. I was the protagonist of my own quest, but I could never have achieved this on my own. It has been an epic story. I lived it with all my heart, surviving through the burning fires of hell which made me stronger, relieved by the intense gratitude of accomplishment, enduring the harsh moments of self-doubt and sharing laughter with everyone.

For their trust, wise advice, discrete tutoring and remarkable integrity, I could never be thankful enough to my supervisors. Jean-Yves Baudouin and Arnaud Leleu have opened so many magic doors, the right doors, and supported me all along this quest. "A thesis is nothing final, it is just the beginning", they said, and it echoed along my path, in the hardest moments, like a lighthouse in the storm.

Like every good story, this one also has its tavern, where people meet, talk, laugh, and replenish themselves in many ways. There, you can always find a helping hand. These gatherings were, and still are, precious. I thank my colleagues, the long-lasting like the more fleeting ones, for making this journey so enjoyable, for providing an open ear, sharing tea at work and beer after work. Present sparser than on a daily basis were also my childhood friends, my anchor of reality in the disconnected world that research can be sometimes. My faithful companions (for better or for worse) have always assisted me across this spatiotemporal journey called life. Finally, so many "minor protagonists", mentors of past days and (unsuspected) role models, who played discrete but valuable role in getting me here and shaping the protagonist I became throughout my epic journey.

Happy she who, like Ulysses has travelled well. I was told to tell a story. This is just the beginning. It has been rewarding in many ways. I have loved living it, I have loved saving it here. You are all part of this story. I hope you will enjoy it as well.

Remerciements

Cette histoire commence en Septembre 2015, à une époque où je ne me représentais pas encore le monde de la recherche, et alors que je commençais tout juste mon master en Ethologie, je considérais les thématiques de recherche de laboratoires sur le comportement chimique des insectes. Comment penser que le seul ajout d'un mot clé dans ma recherche google me ferait tomber sur la page web de l'équipe ? La transdisciplinarité revendiquée a fait écho à ma quête éternelle de connaissances, et j'ai envoyé ma candidature spontanée. Mais ce que je ne savais pas encore, c'était que ce simple battement d'ailes de papillon allait bouleverser ma vie. Je me dois donc de remercier en premier lieu : le hasard et la curiosité.

J'ai fait beaucoup de rencontres sur ce chemin. Bien que protagoniste de ma propre quête, je n'aurais jamais pu réaliser tout cela seule. Elle aura été épique. Je l'ai vécue de tout mon coeur, bravant les flammes déchainées de l'enfer qui m'ont rendue plus forte, récompensée par la liesse du travail accompli, supportant les durs moments de remise en question, et partageant, aussi, les bons moments avec tous.

Pour leur confiance et leurs conseils toujours avisés, leur encadrement discret et leur remarquable intégrité, je ne pourrais jamais assez remercier mes directeurs. Jean-Yves Baudouin et Arnaud Leleu m'ont ouvert tant de portes, les bonnes portes, et m'ont soutenue au long de cette quête. "Une thèse n'est pas une finalité, c'est là que tout commence", m'ont-ils dit, et cela a résonné dans mes pas, dans les moments les plus durs, comme un phare sauvant du naufrage en pleine tempête.

Comme tout bon récit, celui-ci a également sa taverne, où les gens se réunissent, discutent, rient et se ressourcent de bien des manières. Là, vous trouverez toujours de l'aide. Ces rassemblements étaient précieux, et le sont toujours d'ailleurs. Je remercie mes collègues, ceux d'antan et ceux d'un jour, pour avoir ponctué cette aventure d'agreable, pour avoir été d'une écoute attentive, pour avoir partagé des tasses de thé et des bros de bière. Toujours présents malgré la distance, mes amis d'enfance représentent cette ancre qui me maintient les pieds sur terre quand le monde de la recherche, parfois déconnecté du quotidien, essaie de m'embarquer trop loin. Mes compagnons fidèles, pour le meilleur et pour le pire, m'ont toujours accompagnée dans cette aventure spatio-temporelle qu'on appelle la vie. Enfin, d'autres acteurs, aux rôles que certains qualifieraient de "mineurs", d’anciens mentors, des personnes qui m’ont inspirée, ont tenu un rôle presque furtif mais non moins important car il m'aura mené jusqu'ici et aura contribué à faire de moi la protagoniste que je suis devenue à l’issue de cette épopée.

Heureuse qui, comme Ulysse, a fait un beau voyage. On m’avait demandé de raconter une histoire. Ce n’est que le début. Cette expérience aura été plus que gratifiante. J'ai adoré la vivre. J'ai adoré la sauvegarder entre ces pages. Vous faites partie de cette histoire. J'espère qu'elle vous plaira aussi.

* Casting (non-exhaustive)

Co-authors, collaborators and colleagues / co-auteurs, collaborateurs et collègues :
Karine Durand, Benoist Schaal, Bruno Rossion, Renaud Brochard, Bruno Patris, Alexandra Destrez, Fanny Poncet, Fabrice Damon, Alessia Baccarani, Magali Tassone-Kley, Nawel Mezrai, Justine Alary, Logan Magnier.

Friends & relatives / Amis & proches :
The BigFive, Katrin, Eline et Antoine, Tiste, Flomo, Jory et Charline, Lulu, Antoine et Julie, Pierrot, Jeannot, Robin, Myrtille, Thibault, Roman, Jules, Romain, Alexis, Sylvain, Camille, Caro, Julie, Pauline, Flav, Hugo, Maë, Katia, Océane, Ayaka, Pear, Laure, Paul, Olivier, … Lydie, André, Yanna, Mookie, Hime & Umi.

Adjuvants :
Sylviane Martin, Véronique Boulanger, Cédric Serrano, Christine Chabert, Daniella Genet, Vincent Gigot, Josette Thery, Christelle Caillot, Thierry Rigaud, Sabine Duchesne, Benjamin Nourry.

Stunt(wo)man / Cascadeuse :
Diane Rekow

Summary

Introduction

Chapter one

Chapter two

General discussion

Résumé de thèse

List of figures

List of boxes

Abbreviations

BCA: baseline corrected amplitude (μV)

EEG: electroencephalography

ERP: event-related potential

FFT: fast Fourier transform

fMRI: functional magnetic resonance imaging

FPVS: fast periodic visual stimulation

iEEG: intra-cranial EEG

lOT: left occipito-temporal cortex

mO: middle occipital cortex

NIRS: near-infrared spectroscopy

OT: occipito-temporal cortex

PET: positron emission tomography

ROI: region of interest

rOT: right occipito-temporal cortex

SNR: signal-to-noise ratio

VOTC: ventral occipito-temporal cortex

Introduction

This work proposes to evaluate the role of body odor in the development of visual face categorization. In that respect, a main focus will be given to olfactory/visual systems and cognition and body odor/face perception along the dissertation.

The theoretical background will be introduced following two major axes:

In a **first section**, we will consider that our daily experiences are multisensory by essence. We will first explain how perception is analogous to categorization, aiming at clarifying our surroundings by segregating inputs and grouping others. In the light of these subtending functions, insights on their relationship to the development of perceptual knowledge will be addressed. In that respect, the development of sensory modalities will shortly be explained and we will review models of multisensory integration to understand how it may work for the developing brain. The **second section** evaluates the perception of conspecifics from the visual and the chemical senses, by detailing processing mechanisms of face and body odor perception at a behavioral and neural level, across development.

This introduction chapter will conclude on the operationalization of our research question. A brief methodological account will be given, since the general method is a common string to the four studies presented hereafter in the form of independent manuscripts.

I. Through a multisensory journey

A. Making sense of our senses

1. An adaptive perceptual experience

Perception is an active mechanism through which we are able to apprehend our physical environment. It is to be considered apart from sensation, the latter being the stimulation of receptors of our sensory organs, i.e., an isolated response to a local stimulus. According to Gestalt psychologists (Wagemans et al., 2012), perception depends on *patterns* of stimuli organized in space and time, i.e., it goes further than isolated responses to local stimuli. It consists in integrating these sensations into a whole, i.e., a percept, therefore linking biological stimulation (physiology) to thoughts and representations in the mind (psychology). It is at the core of all living life. The topic has been widely studied, from the Antiquity to artificial intelligence today. While the purpose of this dissertation is not to provide an historical description of the concept nor a resolution to ongoing debates, we will establish the bases of our theoretical considerations.

What has fascinated or troubled so many thinkers about perception, is the apparent simplicity and automaticity of how it works. We perceive things around us with an impressive accuracy, speed and almost "universality" (i.e., we perceive the same world and relate to descriptions made by others), without mostly realizing all that we process, as it feels like water flowing down a stream. Perception is by essence multisensory (Gibson, 1966; Stein and Meredith, 1993) as we are embedded in a wealth of continuously changing information from all our senses. It is a fundamental cognitive function, which places us in the world and allows us to act on it, react from it, and interact with it. Although an infinite number of stimuli are continuously hitting our receptor cells, the cognitive abilities of our perceptual system are limited. How come we do not feel overwhelmed? How do our cognitive system and brain manage to handle this amount of information without us noticing it?

It has been argued that the world is ambiguous by itself and perception serves as a filter to make sense of it (Ernst and Bülthoff, 2004). Perception is an accurate mechanism which allows to detect salient inputs amongst a noisy background (i.e., the noise refers to the "non-relevant" elements), which implies that noise is implicitly processed to determine whether information is indeed noise or is, instead, relevant. Robust perception is thus defined as the combination and integration of multiple sources of information; it aims at maximizing the information (by combination) while reducing its variance to increase the reliability of the percept (by integration). Hence, if one sensory modality alone cannot obtain this "robust" percept, it will automatically rely on other channels and integrate multisensory information (Ernst and Banks, 2002; Ernst and Bülthoff, 2004). In fact, perception allows us to act/react/interact immediately with our surroundings, which suggests that it is a very fast and parallel process. From this point of view, perception is not a passive mechanism and sensory stimuli alone (bottom-up processes) cannot result in a robust perception. It necessarily relies on priorly acquired knowledge to rapidly identify inputs based on the most probable interpretation given the available information. Perception is thus a dynamic mechanism able to actualize its interpretation depending on the incoming flow of information. In that respect, it reduces the cognitive cost engaged to analyze and process incoming sensory inputs and contributes to simplify our world, as interpretation can already be inferred from fragmented information (Ernst and Bülthoff, 2004; Gregory, 1997).

Perception is also necessary for acting. For that matter, our brain considers objects by matching sensory inputs with our representations. Objecthood offers a perceptual consistency as it congregates perpetually changing inputs into a viewpoint invariant representation of the object. In addition, objects become salient percept because they are distinguished from the other objects and their perceptual context. In sum, our perceptual experience takes place in a multisensory environment and is the result of the combination of sensory evidence with prior knowledge to respond adequately and immediately to our surroundings (Ernst and Bülthoff, 2004). It is a filter through which we can simplify our world to focus on what is useful for us, usually at the object level (i.e., not molecule/atom level), to bridge the gap between reality and knowledge (Arterberry et al., 2016).

2. Categorization as a perceptual tool

Conceptualization of categorization could provide additional elements to understand perception, as perceiving an object means categorizing it. Indeed, every object we encounter is automatically categorized (i.e., matches a mental representation), by isolating the items from the noise (i.e., discrimination) and gathering similar items together (i.e., generalization), which result in the simplification of our surrounding. It is the most important brain function when it comes to making sense of our senses.

The traditional definition implies that categorization serves to reduce the complexity of our world by understanding and predicting objects so that we can adapt our behavior consequently (Barsalou, 1990). One of the cognitive strategies to that extent consists in considering categorical perception where between-category separation and within-category compression are emphasized (e.g., living vs. non-living), as opposed to continuous categories (e.g., big vs. little things depend on a referential) (Harnad, 2003). Categories are infinite and are themselves organized, as proposed by Rosch (1978)'s taxonomy: the superordinate level comprises broad categories (e.g., animals), on the contrary, the subordinate level comprises much narrower ones and represents the level of the exemplar (e.g., my cat) and the basic level (e.g., pets) corresponds to the most useful category type and most commonly used, being a compromise between the two previous ones. In each of these levels and categories, prototypes exist and the distance from the exemplar to the prototype is thought to be reflected in the time needed for its recognition (Rosch, 1978). Taken together, categorizing consists in assigning mental representation to a set of stimuli perceived as a whole. In that respect, the effect of expertise (i.e., being extensively familiar with one category so that recognition is well performed at the subordinate level) is related to prior knowledge. Indeed, expertise, just like prior knowledge, actively contributes to object recognition to which this knowledge applies (e.g., Tanaka and Curran, 2001).

Categorization constitutes an integral part of our perceptual experience and help making sense of it by drawing meaning from organized categories. By having a structured, yet flexible, organization of object representation, categories thus stand as a useful tool in our perceptual experience because they have the advantage to represent relations between concepts/objects and these relations are relative to the framework at stake at a given time. In that respect, they could operate as the prior knowledge necessary for perceptual abilities. The mechanisms involved are dynamic as they refine with experience, which suggests that they could as well be susceptible to bottom-up influences.

3. The role of context

Interpretation of entering signals from the flurry of cues available is more challenging than we may feel. In that respect, and additionally to prior knowledge (i.e., top-down), contextual information (i.e., bottom-up) can help gathering what belongs together to form a whole and increase our probabilistic inferences.

While considering perceptual abilities, the (multisensory) context provides complementary information to help disambiguate inputs. In line with the contribution of prior knowledge and stored representations, context can even constitute a prime to object identification (Kveraga et al., 2007; Lakatos et al., 2009; Oliva and Torralba, 2007). For instance, intersensory influences could help detect congruent information (e.g., an object and its scent) and combine them into a complete, multisensory, representation (i.e., a fresh fruit), whose facilitated identification translates into an adapted behavior (e.g., Seigneuric et al., 2010). In addition, it has been proposed that the predictive value of contextual information guides our attention to the object (Chun, 2000). Indeed, objects appear to us following structural organization with their context in reality and these links can result in predictions: some objects are expected systematically in a particular portion of the visual field for instance (e.g., clouds in the sky), whereas others are experienced in relation to other objects (a chair facing a table; for a recent review, Kaiser et al., 2019). Contextual associations can thus actively help category – and thus object – recognition (Oliva and Torralba, 2007) at behavioral and brain levels (e.g., Kaiser et al., 2014).

While it feels immediate and automatic, perception functions thanks to a complex mechanism. It is a dynamic process combining bottom-up and top-down processes to give the most probable interpretation of the information as rapidly as possible. Importantly, it serves to simplify our ever-changing environment to help our consciousness grasp the useful elements for our behaviors and mental activities. Our brain relies on prior knowledge to make sense of incoming signals by drawing representations from organized associations (i.e., categories). Context functions as an influence that can tilt the balance in favor of the best interpretation (Oliva and Torralba, 2007). But in this multisensory world, are all senses equal? Most importantly, how do these most fundamental cognitive abilities develop across the senses? According to our goal, we will address these questions with a focus on olfaction and vision. We will first address the neurofunctionality of olfaction and vision and their development, before considering their differences and how multisensory perception could develop in infancy.

B. Sensory development

For each sense, sensory processing follows a similar path: some energy touches the organ and sensory receptor cells, which transform this energy into a nervous signal. Neural inputs go then through different sensory relays and to the central nervous system where the sensation becomes meaningful information, the percept.

1. Neuro-anatomy and neuro-functionality of olfaction

The olfactory system, "highly conserved" across mammals (Ache and Young, 2005), is usually composed of the primary system, the accessory system (i.e., vomeronasal), whose existence in humans is clearly debated; and the trigeminal system, whose sensory function remains enigmatic but is sensitive to irritating properties of chemicals (Doty and Cometto-Muñiz, 2003). Olfaction relies on the perception of chemical substances, arranged in mixtures.

When air is breathed or sniffed (i.e., orthonasal pathway) or aspirated through the mouth (i.e., retronasal pathway), molecules enter the nose and the nasal cavity to meet the olfactory epithelium and its mucus covering the upper portion of the nasal cavity. There, odor molecules are passively transported and dissolve in the mucus. They bind with the cilia of olfactory sensory neurons (i.e., the dendrites were receptor are expressed) which are responsible for signal transduction. Continuously replaced across life, they are the only neurons reaching the external of the brain cavity by crossing the bone and reaching the nasal cavity. Most of olfactory sensory neuron code for only one type of receptor (Saito et al., 2009), and we would have, in each epithelium, about 12 million bipolar receptor neurons (Moran et al., 1982). Their axons cross the cribiform plate of the ethmoid bone and arrive at the ipsilateral olfactory bulb, first relay station of the primary olfactory cortex. There, in specialized glomeruli structures and supported by periglomerular interneurons, they synapse with mitral cells whose axons constitute the olfactory tract connecting to the cortex.

The main component of the olfactory cortex is the piriform cortex located in the ventral temporal lobe (Price et al., 1991). Neural connections are also widely projected across the brain from the olfactory bulb including the orbitofrontal cortex and portions of the limbic system: the amygdala, the hippocampus, the enthorinal cortex, the hypothalamus and the thalamus. Importantly and contrarily to the other senses, the thalamus is a secondary recipient in olfaction, i.e., connections are post-cortical. Unlike knowledge on the visual system, the neural bases of olfaction are still not completely understood. In a recent fMRI study, the functions of these subregions were explored by qualifying their unique and shared connectivity (Zhou et al., 2019). Authors found that subdivisons of the piriform cortex could be involved in combinatory motor planning for grasping and eating (frontal → caudate/putamen and primary motor cortex) and for modulating breathing in a protective way (temporal → brainstem raphe magnus, posterior insula). The anterior olfactory nucleus is highly connected to the orbitofrontal area and additional regions related to object recognition and could thus play a role in odor identification. Finally, the olfactory tubercle selectively connects with areas associated with emotional processing and social cognition, notably, face perception (anterior paracingulate cortex, left frontal pole and left fusiform gyrus), something we will bear in mind for this dissertation work (Figure I-1).

Regarding the anatomical development, as early as 4 weeks post ovulatory, the free nerve of the trigeminal system innervates the respiratory and olfactory mucosae, able to mediate tactile reactivity and thus probably chemosensation in the embryo. In utero, the primordial olfactory bulbs are formed around weeks 6 to 8. By week 7, the axons of olfactory sensory neurons are channeled into the olfactory nerve and during gestational weeks 10 to 11, the dendrites (i.e., cilia) grow out to the membrane of the epithelium. Olfactory sensory neurons are thus morphologically mature and connecting to the olfactory bulbs from at least week 11. At around 6 months of gestation, the amniotic fluid fills the nasal cavity (Schaeffer, 1910) and same age preterm neonates react and can habituate to unfamiliar odorant (i.e., menthol; Sarnat, 1978). In sum, the nasal chemosensory structure benefits from an early maturation, probably supporting chemosensation functioning from at least the last gestational trimester. From 6 months of gestation onwards, olfactory neurons bathe in the amniotic fluid, conveying many and varied chemostimuli that dynamically meet the receptors, as the fetus increasingly performs pseudo-respiratory movements (rhythmic expansion-contractions of the thorax) along with the progress of gestation. While no experimental evidence is reproducible on human fetuses, animal models have shown direct intrauterine learning of odorants (Schaal and Durand, 2017). This ability is inferred in humans by using the mother as a vector and exposing odorant via her diet, then presenting this odor to the newborn. Numerous studies have evidenced this effect with different food products (Faas et al., 2000; Mennella et al., 2001; Schaal et al., 2000) and biological substances from the intrauterine environment (Marlier et al., 1998) in humans.

2. Neuro-anatomy and neuro-functionality of vision

"The eye is not a camera, but a biological tool adapted to detect pertinent visual information in the environment" (Muntz, 1964). In vision, the external energy which comes to our eyes is the light reflected by objects. Electromagnetic wavelengths are refracted by the cornea and lens, and project onto the retina covering the bottom of the eye. The cell membrane of the retina is composed of 3 layers.

Photoreceptor cells are the first step of sensory transduction by converting light into electromagnetic signal and they dwell in the deepest layer. They are of two kinds: rods and cones, each having different topographies and light sensitivity (De Valois and De Valois, 1993). Rods are mostly present on the periphery of the retina and are sensitive to dim light environments, thus mainly sustaining black and white vision. On the other hand, cones (short, medium, large, each sensitive to a dedicated range of wavelength) are most concentrated at the center of the eye, in the fovea, and respond to color vision. The fovea corresponds to the area with the highest acuity. Bipolar cells, which ensure transduction continuity by synapse from rods and cones, are also much more condensed in the fovea area (almost one bipolar cells for each cone) than in the periphery where one bipolar cell channels inputs from a higher number of cells. Finally, the ganglion cells, synapsing with bipolar cells and constituting the outermost layer, are sensitive to local variation of contrast with the relay of horizontal and amacrine cells, themselves converging neural inputs from deeper layers. As a result, the activation of about 130 million photoreceptors converges into 1.5 million axons. The axons of the ganglion cells become the optic nerve (cranial nerve II) to transduce information from the retina to the brain following a retinotopic organization, i.e., the spatial arrangement of visual inputs is preserved and projected following the same mapping within the visual stream.

Following the optic tract, the optic nerve from both eyes meets in the optic chiasma (inferior to the hypothalamus), where axons from the temporal retina area follow their course in ipsilateral regions, while axons from the nasal retina area cross to contralateral regions; allowing inputs from each hemifield to be processed conjointly. Projections then arrive at a thalamic relay in the lateral geniculate nuclei of both hemispheres, where connections project through optic radiation to the primary visual cortex (V1, striate cortex) on ipsilateral bilateral occipital regions. The retinotopic mapping, there, is preserved (the fovea represents approximately half of V1), however, it becomes more complex in the other visual cortical areas. In parallel, two streams of visual processing have been described (Mishkin and Ungerleider, 1982). The dorsal stream is known to process motion, spatial location of object, as well as motor induced responses (eye blink or saccades, reaching) and covers areas from extrasiate regions onto the prefrontal cortex through the parietal cortex. The ventral stream is focalized in the inferior temporal cortex, passing through V2 and V4, and responsible for the object representation and form recognition, relatively invariant of the stimulus characteristics. At these stages, there is no longer retinotopic mapping. More details on the ventral visual pathway, a key area for object identification hence categorization, will be given in the next sections (see II. A. 2).

In term of embryogenesis and fetal/infant development, the visual system takes longer than other senses to install and mature (Graven and Browne, 2008). While visual cortex myelination starts around the 8th gestational week, the axons of the ganglion cells only reach and start stimulating the lateral geniculate nuclei between gestational weeks 22 and 30 (Graven, 2004). Before 32 weeks, no pupillary response to light is observed in preterm neonates and their thin eyelid does not obstruct light from hitting the retina. In fact, at gestational week 36, the photoreceptors, bipolar cells and ganglion cells are still not mature. Yet, most of the visual system develops between gestational week 24 and 40 (i.e., term), but in the absence of visual stimulation. Indeed, if visual stimulation happens too early (i.e., before at-term birth), it is highly susceptible to cause severe damage to the visual system (from photoreceptors to white matter, see Braddick and Atkinson, 2011). The visual system seems tuned to develop progressively and a “good amount” of visual stimulation, starting from birth, ensures a harmonious development of sight (Graven and Browne, 2008). At birth, the system is only rod-based (maturing around week 40), and still develops for 2-to-3 months when the photoptic system (cone-based) starts to mature, which happens progressively (i.e., the color red is the first to be transcribed). Visual acuity improves dramatically over the first 6 months (Maurer and Lewis, 2001). The critical period for the visual system development is quite wide, starting from 20 weeks of gestation to 2-to-3 years old post-natal, with most of it achieved by the end of the first year, but 3D vision extending for instance to 15-to-18 months.

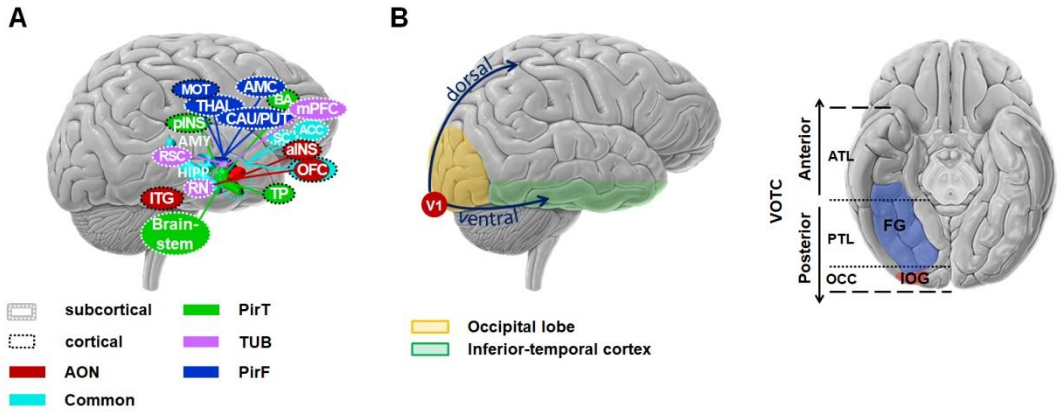


Figure I-1. Brain regions involved in (A) the olfactory system and (B) the visual system from sagittal and ventral views. A. Some brain regions of the olfactory cortex have unique connections to each subregions (colored) while other (in light blue) share connections with the other subregions. AON: Anterior olfactory nucleus, TUB: olfactory tubercles, PirT: temporal piriform cortex, PirF: frontal piriform cortex, mPFC: medial prefrontal cortex, CAU: caudate, PUT: putamen, AMC: anterior mid-cingulate cortex, THAL: thalamus, RN: red nucleus, RSC: retrosplenial cortex, ITG: inferior temporal gyrus, pINS: posterior insular cortex, MOT: motor area, TP: temporal lobe, BA: Broca area, aINS, anterior insular cortex, OFC: orbitofrontal cortex, ACC: anterior cingulate cortex, SC: subcallosal cortex, HIPP: hippocampus, AMY: amygdala. Adapted from Zhou et al. (2019), CC0. Original can be found at https://doi.org/10.7554/eLife.47177.020 **B. Left**: visual information arrives at the occipital cortex (orange) and the primary visual area (V1) and goes along the dorsal and ventral pathways. In the inferior temporal cortex (green), areas are specialized in object recognition. **Right**: ventral view of the inferior temporal cortex, the ventral-occipital temporal cortex corresponds to the superficial layers of the IT. Face-selective regions (see II. A. 2) are the fusiform gyrus (FG) and the inferior occipital gyrus (IOG). ATL: Anterior temporal lobe, PTL: posterior temporal lobe, OCC: occipital lobe. Adapted from Rossion et al. (2018). Original can be found at http://doi.org/10.1111/nyas.13596

3. Differences in sensory functions

Olfaction and vision have their anatomical specificities and they function differently. In brief, vision transduction appears relatively well-defined: photoreceptors are clearly structured and depend on wavelength variations (stimulus dependent activation from the visible spectrum of light; De Valois and De Valois, 1993), properties of the visual receptive fields are explainable from basic rules of optic (spatial frequencies, Gaussian scale space; Lindeberg, 2011) and a retinotopic mapping of signal is preserved from the retina to the primary visual cortex. All of this contributes to a well identified relation between the stimulus and the percept in the mature system and allows consistent and rather accurate prediction of visual perception which has nourished cognitive psychology and optic with a wealth of theories and models of visual perception.

On the other hand, there are still a lot of unknown parameters from olfactory transduction to perception. Overall, the obvious stimulus/percept relation found in the other sensory modalities is harder to grasp in the case of smell, since even our other chemical sense, taste, has five clearly-defined types of receptors (Yarmolinsky et al., 2009). First, olfactory receptor cells are defined by a ligand-receptor complex and seem to activate variably according to the size, volatility (Saito et al., 2009) but also the structural complexity (Kermen et al., 2011) of the odorant, overall making olfactory transduction unpredictable (Laska and Shepherd, 2007; Rossiter, 1996; Sell, 2006; Stettler and Axel, 2009). Consequently, it has been suggested that we perceive *mixtures* more than molecules (Barwich, 2019), as receptors transduction follow combinatory instead of additive principles (Malnic et al., 1999). Second, the retinotopic mapping found in vision has no equivalent in olfaction. While it is argued that glomeruli structures respond to spatial patterns of odor representation (Auffarth, 2013), this spatial pattern of information is lost in further steps of signal transduction. More importantly, this spatial representation happens outside the scope of consciousness (Shepherd, 2006). In fact, the dominant view is that there is no spatial dimension of olfactory perception (see Sela and Sobel, 2010). Third, unlike any other sense, the thalamic relay succeeds to the primary cortex synapse what is often related to the poor conscious attention dedicated to smell, whereas we are very good at explicitly qualifying our visual environment. The thalamic connections of the olfactory pathways with the hippocampus, and more generally with the limbic system, give a large place for emotion processing and memory in odor perception (Bensafi et al., 2002), thus to subjective qualities. This tight link between odor, emotion and memory appears stronger than with any other sense (e.g., Richardson, 2002). Additionally, while there are only a few proposals for perceptual olfactory dimensions in literature (mostly in the perfume retailer business, Zarzo and Stanton, 2009), it has been proposed that the main value given to an odor depends on its pleasantness (Yeshurun and Sobel, 2010; Zarzo, 2008) before its edibility (Zarzo, 2008). Taken together, it appears that the separation between sensory input and cognitive judgment is more categorical in vision than in olfaction and all these elements certainly contribute to the general feeling of the unreliability of the olfactory system (see **Box 1**) and could partly explain the visual dominance sensation in our phenomenological perception. It seems indeed easier to understand visual perception, however complex, as we can more easily explicitly relate to our own experience.

Finally, and importantly for our purpose, both senses organize during embryogenesis but they have a different timing. Our senses do not developed following the same chronology and they do not reach functionality/maturity synchronously. The development of human sensory embryogenesis follows a classical sequence shared across vertebrates (Turkewitz and Devenny, 1993), with respect to adaptive value (e.g., Mezrai et al., 2019). In humans, the order of the emergence of the senses is: touch, chemosensation, audition then vision (Lecanuet and Schaal, 1996). Chemosensation in humans is allowed by the trigeminal, the olfactory and the gustatory system (see above). Neurons of the olfactory and the gustatory systems become mature between gestational weeks 11 and 12 (Beidler, 1961) and intrauterine learning seems possible (e.g., Schaal et al., 2000). While the visual system's anatomy starts during the first trimester as the other senses (the retina begins to form around week 7), it takes longer to mature and needs very little stimulation to achieve its early functionality at birth. Critically, the neuroanatomy of the visual system still undergoes decisive changes for several months post-birth and throughout childhood, when the olfactory system has already accumulated several months of chemical experience.

C. Multisensory integration

A string of research has been interested in the development of multisensory integration. Two main views proposed to describe the emergence of this core ability and empirical evidence further complete these accounts to provide multisensory integration models reliable across measures, species and different stages of development.

1. Views on multisensory perceptual development in infancy

A first view was mostly put forward by Piaget (1952)'s constructivist theories of infant cognitive development. It states that while sensory integration is absent in initial stages of development, with senses developing separately and creating isolated sensations, the infant gradually learns the relations between them. Experience, notably through grasping from the development of motor abilities, along with repeated exposure to co-occurring events, allows infants to fully integrate multimodal information and to apprehend objects through multiple channels. The *integration view* thus states that it takes cognitive maturation and experience for infants to apprehend and represent the unity and intrinsic multisensoriality of objects and it has obtained empirical support (e.g., Grill-Spector and Weiner, 2014; Mareschal and Quinn, 2001).

On the contrary, the *differentiation view* suggests that, at first, infants perceive a unity through the different senses and that they progressively learn to distinguish between different inputs to represent finer and more complex multisensory relations. This view was initially brought by Gibson (1969), who argued that infants are equipped to detect amodal properties of objects from the beginning.

As evidence was obtained for both views (Bahrick and Lickliter, 2000; Lewkowicz and Lickliter, 1994), it is suggested that probably both mechanisms described contribute to the emergence of multisensory integration in infancy (Bremner et al., 2012). Indeed, infants are able to bind multisensory inputs and detect intersensory relations before developing motor skills, but perceptual abilities are not present all at once and some need experience to mature (Bahrick and Lickliter, 2000; Lewkowicz and Lickliter, 1994).

2. Subtending mechanisms

Complementary to modality-specific properties (e.g., color, pitch, sweetness) which can only be conveyed by one modality (Gibson, 1969; Spence, 2011), amodal properties of objects are observed in more than one sensory channel (e.g., temporal synchrony, intensity, rate duration, spatial collocation, rhythm, etc.). They are particularly salient and infants would be readily able to detect at least some of them (Lewkowicz, 2010). In fact, their inherent saliency would allow infants to unify multimodal stimulations and as a consequence, those capture and orient infants' attention. Through this sustained attention, perceptual learning about consistent regularities of multimodal events is promoted. For instance, the synchrony between two sensory events (e.g. a voice co-occurs with a face) is detected before the infant learns the associated specific context-dependent events (e.g., identity, gender, etc.; Lewkowicz, 1992), which is promoted thanks to the bimodal stimulation capturing attention (Bahrick and Lickliter, 2000).

This phenomenon has been further conceptualized as the intersensory redundancy hypothesis, referring to "*spatially coordinated and concurrent presentation of the same information across two or more sense modalities*" (Bahrick and Lickliter, 2000). It explains that redundancy of amodal properties across several senses guide attention and facilitates learning by a selective processing of modality specific information. The effect is expected to be more important during the early learning phases of a domain, i.e., when arbitrary correspondences are to be acquired (see Lickliter and Bahrick, 2004, for a review). Likewise, it has been confirmed that exposure to non-redundant bimodal information had the reverse effect and hindered the processing of signals consequently made competing (Bahrick and Lickliter, 2000; Lickliter and Hellewell, 1992).

The intersensory redundancy hypothesis has been inspired by multisensory integration considerations at brain level, notably the inverse effectiveness principle. In fact, the three rules of multisensory integration are of interest for the present work. The integration of multisensory stimuli is considered the most probable for stimuli approximately coming from the same spatial location, due to the spatial mapping of most of the sensory cortex (i.e., the spatial rule; Meredith and Stein, 1986); and coming from a relative co-occurrence of stimuli in time (the temporal rule), supported by the temporal window needed to process information despite very brief neuronal pikes (Meredith et al., 1987). The third rule predicts that multisensory integration is at its maximum when one sensory stimulus input is weakly effective on its own, so that the combination with another entrant signal magnifies the resulting response (i.e., the inverse effectiveness rule, Stein and Meredith, 1993).

The inverse effectiveness rule has notably proven fruitful at the theoretical level and has built a solid foundation for multisensory integration considerations at the brain and behavioral levels. First investigated in cats' single neurons, it showed that neurons of the superior colliculus followed a non-linear and super-additive activation, as the number of spikes obtained following a multisensory stimulation was greater than their sum across unisensory conditions (audio and visual). In addition, it was evidenced that this enhancement was inversely proportional to the strength of the unisensory response, i.e., the neurons the least effective in one modality benefited the most from multisensory stimulation (Meredith and Stein, 1983). Along the years, a consequent amount of studies on the subject have flourished, contributing to delineate this effect across species and measures (see Wallace, 2004). In humans, we continue gathering evidence of the application of this neural principle at the perceptual (Stevenson and James, 2009) and behavioral levels (Holmes, 2007; Stein et al., 1988).

3. Theoretical perspectives

Sensory modalities have been extensively studied over the past centuries, and multisensory perception (and integration) are experiencing a more recent and growing interest. Today, the technical and methodological advancements have allowed to uncover a large part of sensory (neuro)anatomy from the first stages of embryogenesis in humans, with a good insight of (multi)sensory perception and integrative mechanisms in adults. However, vision studies dramatically dominate the field while vision matures with a delay compared to the other senses. One could thus wonder (1) what role senses other than vision do play in the early stages of perceptual development; and considering the early maturity and peculiar function of olfaction (2) whether this vision-driven theoretical framework could easily integrate olfaction in these models. Likewise, among the amodal properties cited, characterized by spatial and temporal properties of the stimuli, could any of them be observed for olfaction, since it is said that its space dimension is hard to get and that odors can be temporally separated from its source?

Vision is overstimulated from birth onwards; hence newborns have to make sense of visual stimuli from birth maybe more than in other sensory modality for which they can better understand the nature because of in utero stimulations. For this reason, early maturing senses could sustain the acquisition of visual knowledge by relating to past experiences and help interpreting information. For instance, during late pregnancy, the auditory system is sufficiently mature for the fetus to be exposed to its mother's voice (DeCasper and Spence, 1986), leading to a facilitative effect of her voice in the learning of her face at birth (Sai, 2005). Analogously, early olfactory knowledge could help the newborn interpret signals from the surrounding. In fact, it is proposed that odors could serve as landmark to guide infants in their discovery of this multisensory world filled with novelty and apply "tags" to sensory-relevant objects (Schaal and Durand, 2012). In that respect, the flexible quality of odor recognition in humans (Barwich, 2019) could be well suited to this task, that is, the imprecision of the olfactory object could make its relative association easier than if odor identification was highly accurate by itself, and therefore contribute to interpret incoming inputs from other senses.

Although our sensory modalities have their own developmental trajectories and specificities in the way they process information, we continuously perceive the world in a multisensory way with a seeming simplicity. It is more and more suggested that olfaction could play a significant role in helping us make sense of our world, but due to only a relatively recent interest (see Box 1 for more details), the mystery about olfactory perception is still thick. Olfaction appears subjective and powerful at the same time. In the next section, we will consider how we perceive our conspecifics in this multisensory world, by focusing on the state of the art from the visual and the chemical senses separately at first, to understand the cues at stake while apprehending our social surroundings, how do we detect and process them.

Box 1 - The unsuspected importance of odors in humans

The interested reader may find the complete arguments of this box presented in Appendix 1.

- Smell has long been depreciated. Among the reasons why, is a common saying that vision is the dominant sense in humans. Indeed, when asked what sense deprivation would scare them the most, 73% of people answered vision versus 0% for olfaction (Hutmacher, 2019). A representation that may reinforce itself with scientific interest reflected in the number of published papers, consequently gathering more knowledge about visual cognition than any other sense.
- Olfaction has gained a *recent* scientific interest, due a long-lasting misrepresentation of smell, associated with animalistic behaviors. An anatomical argument was used to support this claim, distanciating humans from animals because we have a proportionaly smaller olfactory system compared to rodents or dogs (McGann, 2017; Schaal and Porter, 1991). In the early 19th century, it was thought as the reason why civilized humans are not aware of their olfactory environment but we know now that this is untrue and rather correlated with little awareness along with poor semantic descriptors in western societies (Majid et al., 2018). Nevertheless, a result of this long misrepresentation is that olfaction is still poorly considered, as reflected by our lack of confidence in our olfactory performance (Philpott et al., 2006).
- Intriguinly, despite the claimed unimportance of smell in humans, we appear very kin in using fragranced substances, from cleaning products and cosmetics to flavored drinks, or perfuming our atmosphere to create a good environment. This unawareness of proper odor-related behaviors is thought of to take roots in this misrepresentation of smell, by comparison to other senses, mostly vision and audition. The two latter indeed allow a very fast and accurate localization of the source of the input, and a mostly explicit oriented attention towards it, while it is mostly implicit in olfaction and that relating to our phenomenological experience is not systematic. This difficulty of spatial and temporal representation of smell has been called *change anosmia,* preventing us from noticing changes in the olfactory space, unless drastic (e.g., alert signal) (Sela and Sobel, 2010).
- When looking at other species and other life forms, chemosensory signals have a tremendous importance in survival as they can be sent/received over long distances and in the absence of sound or light. Chemosignals are strongly implied in food foraging, predator or mate identification and recent evidence tends to show that humans are not so different in that matter (see section II. B.). Chemosensory communication among humans play a fundamental role in modulating key functions of human survival (Lübke and Pause, 2015).
- In fact, contrarily to what we individually and culturally consider, we are very good at smelling, even better than dogs and rodents for some substances (Sarrafchi et al., 2013; Sarrafchi and Laska, 2017), and able to detect very low concentrations (Nagata and Takeuchi, 1990).
- In addition, partial or complete loss of smell is related to a decreased quality of life, impacting food intake as well as social relations, mood and libido (Hummel and Nordin, 2005 for reviews), suggesting that olfaction is actively linked to them in healthy adults. Along this line, numerous recent studies have shown odors influence mood (Knasko, 1995, 1992), but also behavior (Kirk-Smith and Booth, 1980) or time perception (Baccarani et al., 2020).

In conclusion, while olfaction has been overlooked and minimized in the past; a growing interest has recently emerged to catch up with our poor knowledge of olfactory function and influences. Odors are very well present in our environment, and may be, in fact, a key element of our interaction with our world, bridging the gap between ourselves and the surroundings.

II. Humans are inclined to perceive conspecifics

Each species need to be able to identify and be recognized by friends or foes for their survival (Snyder-Mackler et al., 2020). It becomes fundamental to social species in order to maintain social cohesion and wellbeing (Holt-Lunstad et al., 2010). In humans, we will review two ways used to communicate and sample information from our conspecifics: the visual categorization of faces and the use of chemosignals through body odor. These two dimensions will be first presented separately, as they are mostly investigated unisensorily, which will allow us to cover the emergence and development of these abilities and consider their neural underpinning, before tackling the state of the art on crossmodal literature on this matter in the next section.

Considering the large and fruitful research undertaken on face perception, the focus will be specifically given on face categorization. Categorization is an essential ability for the brain to reduce the diversity of the physical world, by organizing information and thus allowing equivalent responses to novel as to known exemplars of a familiar category. This cognitive function will be treated separately from finer “face categories”, that is the different categories of faces (e.g., identity, gender, age, ethnicity). By face categorization, we thus mean the generic and fundamental selective processing of visual object as faces, i.e., providing a different response to that of nonface objects and generalized to all faces (i.e., regardless of viewpoint, identity, age, gender and ethnicity). While this generic ability is included in models of face perception (Bruce and Young, 1986; Haxby et al., 2000), the descriptions and hypothesis of how it may work are left elusive.

In the second phase, we will explore chemical communication in humans. Less known, the production and perception of body odor is actually strongly involved in conspecific perception and influences our behaviors. A thorough account of body odor’s influence across the life span, with a particular focus on maternal odor in infancy will further be given.

A. Conspecifics in the visual realm: seeing faces

Face perception in human benefits from a long-lasting and intensive interest in Psychology, Neuroscience and Developmental sciences. Covering it all in the following sections would be out of scope for this dissertation. We will thus focus on two facets to answer the following questions: how does visual face categorization manifest and develop? What do we know about the underlying brain network of this fundamental function?

1. Generic face categorization

Faces are a special type of objects. They are robustly salient, as observed from birth (Reynolds and Roth, 2018 for review) and provoke an irrepressible and impressive visual attraction in adults (e.g., Crouzet et al., 2010). Rich objects, they are defined by a basic configuration and seeing a face does not necessarily calls for a complex stimulus, as two-tone pattern can easily evoke one (i.e., Mooney faces; Mooney, 1957 see Box 2 for examples). More than of other objects, face perception particularly suffers from picture-plane inversion (Yin, 1969) which hampers memorization/recognition and delays reaction times at the exemplar level. These two elements illustrate the fact that faces are processed holistically rather than part by part (Hoehl and Peykarjou, 2012; Rossion et al., 2011). Also, the fact that brain damage can lead to a selective deficit in recognizing individual faces, that is, without hindering any other cognitive ability (i.e., prosopagnosia; Bodamer, 1947; Damasio et al., 1982; for a review Rossion, 2018a), suggests a particular and somehow independent neural processing of these visual objects. Corresponding to the visual category for which we acquire extensive expertise without formal training, faces are represented at the subordinate rather than basic level (i.e., we recognize individuals very efficiently). For all these reasons, a fruitful line of research on face perception has been drawn over the last century, including face individuation (for a recent review; Rossion, 2018b), facial expression discrimination (e.g., Ekman, 1993), or face sex (e.g., Rekow et al., 2020a), from the identification of very low-level cues to higher-level, abstract representation of the face. First and foremost, to be able to process these face categories; the brain has to consider the input as a face.

Generic face categorization is a primitive and fundamental function of face perception. Despite its seeming simplicity, the perceptual task may in fact be more complex than it seems, as it relies on the discrimination of faces from other objects with which they may share visual features (e.g., colors and shapes) and implies that different faces are processed equivalently despite variability in size, viewpoint, identity, expression, etc.

a. Behavioral evidence for the categorization of faces

In adults, animal faces are categorized very fastly (Kirchner and Thorpe, 2006), with an accuracy close to that of human faces (Rousselet et al., 2003) and independently of their location in the visual field (Drewes et al., 2009). However, human faces have a processing advantage over other category exemplars as they "pop-out" of display presenting lots of natural images (Hershler and Hochstein, 2005) and elicit faster saccades (Fletcher-Watson et al., 2008). In addition, the attraction to human faces seems automatic as it happens even when participants are instructed to detect the other target (Crouzet et al., 2010) and make the looking-away saccade initiation more difficult when looking at upright faces (Gilchrist and Proske, 2006). In complex visual scenes, the presence of human faces (Buswell, 1935; Yarbus, 1967), as well as the body (Fletcher-Watson et al., 2008), orients the direction of the gaze suggesting a preferential mechanism for cues indicative of a person. While adults participant have the advantage of being able to verbalize they performance in face detection, developmentalists need become more creative to investigate infant's abilities to detect, and categorize faces.

Very young infants are already good at categorizing visual objects (Mareschal and Quinn, 2001, for a review). Behavioral studies developed elegant and innovative designs to explore the emergence and development of category formation which nourished an extensive literature (see Quinn, 2011, for a review). From around three months at least, infants are able to perform online category learning, which means they form new categories during the course of the experiment, a useful ability allowing the investigation of initially unfamiliar categories (furniture, animals, vehicles, etc.). Subtle categorical mechanisms were thus evidenced, showing for instance that female lion is included in the cat category, but tigers are not (Eimas and Quinn, 1994). Aside this very active cognitive function and from birth onwards, infants show a spontaneous preference for face stimuli over stimuli of equivalent complexity (e.g., Johnson et al., 1991; see Reynolds and Roth, 2018; and Simion and Di Giorgio, 2015, for reviews). By three months, face categories are already formed since female rather than male faces (Quinn et al., 2002), same- rather than other-race faces (Kelly et al., 2005), and canonical faces rather than to equally top-heavied scrambled faces (Turati et al., 2005) are respectively preferred by infants, thus suggesting that a form of face representation is acquired at this age. (Passive) experience plays thus a significant role in the development of visual categories (see Quinn, 2011, for a review) and faces are arguably the most present object in infants' visual scene, especially during the first year (e.g., Jayaraman et al., 2015). Overall face categories have been explored extensively over the first year of life (e.g., race and gender; Quinn et al., 2019; Pascalis et al., 2011) but knowledge about the categorization of faces among objects is scarce. Maybe because of the spontaneous detection for a face at birth, suggesting that infants recognize faces and inferring they would be able to categorize them, only a limited number of studies have directly tackled the contrast between faces and other objects.

In fact, recent studies are suggesting that face detection in more naturalistic settings is challenging and infants are able to do it from the second half of the first year only (Leppänen, 2016). Indeed, in displays presenting numerous stimuli at once, face detection is reported for color (Elsabbagh et al., 2013; Gliga et al., 2009; Gluckman and Johnson, 2013; Jakobsen et al., 2016; Kwon et al., 2016), but not for grayscale images (Di Giorgio et al., 2012), and only from 6 months of age and older. However four month-old infants seem to show face preference when the task is simplified and includes pairs of stimuli of equivalent salience (e.g., faces versus toys; DeNicola et al., 2013; Kwon et al., 2016), although evidence for an earlier ability in lacking (Libertus and Needham, 2011). In addition, the previous studies used faces and objects segmented from their original background which facilitates the figure-ground segregation. When it comes to faces embedded in complex visual scenes, the task is even more challenging, albeit more ecological, confirming infants require at least 6 months to display a reliable face preference (Frank et al., 2009; Kelly et al., 2019).

Box 2 – Categorizing faces without faces

Our expertise in face categorization lies also in the fact that we can perceive faces in nonface stimuli.

Mooney faces are only composed of simple black and white shapes (Mooney, 1957) yet they are perceived as faces differing in expression and identities. They are already discriminated by newborns (Leo and Simion, 2009) and reliably preferred around 3 month old (Otsuka et al., 2012), suggesting the detection of the face pattern.

A."Which one is a face ?" Example of a Mooney face (left) with distractors (middle, right) from an online version of the Mooney face test © Verhallen et al. (2014), reproduced with permission (Licence 4822500026222) **B.** Face pareidolia in common object (coffee stain and wooden shelf), from my personal collection.

Quite more complex, face pareidolia is a strong phenomenon where common objects can evoke complex and often expressive faces. It was identified that the perception of eyes were important to induce the effect, but are not exclusive (Ichikawa et al., 2011; Omer et al., 2019). Face pareidolia were notably made popular by the object arrangements of Arcimboldo's paintings. Recently, it was shown that face pareidolia relies on the processing of social qualities projected to these objects (Palmer and Clifford, 2020). It was evidenced that 7-month-old infants (but not younger ones) preferentially looked at Arcimboldo's paintings when presented in their upright orientation versus upside-down, suggesting the face pattern was detected by young infants (Kobayashi et al., 2012).

The interested reader may find more on the question in Study 3 and 4 and in Appendix 5.

b. *Brain activity corresponding to face categorization*

Investigating infants' neural development is particularly challenging. A small handful of studies have contrasted the neural processing of faces versus objects and has enabled the identification of several face-selective components. Indeed, most of these studies used electrophysiological measures and analyzed event-related potentials (ERPs), where components of neural activity are qualified by the polarity (negative or positive) and latency (in ms) of the peak. Contrasting individual faces (the mother's or a stranger's) to a toy (own or stranger's), the infants' P400 component (i.e., positive wave ~400ms after stimulus onset over occipital sites) was measured with a shorter latency for faces than toys in six month-olds (de Haan and Nelson, 1999) but showed no variation depending on the category in other studies and age groups (from 3 to 12 months), as reported by Conte et al.'s (2020) synthesis (gathering data collected with the same contrast cross-sectionally from Guy et al., 2018, 2016; and Xie and Richards, 2016). However, converging evidence orient toward a face selectivity of the negative N290 (recorded over mid parietal sites), considered the precursor of the N170 in adults (Bentin et al., 1996; de Haan et al., 2003, for a review on face components in infancy), as measured when faces are contrasted to cars in 3 month-olds (Peykarjou and Hoehl, 2013), to toys from 3 to 12 months (Conte et al., 2020) and even to faces of other species (de Haan et al., 2002; Halit et al., 2003).

Jumping to children, different responses between a face and another object are observed in preschoolers (4 years old) and are reliably maintained across development until adulthood (versus cars; Kuefner et al., 2010; versus houses; Mares et al., 2020), in line with fMRI studies starting at 5 years old (Gathers et al., 2004; Scherf et al., 2007). As human adults are considered face experts, the development of face perception is the focus of a large pan of research in human cognition and its emergence have largely been investigated and debated. Accumulated evidence and recent views converge to consider that although genetics play a imporant initial role in shaping face perception abilities, the neural specialization of face perception is further shaped by experience in a dynamic manner (for reviews Johnson, 2011; Rossion and Retter, 2020).

As for activations in the mature adult brain, numerous studies have evidenced that faces and objects recruit different regions (Grill-Spector and Weiner, 2014; Haxby et al., 2000; Puce et al., 1995; Sergent et al., 1992) and solicit different brain activations. Notably, electrophysiological measures have investigated the time course of face-selective processing. As evoked above with the infant's N290, the N170 in children (Kuefner et al., 2010) and adults (for reviews, see Eimer, 2011; and Rossion and Jacques, 2011) is considered strongly related to the perception of a face in the stimulus. The N170 is larger for faces than objects, and in fact for any stimuli evoking a face, even from the interpretation of two-tone Mooney faces (George et al., 2005), or Arcimboldo's paintings (Caharel et al., 2013), suggesting it is related to the high-level representation of a face. Indeed, picture-plane inversion, disrupting the perception of configural information of the face, impacts the N170 for faces by producing a larger amplitude and delaying its latency whereas inverted objects elicits equivalent N170 amplitude and a much smaller delay (Itier and Taylor, 2004; Rossion et al., 2000; in children, Mares et al., 2020). Likewise, Mooney faces, which are only perceived as faces in their upright orientation, do not show a face-typical larger response following inversion, as they lost their evocation of a face (George et al., 2005). Another ERP component, P1, from an early time window (80-100ms) was originally considered as face-specific but later showed to be related to low-level confounds, thus stimulus driven (Rossion et al., 2011; Rossion and Caharel, 2011). This component is also found in infancy, with a similar apparent advantage for processing faces, but as it seems also sensitive to attention allocation and low-level cues in the stimuli used as well, it was recently concluded that it may not be face-selective in infancy as well (Conte et al., 2020).

c. A recent approach to measure direct, automatic and implicit face categorization

All these studies report important findings for our understanding of face perception versus other objects across development. They highlight the early existence of face-selective processing and suggest specific responses recruiting dedicated regions. If the interpretation toward the ability to *categorize* can be inferred from these studies, responding differently to isolated exemplars based on their category however is not strictly equivalent to elicit a categorical response independent of the stimulus nature but according to its category. In other words, category-specific processing is not directly measured from differences in processing two stimuli from separate categories, as it is the case in the aforementioned studies.

Proposing a design specifically addressing the question of face categorization among variable objects, de Heering & Rossion (2015) took advantage of the high temporal resolution of EEG to adapt a fast periodic visual stimulation paradigm (Farzin et al., 2012; Norcia et al., 2015; Rossion et al., 2015, see below) in 4-to-6 month-old infants. First to use images of objects unsegmented from their background coupled with a neural measure in an infant study, authors contrasted numerous faces varying in size, viewpoint, gender and expression, to a large amount of object categories and presented them within a fast track of periodic stimulation (e.g., 6 images per second), that is, at regular interval (without interval inter stimuli), and relying on the brain activity to synchronize with the rate of stimulation (Figure II-1A). As faces were inserted periodically in the fast stream of images (every 5th image), a selective response was expected at the predefined frequency (i.e., at 1.2 Hz). If observed, it would correspond to a brain activity selective to responses to faces and independent of stimulus-related properties. To exclude the contribution of low-level confounds, images were also presented in their phase-scrambled version in dedicated sequences, where "scrambled faces" were not expected to elicit such brain activity. This is precisely what they revealed, by recording a clear response over occipito-temporal regions (with a strong right-hemispheric dominance) at the exact frequency of stimulation for intact faces only (i.e., 1.2 Hz, Figure II-1B and C), and directly distinct from the general visual response elicited by the rapid visual stimulation from all images over middle occipital regions at 6 Hz. The infant brain is thus able to process images very rapidly and to provide a selective response to faces appearing every ~833ms, that is, face-selective population of neurons are specifically recruited and respond reliably to extremely varied faces, as early as from 4 month after birth (de Heering and Rossion, 2015).

The same approach was also used in 5-year-old children to investigate how the response evolved across development (Lochy et al., 2019a). Compared to infant response, the brain activation was found (1) stronger in amplitude with more significant harmonics in the frequency spectrum, but also (2) qualitatively different, as it was equally distributed over bilateral occipital temporal regions (see also Lochy et al., 2019b). Brain and visual maturation, are proposed to explain this observation, in addition to a cumulative experience to visual objects in general, including faces. Because this type of paradigm relies on the automatic discrimination of a target category among distractors (and the generalization of the response across its exemplars), the face-selective response enhancement is as well a consequence of better processing of faces per se, as the result of more accurate visual object recognition ability in general.

As illustrated by implementing the same type of stimulation in infancy and childhood, one of the strengths of the method is that it can be applied to all ages using roughly the same parameters (see section III. B. 2). Accordingly, the studies presented hereafter use the same

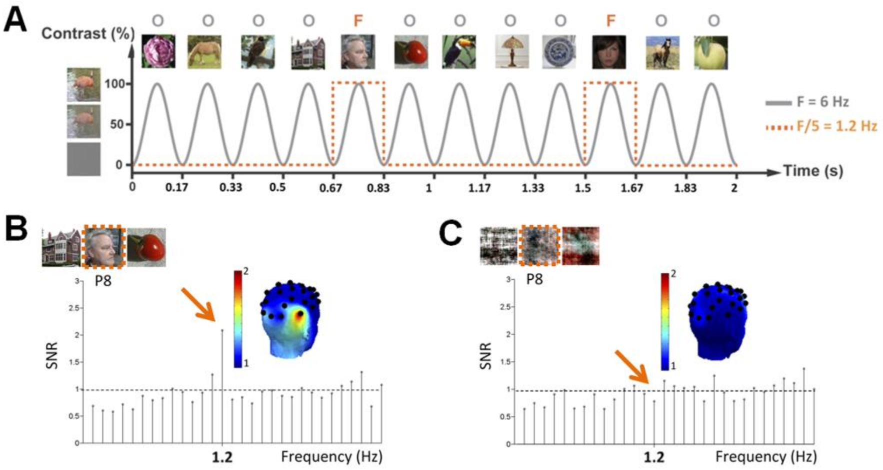


Figure II-1. Methodology and main results from de Heering & Rossion (2015) A. Fast periodic visual stimulation using sine wave contrast modulation presenting one face (F) every five objects (O) in a stream of 6 images per second (i.e., 6 Hz), thus indexing a face-selective response at 1.2 Hz. **B.** In experiment 1, intact images are used and elicit a face-selective response in 4-to-6-month-old infants at the predefined frequency of 1.2 Hz over the right hemisphere. **C.** In experiment 2, the same images in their phase-scrambled versions were also tested in dedicated trials, showing an absence of response for faces in that case, ruling out a different power between stimuli being responsible for the main response. © de Heering & Rossion (2015), CC0 License, modified. Originals can be found at https://doi.org/10.7554/eLife.06564.003 and https://doi.org/10.7554/eLife.06564.0039

approach and a very similar design (varying sometimes the presentation rate from 6 Hz to 12 Hz). In adult, this line of studies has demonstrated the adult brain ability to categorize faces at a glance. In line with results in developing brains, variable exemplars of faces are accurately categorized among other objects, living and non-living (Rossion et al., 2015), whether presented in color or greyscale (Or et al., 2019). Also, participants process faces in a similar manner whether they are implicitly and automatically categorizing faces (i.e., while focused on an orthogonal task) or during an explicit face-detection task (Quek et al., 2018b). The categorization response to faces is stronger than to any other visual category (biological or not) and differs qualitatively also (Jacques et al., 2016a), emphasizing the special status of faces in the human perceptual world. Recently, it was also evidenced that human face categorization occurred in an all-or-none fashion, as the amplitude of brain activation is significantly correlated with participant's performance in detecting faces one by one in streams of FPVS trials varying in speed presentation (Retter et al., 2020). Finally, this design was further adapted to fMRI in order to measure face-selectivity cortical organization (Gao et al., 2019, 2018). We will expose next the brain architecture subtending face perception and its categorical processing.

Collectively, these studies demonstrate that from the earliest stages of development, faces benefit from a preferential processing. Even if behavioral studies in infancy are constrained by infants' behavioral development which limits the comparison of the same paradigm across ages, electrophysiological studies bring forth strong evidence for neural marker of early visual categorization from 4 months of age at least. Faces are definitively special kinds of stimuli for humans, as substantiated by accumulated evidence from newborn attraction to face patterns to a quantitative and qualitative differential perception of faces compared to any other objects in the adult brain even when implicitly perceived at a glance (Jacques et al., 2016a).

2. Neural architecture subtending face perception

a. Dedicated pathways

Visual recognition of objects, including faces, is subtended by ventral areas of the occipital-temporal cortex (VOTC, Figure I-1), and follows a hierarchical organization having for instance broad regions dedicated to process living object categories and finer categories like human body, corresponding to a cluster of neurons in this broad region (Grill-Spector and Weiner, 2014). It was recently evidenced that domain level representation is stronger in lateral VOTC whereas domain and categorical levels activate in similar proportion the middle VOTC, and that activation was quantitatively greater in superficial layers of the cortex, the structural organization being maintained through deeper layers (Margalit et al., 2020). The face-selective network was identified on the right VOTC mainly. A neighboring region is also considered in the face-selective network, the superior temporal sulcus (STS), but it appears more involved in the processing of dynamic aspects of the face (e.g., expression) (Grill-Spector et al., 2017; Haxby et al., 2000).

A preferential processing for faces vs. objects or scenes was found in different areas of the right VOTC: the inferior occipital gyrus (IOG, sometimes referred to as the *occipital face area,* OFA), the lateral fusiform gyrus (latFG, encompassing the *fusiform face area,* FFA) and the anterior temporal lobe (ATL, Hagen et al., 2020). In the IOG and latFG, the preference for faces was repeatedly found across neuroimaging (Haxby et al., 2000; Kanwisher et al., 1997; Margalit et al., 2020; Mattioni et al., 2020; Puce et al., 1995) and intracerebral recordings (Allison et al., 1994; Hagen et al., 2020; Jonas et al., 2016; see Rossion et al., 2018, for review). Remarkably stable across individuals, face-network areas are also strongly interconnected (Gschwind et al., 2012) and integral part of the visual cortex, through which, it is thought, they connect for an efficient face perception (Grill-Spector et al., 2017). Evidence from intracerebral recordings suggest that something that was previously interpreted as overlaps between face-selective and object-selective neuron populations (Haxby et al., 2001) does in fact come from close but isolated populations of neurons and that there is no such overlap (Hagen et al., 2020). In addition, while the FFA has been extensively studied for the last decades (Kanwisher et al., 1997; for review Grill-Spector et al., 2017), the use of direct intracranial recordings have allowed the exploration of regions hardly accessible through fMRI, in the anterior part of the temporal lobes (the closeness to the ear canals inducing strong magnetic artifacts). Thanks to this, face-exclusive populations of neurons were additionally found in the anterior temporal lobe (Hagen et al., 2020; Jonas et al., 2016), using a FPVS-iEEG paradigm on a large number of participants. In this area, neurons are even described as face-*exclusive*, instead of *selective*, because they activate at the face presentation rate (the target category) and not at the general visual stimulation rate (i.e., the objects, living and non-living, used as contrast; Jonas et al., 2016), but also because they do not respond when another target category (e.g., houses) is used in the sequence (Hagen et al., 2020). Authors suggest that the ATL could be linked to the cross-modal representation of persons, as the area is shared with other modality-specific regions and appears related to highly semantic representations (Lambon Ralph, 2014; Rice et al., 2018; Volfart et al., 2020).

In infancy, neural processes and structures underlying such ability are still scarcely unveiled, despite a very strong interest. Recently, an fMRI design was successful in recording low-motion brain activity from awake infants. Denn et al. (2017) tested 4-to-6 months olds infants and showed that at this age, adult-like face-preferring regions were already strongly present (observed on 6/8 individual infant data). Indeed, faces versus scenes showed preferred activations for faces in the latFG, the lateral occipital cortex, the STS and the middle prefrontal cortex. However, when comparing faces versus other objects, no difference was found in infants, unlike for adult brains. Authors propose that the subtending network is not mature enough to produce selective responses to faces and other objects. However, de Heering & Rossion (2015) showed a neural activation that could emerge only if 4-to-6 month old infant brain processed faces differently than other visual objects; and Conte et al. (2020) observed that the N290 ERP component was face-selective in 3-to-12 month olds infants while they discriminated faces from toys. Moreover, using source reconstruction, Conte et al. (2020) estimated its generator to be linked to the fusiform gyri, suggesting that the premises of adult face-selective regions were already formed and functional.

Several hypotheses have been proposed to settle the apparent discrepancies emerging from infant studies using varied methodologies in humans but also when considering nonhuman primate brain studies. Particularly, Powell et al. (2018) propose that cortical face selectivity could emerge from different mechanisms working together and methods often lack sensitivity to reveal this. Our brain architecture would include a neural proto-organization that needs to be reinforced by experience, since this organization is observable at birth (prior to proper visual experience) and depriving monkeys of early visual exposure to faces is deleterious to the specialization of these structures (Arcaro et al., 2017). This reinforcement would be facilitated and accelerated by an innate face template, responsible for face attractiveness during the first stages, which would rapidly nourish the neural acquisition of face-selectivity. Finally, this initial template would be replaced by a more adaptive mechanism preferring dynamic and interactive faces to static and silent faces for instance, based on evidence showing that the social interaction contingency of the face during the early months is very rapidly acquired, sought for and overtly preferred (e.g., Field et al., 1988). This last social dimension of the face would include more than the face network and extend to areas of the middle prefrontal cortex, associated in adults with self-relevant social interactions (Grossmann, 2013; for a developmental review). In any case, it seems that the blueprint of the mature neural structure is already perceivable at early ages, with already a right hemispheric dominance in processing face information in infancy (Adibpour et al., 2018; de Heering and Rossion, 2015).

b. A right hemispheric specialization for face perception

Despite apparently similar brain architecture on both hemispheres, the specialization of each region can have a hemispheric dominance, and faces are preferentially processed in the right hemisphere. Indeed, brain lesions localized in the right hemisphere can lead to the selective impairment of face recognition (i.e., prosopagnosia, Rossion, 2018a). Apparently found only in humans (Tsao et al., 2008), several hypotheses have been proposed to account for this asymmetry, suggesting either the existence of a proto-organization determined by genetic factors constraining visual pathways then reinforced by the environment (Rakic, 1988); or being the result of competitive mechanisms processing visual categories (de Schonen and Mathivet, 1989).

The right hemispheric advantage in face processing is clearly established in the adult brain (Sergent et al., 1992; Grill-Spector et al., 2017, for review), however its emergence is less understood. Developmental studies seem to go in favor of an early right hemispheric dominance but the question is still under debate as the development of this lateralization appears non-linear (Lochy et al., 2019b, 2019a). In infancy, evidence from the processing of face information have been found right lateralized using different approaches, like EEG (Gliga and Dehaene-Lambertz, 2005; Scott et al., 2006) and ERPs (Adibpour et al., 2018), PET (Tzourio-Mazoyer et al., 2002), NIRS (Honda et al., 2010; Nakato et al., 2011; Otsuka et al., 2007) or behavioral paradigm using hemifield presentation (Adibpour et al., 2018; Dalrymple et al., 2020; de Schonen and Mathivet, 1990; Rizzolatti et al., 1971) and neural face categorization appeared strongly right lateralized in infants (de Heering and Rossion, 2015). However, several other studies did not evidence such a lateral preference (de Haan and Nelson, 1999; Deen et al., 2017; Gliga and Dehaene-Lambertz, 2007; Peykarjou and Hoehl, 2013). In addition, while the face-sensitive N170 component is clearly right lateralized in children and adults, the homologous N290 in infants has been recorded over medial occipital regions.

The emergence of the visual processing of words, a prerequisite for reading abilities, is thought to account for the right lateralization identifiable later in development (for a recent review, Behrmann and Plaut, 2020). Notably, the parallel between faces in the right hemisphere and the left hemispheric dominance for the visual word form processing is subtended by a reduced asymmetry in dyslexic children (Monzalvo et al., 2012), thus relating the strength of the ability to its hemispheric balance. In line with this, testing 5-year-old preschoolers, Lochy et al. (2019a) showed that the face categorization response was found over bilateral occipital-temporal regions and that the response of the right hemisphere was positively correlated to their score of grapheme-phoneme recognition. The latter correlation had been previously evidenced in older children and adolescents from their reading ability (Dundas et al., 2013), and their cortical face response was also found bilateral (Dundas et al., 2014).

In sum, the neural response for faces is stronger over the right hemisphere early in infancy and in adulthood, but consensually shows a bilateral response in childhood, suggesting that reading acquisition is not the sole responsible for the initial right hemispheric dominance of face processing (Behrmann and Plaut, 2020 for a recent discussion).

When it comes to perceiving conspecifics from visual cues, the face is central from the first moments of life. Behavioral studies show that at any age, we are reliably attracted to faces when opposed to other objects or embedded in more naturalistic views. Accordingly, a neural network is dedicated to the process of face cues with a stronger contribution of the right ventral occipital-temporal region. Finally, we saw that using a fast periodic visual stimulation coupled with EEG recording of the brain activity, the neural underpinning of face categorization at a glance could be isolated using the same material across the lifespan, what seems ideal in tackling developmental questions including difficult-to-test populations and appears interesting for our question.

B. Conspecifics in the chemical realm: body odor

Contrarily to visual perception of conspecifics, social communication through chemical cues in humans has only emerged quite recently in the scientific horizon (see **Box 1**): much is still under investigation and sometimes tinted with speculations. It is based on complex mixtures emanating from body odor secretions, almost all of which produce an odor. These cues provide insight of the sender physiological state, and may modulate the receiver's behavior and internal state (see **Box 2**). A review of what kind of substance is considered, their observed effect across development and their neural underpinning will be addressed in the following paragraphs.

Box 3 – Are there human pheromones?

- The successful isolation of a pheromone was made by Butenandt (1959) observing that male moth Bombyx (Bombyx mori) were able to detect a fertile female as far as from 10 km. Based on this observation, pheromones were defined as "*substances which are secreted to the outside by an individual and received by a second individual of the same species, in which they release a specific reaction, for example, a definite behavior or a developmental process*" (Karlson and Lüscher, 1959).
- Does this definition apply to humans? After sixty years of research, the quest is quite unsuccessful... Despite the more inclusive definition – a pheromone is a *single molecule* powerful enough to trigger a *systematic and automatic response* in the receiver – no such signal has been identified in humans to date (Hare et al., 2017; Wysocki and Preti, 2004).
- By contrast, a strong line of evidence show various and robust effects of conspecifics' odors in humans, which will be addressed as *chemosignals*, or *chemical cues*.

For a comprehensive overview and review, the reader may find Wyatt (2017), as well as Wysocki & Preti (2004) and the alternative proposal of de Groot et al. (2017) to be of interest.

1. Body odor production

A lot of human secretion could be designated as "body odor": sweat, saliva, urine volatile compound, feces, tears, sebum, etc. In this dissertation, we will focus on a well-defined and highly documented category of body odor secretion, axillary sweat. Contrarily to some of the aforementioned other secretions, human axillary body odor is subtler and usually less obvious to detect. In fact, the odorous quality comes from the interaction between the substance produced by our axillary glandular system and the axillary microbiome. We have known for over 70 years that fresh human sweat is odorless and that the typical malodorous sweat odor, which gives the signature of human sweat, comes from microflora activity (Shelley et al., 1953; see James et al., 2013 for a recent review) which undergoes physiological modifications with age (Somerville, 1969; Yamazaki et al., 2010).

Sweat is mostly produced by apocrine glands, which can be found with the highest proportions in underarm regions (the axillae), yet also present in the eyes, nipples and pubis area, and ears wax (Smallegange et al., 2011). After puberty, these glands start secreting the complex substance we simply designate as sweat (Wilke et al., 2007). Human sweat has a unique signature composed of carboxylic acids, sulfur compounds and steroids (the most frequently studied are androstenone, androstenol and androstadienone). Note that these compounds are listed here as the most consensual and relevant to date, as we are still uncovering the exact composition of human sweat (for a review, Starkenmann, 2017). Resident skin bacteria, especially one enzyme (Rudden et al., 2020), found in the moist and warm underarm region actively contribute to the release of volatile organic compounds (VOCs) by degrading the water-soluble chemical precursors of these compounds (Shelley et al., 1953). As our work will not further consider body odor at a molecular level, the reader can turn to the exhaustive chapters of Starkenmann (2017) & Natsch (2017) to dig deeper into this topic.

The production of sweat can be influenced by a variety of factors. Intrinsic factors like hormonal status seems to modify its composition as it modifies its perception (Gildersleeve et al., 2012; Lenochova and Havlícek, 2011; Thornhill et al., 2013). Other physiological modifications, like metabolic disorder (e.g. phenylketonuria, Cone, 1968) or infections (e.g., typhoid fever, Liddell, 1976) give a specific scent to axillary odor. Surprisingly, personality traits also induce changes in the perceived quality of body odor (Sorokowska et al., 2012) as well as transient emotional states (Smeets et al., 2020). Diet is also a famous, and obvious, influence of body secretions. The small size of volatile molecule conveyed by food allows them to pass through the epithelium barrier to the blood stream and contaminate the whole body, including breath, odor of urine or feces, and sweat. For instance, while garlic is known to badly alter the pleasantness of breath, its antibacterial activity actually improves sweat's attractiveness and lowers its intensity (Fialová et al., 2016). On the contrary, a *high* consumption of red meat (i.e., twice a week) has the reverse effects on the perceived quality of sweat (higher intensity and lower attractiveness, Havlícek and Lenochova, 2006).

Sexual dimorphism in sweat production leads to distinguishable differences between male and female donors despite a similar composition (Troccaz et al., 2009; Zeng et al., 1996), due to specific microflora differences (Jackman and Noble, 1983; Troccaz et al., 2009), inducing an identifiable gaseous profile (Penn et al., 2007). Body odor is nonetheless relatively stable within individuals (Kuhn and Natsch, 2009; Roberts et al., 2005); indeed, the comparison of samples from both armpits and different days yielded equivalent judgments (Penn et al., 2007; Roberts et al., 2013; Shehadeh and Kligman, 1963).

> Human axillary sweat odors, henceforth designated as "body odor", are a complex substance, subject to a myriad of more or less transient influences (internal: hormonal status, external: diet) to their composition and vary across individuals (genetically induced individual odorprint). These characteristics have been identified thanks to our ability to detect them. Body odor could therefore constitute social cues helping us navigate among our conspecifics.

Box 4 – Methodological considerations on body odor

No systematic methodology has emerged over the years yet. The following methods of sampling and storage will thus be presented as a guideline for the reader (for a review, see Parma et al., 2017).

- **Instructions**: three types of body odor can be found in literature. The most common methodology is to seek for standardized odors, with restrictions to donors which include limitation or exclusion of specific food (e.g., spices), tobacco, and alcohol and the use of scented products (soap, antiperspirant, perfume) generally starting a few days ahead of collection. Recent work has chosen to use "diplomatic odor", that is, non-standardized body odor preserving the donors' habits (Gaby and Dalton, 2019; Gaby and Zayas, 2017). A compromise between highly controlled and uncontrolled body odor is the addition of a mask odor (e.g. neutral essential oil) to standardized body odor, in order to evoke scented cosmetic product while controlling for intensity across samples (e.g., Cecchetto et al., 2019).
- **Collection**: in most cases the substrate used is cotton (pre-washed t-shirt or sterile cotton pads with surgical tape) and donors are provided with short-term storage material if it happens outside the laboratory. Duration varies greatly, ranging between half an hour to several days (for night wear).
- **Sampling**: Activities done by donors also vary and depend on the aim of the collection. Sometimes the collection is made while sleeping or at rest state (inside or outside the lab), while studies investigating the emotional content of body odor use more specific designs (e.g., stressful events like parachute diving versus physical activity sweat).
- **Storage**: until recently, only one study had investigated the effect of storage duration (Lenochova et al., 2008), the consensus was thus to use frozen samples within 6 months as no longer duration was tested to date. A recent study on fear odors showed they could be reused after being unfrozen without impairing their effect (Gomes et al., 2020).

2. Perceiving body odor

In the following paragraphs, we explore the perception of body odor across the lifespan. Most of the research focuses on neonates and young adults, with a gap from infancy to adulthood, and no study found in old age. The ability to detect body odor and its influence on our mood and behavior are suggested below and one can assume that these preserved abilities over evolution may express an evolutionary advantage in the context of intraspecific relations.

a. Particularities of maternal odor

In neonatology and probably still months afterwards, the most salient body odor newborns will encounter is their mother's body odor. Compared to any body odor, the mother's odor has a special status and benefits from a strong associative learning through the reinforcement of caring. This odor, hereafter designated "maternal odor", represents the secretion from axillary and areolar regions from the nipple, where apocrine, eccrine and sebaceous glands secrete colostrum, milk, sweat and a latescent fluid from areolar glands (Doucet et al., 2012; Schaal, 2010, for a review): it is basically axillary odors with additional breast odors.

It has been evidenced that the chemical composition of breast-milk had similarities with amniotic fluid, allowing transnatal familiarity (Porter and Winberg, 1999; see Loos et al., 2019, for a recent review on human milk composition). This powerful ensemble allows the neonate to find the nipple as fast as 10 min after birth (Varendi et al., 1994) and isolated components (i.e., sources or odorants) elicit similar oral activation compared to a scentless breast (i.e., isolated nipple, areolar region, milk or whole breast, Doucet et al., 2007), head turning behaviors (amniotic fluid versus colostrum, Marlier et al., 1998) and oro-facial responses (amniotic fluid versus breast milk, Soussignan et al., 1997). The literature is very rich on the question (for a recent review, Schaal et al., 2020). Aside these prompt and early attractive substances, associative learning completes the maternal odor panel very rapidly after birth (evidenced from 30 min postnatal, Romantshik et al., 2007) which lasts up to a 21 months duration (Delaunay-El Allam et al., 2010, 2006); and could explain the wealth of maternal odor stimulation, as different sources and substances will be rapidly associated with them (Cernoch and Porter, 1985; Schaal et al., 1980). In conclusion, maternal odor has a particular weight in the sensory bubble of the baby during the first months, which is shared across mammalian species (Porter et al., 2001; Schaal, 2010), suggesting a strong evolutionary advantage for such dedicated systems (i.e., production from the mother and reception from the baby) in the survival of the species.

b. Pre- and post-natal perception of maternal odor

Investigating the human fetuses is still refrained by methodological constraints. However, preterm neonate abilities offer an insight to the functional stages of development from ~30 weeks of gestational age, even if chemo-sensation may differ between liquid (intrauterine) and aerial (extrauterine) environments. The first study on human preterm neonates showed an olfactory responsiveness to peppermint odor from 28 week old (Sarnat, 1978), confirming that olfactory stimulation could happen in utero as it is observed in other mammals (Smotherman and Robinson, 1987). Intrauterine learning is possible, as studies showed a recognition of the familiar amniotic fluid versus an unfamiliar one (Schaal et al., 1998) and reactions in favor of amniotic fluid versus breast milk with a shorter crying duration (Varendi et al., 1998) showed immediately after birth (the test was made ~30min after full term birth). Along this line, a soothing effect of maternal odor was evidenced recently on preterm neonates (using breast milk odors), characterized by a reduction of pain reactions during a routine blood test puncture (Jebreili et al., 2015; see also Küçük Alemdar and Kardaş Özdemir, 2017). These behavioral observations are confirmed by a reduction of cortisol level, suggesting a physiological analgesic effect of breast milk odor on preterm neonates (Badiee et al., 2013; see Zhang et al., 2018, for a review).

Amniotic odors could be very important in establishing transnatal continuity. Presented with maternal odor on a cloth, very preterm (28-32 weeks) and late preterm (33-36 weeks) neonates show an activation of unilateral orbitofrontal cortices, whereas full-term (37-41 weeks) neonates show a bilateral activation, a difference that the authors interpret in term of improved awareness to the olfactory cues in the environment (Frie et al., 2019). Full term newly born infants' orbitofrontal regions react differently to vanillin, colostrum and water (Bartocci et al., 2000), suggesting that these odorants may elicit different behavioral responses. Importantly, compiling evidence shows an acute sensitivity of the newborn to maternal odor, enabling the recognition of the mother, but also the engagement of feeding behavior, both decisive factors in early mother-infant bonding ensuring ontological survival (Schaal, 2014; Schaal et al., 2004). Indeed, newborns are sensitive to biologically relevant odors as they are able to discriminate between their maternal odor and another mother's odor (Cernoch and Porter, 1985; Macfarlane, 1975; Schaal et al., 1980). Smell serves as a powerful guide to rapidly direct the newborn to the appetent nipple (Varendi et al., 1994). Moreover, appetitive behaviors are observed in greater proportion towards the familiar versus an unfamiliar night gown worn by the mothers (Sullivan and Toubas, 1998), but also in the presence of the amniotic fluid (Contreras et al., 2013) or breast odors (Doucet et al., 2007), which are even able to activate crawling behaviors from the newborn in order to reach to source of the odor (Varendi and Porter, 2001). Breast milk odor is preferred over formula milk odor even when newborns have never experienced the reinforcing situation of breastfeeding (Porter et al., 1991), and it activates the orbitofrontal regions more than formula milk odor (Aoyama et al., 2010). As delayed breastfeeding as been correlated to increased risk of infectious diseases and higher neonatal mortality (Edmond et al., 2007, 2006), these odor-induced behaviors may be of vital importance.

The baby is thus pre-equipped in detecting and actively reacting to maternal odor from the first stages of development (Porter et al., 2001). These observations are probably partly the result of very early and effective learning, starting in the intrauterine environment. The already mentioned chemical similarities between intra and extra uterine olfactory cues are reflected in the verbal description of parents when qualifying the amniotic fluid itself (Schaal and Marlier, 1998). In fact, the baby is not the only active part in the mother-infant dyad to create and nurture the bond. The mother is able to recognize her newborn's body odor (Kaitz et al., 1987; Porter et al., 1983; Russell et al., 1983) and her amniotic fluid with a very good accuracy shortly after birth (i.e., 80%; Schaal and Marlier, 1998). In addition, her disgust perception is reduced when exposed to soiled diapers of her infant versus another's women infant, ensuring her unconditional care even in case of disease which can cause repulsive malodor (Case et al., 2006). A baby's odor exposure was also linked to activation of the neural reward system (Lundström et al., 2013) and the prefrontal cortex (Nishitani et al., 2014), suggesting reinforcing mechanisms (or reinforcement) of this bond. This reciprocal recognition is a key element in shaping the bond and ensures its continuance. The neonate recognition by body odor smell is also achieved by other family members (e.g., the father, grandparents and aunt/uncles; Porter et al., 1986; but see also Bader and Phillips, 2002) and the father is equally able to identify the amniotic fluid of his newborn, often described as related to the mother's odors (Schaal and Marlier, 1998). Olfactory cues appear to be very strong vectors of inter individual relationships from the earliest moments of life.

Aside these feeding and bonding effects, as we saw for preterm neonates, neonatology care units benefits from a line of research aiming at reducing distress in newborns (for a review, Zhang et al., 2018). Maternal odor thus also appears to have a soothing and distress-relieving effect during the first month, at least. Breast milk odor alone is able to reduce, during a painful event: crying and agitation (Rattaz et al., 2005), heart rate and oxygen saturation (Akcan and Polat, 2016) but also cortisol level (Nishitani et al., 2009); and after the event, it reduces crying duration (Mellier et al., 1997), an effect also observed with overall maternal odor (Doucet et al., 2007; Sullivan and Toubas, 1998). Likewise, less pain reactions are observed for newborns exposed to familiar breast milk or the odor of their amniotic fluid (Akcan and Polat, 2016).

In older infants, olfactory literature is overall sparser, due to the difficulties associated with infant studies. However, associative learning has been evidenced by using maternal odor coupled with an arbitrary odor. Schleidt & Genzel (1990) asked mothers to wear a perfume during the first two weeks following birth. At one week, the infants oriented preferably towards the perfume odor opposed to a control odor (vanilla, anise or rose oil) and maintained the preference at 4 weeks if the mother had occasionally continued wearing it. Using a more specific situation of breastfeeding, Delaunay et al. (2006) showed that 3-day-old chamomile-exposed newborns preferred chamomile over a scented control, but displayed no head-turning preference between chamomile and breast milk odor, suggesting they considered the odorants of equivalent quality or motivational value. Some of these infants were tested again as toddlers in an object manipulation paradigm (Delaunay-El Allam et al., 2010). At 7 then 21 month-old, they showed very clear differentiated behaviors compared to non-exposed infants in manipulating the chamomile objet (more and longer mouthing, less negative facial responses) versus the scented control (i.e., violet). The chamomile had not been presented since the 4th day postpartum, which allowed the authors to conclude in a long-lasting retention of the early positive association between maternal odor and chamomile through breastfeeding. These studies provide very interesting insights on the vectorial quality of maternal odor, itself probably being the result of intrauterine learning transference. In a way, they show that maternal odor can act as a cornerstone to associative learning for very arbitrary cues, provided they are reinforced. Odorants/flavors are also learned through the mother's diet by transferring to the intrauterine environment, and later to breast milk, and the retention of this exposure could even manifest into childhood/adulthood. Carrot (Mennella et al., 2001), anise (Schaal et al., 2000), alcohol (Faas et al., 2000), garlic (Mennella and Beauchamp, 1993) or vanillin (for a bottle-feeding experience; Haller et al., 1999) have been shown to elicit discriminative or preferential responses post-birth from days to years after initial exposure. One may thus wonder the extent of this capacity: what type of stimuli can benefit from the maternal odor's saliency? Does it work only with stimuli of similar nature (i.e., olfactory cues) or can it transfer to other modalities as well? Does it only manifest in experimental paired-choice settings or does it spontaneously and profoundly modulate one's behavior?

c. *From childhood to adolescence*

Children are equally sensitive to the body odor encountered in their environment. Children (i.e., 2 to 16 years-olds) show olfactory competence with an impressive precision, along with the physiological transformation their own body experience, leading to marked body odor secretions.

Body odor conveys olfactory cues mediating social interactions in children, suggesting a social group cohesion mechanism. Indeed, they recognize a friend's body odor (Mallet and Schaal, 1998) and reject pairs whose body odor is poorly judged (Todd, 1979). Before puberty, children are apparently not discriminating sex differences in the body odor of their pairs (9 years-old; Mallet and Schaal, 1998). However, later in childhood, body odor cues are strongly suggesting attraction/repulsion behaviors driven by incest avoidance and the identification of potential sexual partners. First, numerous evidence show that from an early age, children are able to recognize their siblings (Porter and Moore, 1981; Weisfeld et al., 2003), which translates into a dislike for brothers or sisters' odors into adolescence (Weisfeld et al., 2003). In addition, adolescent girls (16-17 years old) strongly react to male sweat (i.e., judged unpleasant) whereas boys of the same age and younger children (8-11 years old) do not, suggesting a switch in body odor perception due to physiological changes. As young pubescent men experience the activation of their own apocrine glands, which expose them to similar sweat characteristics, this sex-dimorphism habituation could partly account for this discrepancy (Stevenson and Repacholi, 2003). Finally, this may also result in the aversion of the father's odor expressed by both adolescent girls and boys (i.e., 9-15 years old) but not at a younger age (6-8 years old); along with the maternal odor recognition, which had faded in children (6-8 years old) but seems reactivated in adolescence (9-15 years old), suggesting incest-avoidance mechanisms at work (Weisfeld et al., 2003). As in infants, kin recognition is reciprocal. Mothers recognize their children's odor (Ferdenzi et al., 2010; Schäfer et al., 2020) and even classify with 72% accuracy the pre-pubertal odor (Schäfer et al., 2020). Likewise, using questionnaires in 163 mothers and 72 fathers (i.e., 235 independent families), Croy et al. (2017) showed that infant and children's body odor (all pre-pubertal) were perceived more pleasant compared to teenager's odor, a difference which can promote early bonding and care at younger ages and contribute to incest avoidance in post-pubertal individuals.

Recently, mirroring a line of research extensively investigated in adults (see below), a study investigated the effect of adult stress odor (versus sport odor) on children (Lübke et al., 2017). Authors found that prepubertal girls (9-13 years-old) were sensitive to stress odor collected from adult males as it enhanced their startle reflex. This suggests that stress odor influence could be unrelated to physiological changes induced by puberty, but more investigation on that matter should be undergone.

In atypical developmental children, maternal odor still bears a specific position as autistic children are spontaneously attracted to them (Bogdashina, 2016) despite sensory abilities considered overall impaired (Larsson et al., 2017). A group of researchers recently yielded interesting findings of maternal odor in autism (Parma et al., 2014, 2013), highlighting their beneficial effect in the context of social imitation. These studies open venues to modulatory effects of familiar and ecologically salient odors in atypical development where social cognition impairments are characteristic symptoms.

d. In adulthood

In line with findings at younger ages, adults are still able to recognize familiar individuals by smell. In addition to a good identification of (one's) infants and children reviewed above, we are able to recognize our own body odor among others (Lord and Kasprzak, 1989; Platek et al., 2001), but also our partner's odors (Lundström et al., 2009). This is particularly interesting considering that the disruption of male individuals' body odor using perfume (via a scented antiperspirant versus a scentless and inactive one) resulted in modified behaviors, so obvious that it correlated with attractiveness ratings from women judging their behavior from videotapes (Roberts et al., 2011). In fact, recent evidence converges to show that we are very sensitive to body odor in adulthood, despite an overall unawareness. For instance, we tend to smell our hand after a handshake with a stranger, as if to sample chemical cues from this encounter (Frumin et al., 2015). In a large-scale online-survey individuals (137 men & 260 women, from 19 to 74 years old and 19 different countries) were asked to report auto and allo-smelling behaviors (Perl et al., 2020). Sixty-one percent of responding people reported smelling strangers, 94% reported smelling/sniffing their relatives (partner or children) and more than 92% reported being conscious of smelling their own armpits and hands. Hands are also used to sample odors from parts of the body (armpits, 55%, or genitals in 74% of men and 56% of women). Of course, online questionnaire can present the bias of being completed mostly by individuals interested in the topic and thus lack representativity; however, it also presents with the advantage of diminishing the social desirability bias and promote honest disclosure on somehow intimate and delicate questions. The underlying reasons for these frequent behaviors are still unknown, by lack of investigation on the matter. Nonetheless, they appear as active and intentional behaviors, even if unconscious, which could contribute to sampling cues from our surroundings leading for instance to an increased feeling of security when smelling the odor of our romantic partner during our sleep (Granqvist et al., 2019; Hofer and Chen, 2020).

In line with functions of chemical communication across taxa (harm avoidance, feeding and reproductive behaviors, **Box 1**), accumulated evidence confirms the body odor involvement in the detection of cues maybe helping potential mate identification in humans. We have the ability to detect the major histocompatibility complex (Milinski et al., 2013), responsible for protein coding which directly affects the human leucocyte antigen (HLA) and would translate to the body odorprint. In that respect, several studies have shown a preference for dissimilar HLA profile in an experimental mate choice design (e.g., Jacob et al., 2002) while this was not confirmed by actual couples studies (e.g., Hedrick and Black, 1997) making these results overall inconsistent (for a review, see Havlícek and Roberts, 2009). Aside this potential genetic identification, others studies have shown that men reported relying more on visual cues while women declared to be more prone to use body odor cues to identify a potential partner (Havlícek et al., 2008; see also Herz and Inzlicht, 2002), and that especially malodorous body odor is a rejection criterion for women (Herz and Cahill, 1997). Body odor could also signal sexual orientation (Martins et al., 2005; Sergeant et al., 2007), maybe via hormonal variations, which is responsible for the variability of women's body odor due to their menstrual cycle. Indeed, women's reproductive status seems detectable by men via odors (with a higher appreciation for high-fertility odors; Gildersleeve et al., 2012) and influences close women's cycles (Mcclintock, 1971; Preti et al., 1986). Likewise, maternal odor modulates the menstrual cycle (Jacob et al., 2004) as well as sexual motivation (Spencer et al., 2004) in nulliparous women, interpreted as cues indicative of a suitable reproductive environment. These effects may also stem in non-hormonal factors, since women committed in a romantic relationship presented a lower sensitivity to non-partner's body odor (Lundström et al., 2009). However, despite chemical distinguishable profiles according to sex, explicit sex judgment of body odor samples (i.e., classifying an odor to belonging to a male or a female) is not achieved in western industrialized cultures (Mutic et al., 2016; Schleidt et al., 1981).

Body odor may also mediate emotions and emotional reactions amongst individuals. The partner's odor improves sleep quality (Hofer and Chen, 2020), whereas unfamiliar (neutral) body odor in a competitive (i.e., stressful) situation is related to cardiac acceleration in women (Mutic et al., 2019). Emotional states induce physiological variations which are transferred into sweat secretions and can be perceived by receivers. A line of research specifically explores if these cues are also provoking emotional detection/contagion (i.e., the detection of the emotional property may induce a similar state in the receiver; Hatfield et al., 1993) or reciprocity (i.e., feeling anxious in the presence of odor collected from an angry person). Numerous effects were reported (Chen et al., 2006; Dalton et al., 2013; de Groot et al., 2012, 2015a; Gasper and Clore, 2002; Haegler et al., 2010). In fact, stress odor is characterized by the release of adrenalin (Harker, 2013), which help stress odor be particularly well discriminated (Ackerl et al., 2002) independently of their intensity (Cantafio, 2004) and producing robust effects in the perceiver (for a recent meta-analysis, see de Groot and Smeets, 2017). Similar mechanisms may be at stake for other emotional or transient states.

For instance, dominance can be manifested by higher levels of testosterone, which modulates body odor secretions similarly to hormonal variations due to the menstrual cycle. As a result, body odor from dominant individuals has been shown to elicit a higher skin conductance in perceivers, what authors interpret as the detection of a threat signal (Adolph et al., 2010) and conversely, it has been recently evidenced that body odor collected from individuals after they had lost a combat smelled more unpleasant than sweat from the winners (Fialová et al., 2020). These chemical cues signaling a (transient) state in the producer can nevertheless result in a fight/flight response from the receiver. For instance, while tested in a virtual environment, women exposed to stress body odor showed less trust towards the virtual character (posing as an ecologically valid encounter) than women exposed to usual body odor (Quintana et al., 2019). Besides, distinguishing between healthy and sick individuals may be a useful ability to avoid potential contagion (Cone, 1968; Liddell, 1976; Regenbogen et al., 2017) and can be a cue to a poor health quality (Sarolidou et al., 2020), the probable underlying cause for women's mate rejection in case of malodorous body odor (Herz and Cahill, 1997). On the other hand, pro-social behaviors have also been observed in these contexts: as unpleasant body odor is also invoking pity, detecting it may lead to helping behaviors, especially when the cause of the malodor is considered outside the individual's scope (Camps et al., 2014). It seems thus that body odor is accurately detected among individuals and actively mediates interindividual relationships in private and less familiar encounters.

Body odor cues are a complex mixture conveying a wealth of information: available from the first stages of life, we make use of them to connect with other individuals. Along this review, it became clear that even if we do not spontaneously report being aware of olfactory cues in our surrounding; we can ascertain using these cues to sample our own body, our loved ones and even strangers. Chemical signals are thus very important to identify conspecifics, based on their identity, physiological or emotional state, and contribute to the way we interact with those individuals. In fact, the neural processing of our own body odor is done faster than the odors of a stranger (Pause et al., 1998). To conclude this section about perceiving conspecifics from chemical cues, we will now describe the neural underpinnings allowing these competences.

3. A dedicated neural network subtending body odor processing

As reviewed, human body odor is ecologically relevant and thus in a good place to benefit from a particular processing, mirroring the large network of the VOTC engaged in visual face categorization. Several neuroimaging studies have observed cortical activation in mainly: the occipital gyrus, the angular gyrus, the anterior and the posterior cingulate cortex (Lundström et al., 2009, 2008; Mujica-Parodi et al., 2009; Prehn-Kristensen et al., 2009; Zhou and Chen, 2008;

see Parma et al., 2017 for review). Importantly, these observations were made while participants were unaware of the diffusion of odors (body odor and control).

Compared to common odor, body odor is shown to activate neurons in the primary visual cortex: in the occipital gyrus. However, this activation had already been observed in processing social information from other modalities (Haxby et al., 2002). It is suggested that it may induce a priming resulting from the alerting value of body odor (Lübke and Pause, 2015), and prepare the visual system to detect objects in the environment (Lundström and Olsson, 2010). In line with this hypothesis, the angular gyrus is usually related to the perception of the body (Seghier, 2013), and its activation in the context of smelling body odor could depend on the same mechanism of preparedness for perceiving person-related cues. The anterior section of the cingulate cortex suggest an heightened attention to odors of this nature as this area is often related to attention processing (e.g., Botvinick et al., 1999). Finally, the posterior cingulate cortex is linked to emotion responses and actions (Cato et al., 2004; Maddock, 1999). For that reason, Lundström and Olsson (2010) propose that both structures (anterior and posterior cingulate cortex) tune activation to determine and process the emotional quality of the stimulus (Fredrikson et al., 1995). Less distributed than the wide network subtending face perception, body odor processing benefits nonetheless from an interesting network reflecting the social value and ecological relevance of these types of inputs.

Just like faces are a special type of visual object, body odor is undeniably a special type of odor. Both cues appear essential in our interaction with others, and they benefit from a special attraction observable in early ages, continuously found across development. In addition, body odor modulates our physiology, cognitive abilities and behaviors. In our environment, body odors and faces co-occur extensively and unfortunately little is known on how this co-occurrence is processed, and what contribution each cue has to the processing of the other, if any.

III. Body odors and faces intertwined

A. What your nose tells your eyes when you see faces

In the first section, we explored how multisensory our perception was; then, we developed the visual and olfactory abilities of human toward the identification of their conspecifics. However, only a few studies to date have explored how we perceive conspecifics using both types of sensory inputs. We will thus address here a thorough review of the state of the art regarding olfactory-visual processing of faces using body odors, as only a small portion of the literature has investigated this question. It is true, so far, knowledge of body odor and cognitive influence remains relatively unexplored, along with potential methodological difficulties in sampling and/or diffusion of olfactory stimulation, as methodological standards are lacking.

Yet, the field is gaining rapid interest and curiosity. This review will include face perception to a larger extent than face categorization, as this question has not yet been tackled.

1. In adulthood

The integration of multisensory information is expected to happen spontaneously, i.e., without explicit directed attention. Along this line, and based on the emotional link of olfactory processing, an interesting study suggests to consider the importance of body odor perception while witnessing a crime (Alho et al., 2015). This work assesses the impact of the emotional content of a scene on the memorization of body odor associated to a person's identity (among which, the face) and the fast and accurate learning abilities measurable in a brief digital encounter (i.e., 1-min video) of a stranger. Indeed, in an experimental setting, participants viewing a crime scene associated to a body odor recognized the odor better when it was presented amongst other equivalent body odor, whereas participants who viewed a non-violent interaction proved no such associative learning of the odors. Along the same line, creating an aversive conditioning with an electric shock, Gaby & Dalton (2019) showed that conditioned body odor altered a neutral face judgment by rendering it more "surprised", whether the body odor was standardized or using the usual cosmetics of the donor (diplomatic odor, see **Box 3**), suggesting that the individual odorprint is still available under more ecological circumstances and can further bias our social interactions. Another study tested the influence of masked body odor cues during the encoding of unfamiliar faces (Cecchetto et al., 2020) and showed that the recognition of face was improved in the presence of the body odor (masked by clove oil) versus only the mask. In addition, using fMRI, the authors related this performance to as greater activation in regions known to process memory (dorsolateral prefrontal cortex), olfactory information and multisensory integration (orbitofrontal cortices). Taken together, these studies confirm that odors are part of the visual experience we have of others and actively contribute to our recognition skills.

The research on olfactory-visual face perception in adults using body odor was most concentrated on facial expression processing, especially using stress odors. Exposing participants to stress odors while making them judge fear from morphed faces (from neutral to fearful) had the effect of enhancing the fear judgment (Wudarczyk et al., 2016) or made the judgment better approximate the categorical model (i.e., sigmoid) of fear perception (Mujica-Parodi et al., 2009). Other congruent effects have been noted, for instance, priming a neutral face with either a happy, fearful or sad face elicits a priming effect for happy faces, but when this task is performed in a stress odor context, the priming effect is disrupted (Pause et al., 2004). Likewise, stress odors reduces the rating of happiness in neutral-to-happy morphed faces (Zernecke et al., 2011) and increases the rating of fear in happy-to-fearful morphed faces (Zhou and Chen, 2009), although only for intermediate morph steps in both studies. Using an electrophysiological measure to record the cortical activity while passively viewing neutral-to-angry morphed faces, Rubin et al. (2012) observed a stronger late positive component in the presence of stress odors, again only for the intermediate steps of the morphing sequence. In parallel, other studies revealed shorter latencies in the judgment of undifferentiated emotions due to the presence of stress vs. sport odors (for neutrality, happiness, fear and disgust; de Groot et al., 2015b; for happiness and anger; Rocha et al., 2018), what the authors interpreted as a contagion effect from stress odor inducing a more alert state. It thus appears that an emotional odor can modulate cognitive abilities of visual face perception: better performance, accentuation (higher extreme ratings) or disambiguation (more categorical ratings on intermediate steps). Since, these studies used unequal and limited sets of emotions (either positive or negative, or sometimes both morphed together) making the stress odor effect hard to conceptualize, a recent and elegant study tested whether the effect of stress odors was discrete (i.e., congruency with fear but not with other negative emotions), or having a general negative evaluative state (the negative polarity of the odors acts as a negative factor), by contrasting fear to anger, disgust and neutrality (Kamiloğlu et al., 2018). Authors showed a reduced response time only to fearful faces, thus in favor of the discrete hypothesis (i.e., the general negative state would have been validated if the response times of all three negative emotions differed from neutral ratings), which could be dominant when both are at stake.

2. In infancy

Aside this dissertation work, only three studies to date have explored the effect of body odor on face perception in infancy, which seems surprising considering the extensive literature on both maternal odors and faces in infancy. The underlying reason probably lies in between the two distinct disciplines they both concern, i.e., psychology and ethology, despite the wealth of studies on face perception in infancy and the assessed importance of chemical signals in the first months of life.

The first study to be interested in body odor effect on face perception questioned a broad phenomenon: face preference (Durand et al., 2013). Authors tracked 4-month-old infants' visual exploration of a pair of images (an unknown face and a car). Additionally, two groups of infants were presented with either a t-shirt impregnated with their mother's odor or an unworn t-shirt. While exposed to maternal odor, they looked significantly longer at the face and particularly the eye region, without reducing the time spent on the car. This study gave the first evidence for olfactory visual association involving maternal odor in infancy and highlighted that odors could help visual exploration of socially relevant objects. Particularly, maternal odor could induce a greater attention to social cues by effect of congruency and motivate the infant to seek for interactions. Indeed, maternal odor is continuously reinforced by social interactions between the baby and the mother, thus the mere presence of the mother's odor could make the baby generalize the interactions with the mother to broader social interactions.

More recently, 4-month-old infants again were tested in a visual face preference task opposing the mother's face vs. a stranger's face while babies were exposed either to no odor, their mother's odors or stranger mother's odors (Durand et al., 2020). The spontaneous preference for the stranger's face is reliably found in every odor context in accordance with the 4-month-olds literature (Bartrip et al., 2001), but the time allocated to the mother's face significantly increases in the presence of any mother's odors (i.e., own or stranger's) while no gaze difference is observed for the stranger's face. This result goes in favors of an olfactory similarity present in both mother's odors. However, whether this characteristic is specific to maternity even 4 months after birth or the fact that they are both female adult odors is still unknown. In any case, associative learning may have favored this association to reorient the infant's gaze toward his mother's face while in the presence of a body odor, as if to remind of her presence.

In 7-month-old infants, Jessen (2020) measured event-related potentials while they viewed happy vs. fearful faces, and were exposed to either their own mother's odors, a stranger morther's odors or no odors. Using ERPs, she showed that while the fearful face elicited a stronger Negative Component (i.e., Nc; Peltola et al., 2009) in infants in the unfamiliar and no odor group, the activation recorded for fearful or happy face was similar for infants exposed to their mother's odor. In addition, a breastfeeding effect was highlighted, since this effect was reliably found in breastfed babies, irrespective of the odor group they belonged to. This study evidences a momentary as well as a long-lasting effect of maternal odor on the reduction of a fear marker (measured on the Nc). The author interprets this finding by linking the maternal odor with maternal presence, which would help promote wellbeing and act as a "safety signal". In this sense, by reducing resource allocation to fearful cues, familiar maternal odor would potentially have an effect in bonding with strangers at an age when locomotion develops and stranger anxiety emerges (Leppänen and Nelson, 2012).

Taken together, these studies suggest that (maternal) body odor actively takes part in infant's social behavior as it directs infant gaze toward socially relevant information, structures visual cognition from visual discrimination to neural activity and guides face processing up to adulthood. This review also revealed a systematic interaction between face and body odor perception. Although it appears difficult to draw a clear conclusion from apparent conflicting results, due to the diversity of questions addresses and methodologies used, body odor influence seems to go in favor of a congruency which is inherent to the association or rapidly acquired through associative learning. Indeed, studies on facial expression perception suggest that the odor effect can be somewhat flexible and adapt to associate with the most congruent cue available (e.g., stress odor either reducing a positive priming or increasing a negative rating).

B. Hypotheses, prediction and proposed methodology

Along this introduction, we have explained that perception is multisensory by essence and functions by grouping signals into whole percepts in order to make the world more intelligible at a lesser cognitive cost. It is mainly achieved based on categorization, a core cognitive function for grouping inputs by providing similar responses despite their variability (Rosch, 1978). We then reviewed the neuroanatomical structure of dedicated senses to evaluate our knowledge about the emergence of interactive perception across the senses. Evidence tends to show that senses are more collaborating than interfering with one another (Bahrick and Lickliter, 2012). Moreover, since olfaction starts to function earlier than vision and that odor perception is more stable in space and time than visual information, it appears in a good position to support the development of category formation in other senses, especially vision (Schaal and Durand, 2012). We further exposed that olfaction is crucial in perceiving our conspecifics (Lübke and Pause, 2015). While it is true that vision provides key elements in this endeavor, as reviewed with an excerpt of the extensive literature on face perception and focusing on face categorization, olfaction also conveys a wealth of social information that we are able to detect and which modulate our behaviors and neural activity (Schaal et al., 2020). The few investigations undertaken in the intersensory association between body odor and face perception inform us that this chemical sense does indeed influence the visual processing of face characteristics and one study in infants suggests that body odor particularly orients towards a face paired with a car (Durand et al., 2013), suggesting a heighten discriminative ability. However, whether body odor helps in categorizing faces, i.e., distinguishing them from other objects, and in which circumstances, is still unknown.

1. Mechanisms and hypotheses

Considering that odors convey a wealth of information we are able to detect, **our main hypothesis is that odors actively contribute to process congruent visual information.** We will test this hypothesis with four studies **illustrating this olfactory-visual association by integrating body odor and the face category.**

Faces and body odors are both very important cues for conspecific perception. They share ecological relevance, which translates into a heightened attention allocation at behavioral level and is reflected by a dedicated processing in the brain. Hence, since they also co-occur in daily interactions, they benefit from associative learning which strengthens their congruency. Accordingly, we thus predict that **(1) body odor influence is in fact selective to the perception of conspecifics**. By presenting odor as a context, it could act as a prime to indicate person-related inputs to other senses (Durand et al., 2013). For that matter, **no body odor effect is expected for nonface objects, and accordingly, a nonhuman odor is not expected to influence the categorization of faces**.

In addition, evidence showed that congruent odors could modulate face processing when the visual input is somehow ambiguous (e.g., emotional face morphs), in line with a compensatory mechanism across the senses when one of them is not sufficient (Ernst and Bülthoff, 2004). We thus also predict that **(2) odors facilitate perceptual interpretation when the visual input does not provide sufficient information by itself**. This prediction will be tested in two cases: **when the visual system is not yet mature**, and in the matured visual system **when inputs are difficult to interpret and lead to ambiguous categorization**.

The four experiments proposed to test these predictions are grouped as follow:

Chapter 1. During early development, when vision is not yet mature and that body odor particularly drives early behaviors, **maternal odor** could selectively promote the visual categorization of faces. This will be tested in the first set of studies. Aiming at **delineating the selectivity of maternal odor**, three groups of 4-month-old infants will be tested, each with a different visual category (Study 1 to 3).

Chapter 2. When the visual system matures, visual categorization is more efficient by itself. It is expected that **odor will lose its facilitating effect, unless visual inputs are ambiguous**. This hypothesis will be tested by a fourth study: an experiment conducted in adults will verify that a **body odor** effect is found according to multisensory congruency and only for ambiguous stimuli.

2. Methodological considerations

The work presented in this dissertation was conducted using a common methodology, which will be shortly introduced here from a general perspective.

Electrophysiological measures consist in a direct recording of the electric fields elicited by neuronal activity. We will only use non-invasive scalp electroencephalography (EEG) which captures the synchronous activation of populations of cortical neurons generating current spreading to the surface of the scalp. While this property gives a roughly-drawn topography of the response over the scalp, EEG recordings are by nature very precise in their temporal resolution (in ms) and are typically used to observe the time course of a given brain activity (Giard and Besle, 2010; Jackson and Bolger, 2014 for an accessible review).

However, the present work will not analyze the time-course of perceptual activities. Instead, capitalizing on this high temporal resolution, the present method was designed to isolate perceptual functions based on an experimentally-induced periodicity, which can be captured thanks to the ability of the brain to synchronize with the periodicity of a given stimulation (Adrian and Matthews, 1934) and observed in the frequency domain in amplitude (μV) at defined frequency bins (Regan, 1989). First developed to study low-level sensory responses, this “frequency-tagging” approach (i.e., whereby information of interest are tagged at defined frequencies of stimulation) has been more recently declined to investigate higher-level cognitive functions, particularly in visual cognition: face perception (e.g., Rossion et al., 2020) and literacy (e.g., Lochy and Schiltz, 2019), for instance.

We will use *dual* frequency-tagging paradigms with fast periodic visual stimulation (FPVS-EEG), where spatially distinct classes of stimuli are tagged at separate frequencies, allowing discriminating the signal of interest from surrounding noise, within the same stimulation sequences. Visual stimuli (i.e., natural images of very diverse categories) are presented at a fast rate of stimulation (e.g., $F = 6$ Hz), thus each image is presented at 1/F second (e.g., ≈ 167 ms). Among this fast stream of images which serves as a base (Figure III-1, "B" objects), one target category ("C") is presented at a fixed (sub)rate (e.g., $F/n = 6/6$ images, i.e., as every 6th image, = at 1 Hz). Hence, the category-selective frequency (F/n) is inherently separate from the base rate of all images (F).

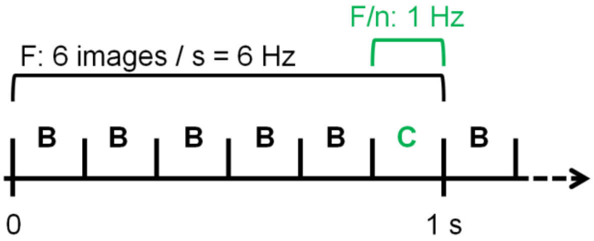


Figure III-1. Illustration of the EEG dual-frequency-tagging paradigm with fast periodic visual stimulation (FPVS-EEG). Excerpt of 1.167 s of stimulation presenting 6 images per second at a F = 6 Hz rate (black), and introducing a category-selective rate of F/6 = 1 Hz (green) by interspersing a defined category exemplar as every 6th image. This frequency-tagging approach elicits distinct neural responses corresponding to separate perceptual functions (see text).

This dual frequency-tagging elicits distinct neural responses according to the rate of stimulation. The base rate of visual stimulation (6 Hz in our example) elicits a **general visual response** which captures processes common to all images (e.g., responses to low-level cues) and is typically reflected by a strong middle-occipital response over the scalp. On the other hand, the category-selective rate triggers a **category-selective response** which results from the neural activation of dedicated functions responding differentially and reliably to the processing of the category of interest, e.g., shape and color characteristic of the category which makes its identification possible. As the two responses superimpose during the same stimulation sequence, the category-selective response corresponds to a differential response which specifically isolates processes that occur exclusively for the category of interest. Indeed, while in the time course of the stimulation the brain will process each exemplar one by one in a discriminative way (e.g., a face will be processed with its individual attributes and the background of the image), the representation in the frequency-domain will show the generalization of the discrimination between the base objects and the category exemplars (i.e., what makes a face a face). Theoretically, the differential response can induce a change of variable form (time-shift, increase/decrease in amplitude), but the fact that a systematic difference occurs will translate into a positive difference in the frequency-domain (expressed in absolute amplitude). By using variable natural images wherein the items are presented in their original background, the response is generalized across exemplars despite their variation in size, viewpoint, exposure, etc.

This paradigm presents with a number of advantages. Relatively simple to implement, it yields a valid measure of the category-selective response (Retter et al., 2020), sensitive enough to show differences in magnitude and localization according to the category (Hagen et al., 2020; Jacques et al., 2016a) and is immune to temporal predictability (Quek and Rossion, 2017). The responses are measured at the predefined frequencies and their harmonics (i.e., integer multiples, usually combined together; see Rossion et al., 2020 for review) making the approach highly objective. In addition, the stimuli are generally presented in long sequences (e.g., 30 s) resulting in a high frequency resolution (1/30 = 0.033 Hz, i.e., one bin value every 0.033 Hz) where the signal is recorded in tiny frequency bins and the noise spreads to broader frequency ranges. This makes the approach quite resistant to artifacts and produces a high signal-to-noise ratio (SNR). Several indices can be calculated by comparing the signal to the surrounding noise, from a relatively small number of trials, i.e., in a short testing time, even at the individual level,. The paradigm measures automatic perception and thus does not require a direct explicit task to elicit a neural response. Altogether, it can easily be applied across ages using the same material and parameters (e.g., infants: de Heering and Rossion, 2015; children: Lochy et al., 2019a; Vettori et al., 2019; and adults: Rossion et al., 2015).

Using this FPVS-EEG approach, odors will be presented as contexts throughout the visual stimulation, maintaining a form of ecological exposure induced by olfactory stability.

Chapter one

Chapter one

IV. Delineating the maternal odor influence over visual categorizations in the developing brain

One way to verify the effect of congruent odors on visual categorization is to test a very relevant category onto which an effect is strongly expected. If an effect is effectively found, the selectivity of the association should be further confirmed by ensuring it is not measured during the categorization of a noncongruent object. Additionally, to go further into understanding how and in what circumstances congruent inter-sensory associations are useful in early visual cognition, a third category can be tested – ideally one as relevant as the first one, but less well defined thus rendering its perception less obvious.

In this chapter, the focus will this be given to maternal odor effect on visual face categorization (**Study 1**), nonface categorization (car, **Study 2**) and illusory face categorization (facelike, **Study 3**) in 4-month-old infants. Evidence shows that from this age, infants experience a dramatic improvement of face perception abilities (Pascalis et al., 2011) and volitional visual processing (Braddick and Atkinson, 2011; Bronson, 1994). This work takes its roots in two studies which we already described: the FPVS-EEG measure of face categorization in 4-to-6 month olds (de Heering and Rossion, 2015) and the enhancement of the face preference in the maternal odor context at 4 months (Durand et al., 2013). We hypothesize that at brain level, maternal odor will influence the neural categorization of faces (**Study 1**) but not of cars (**Study 2**). This step is important in proving that the selectivity of the olfactory-visual association does not rely on general physiological effects (e.g., increased arousal) or sensory characteristics (e.g., the stability induced by *any* odor stimulation as a context which could enhance the response to *any* periodic stimulation).

While **Study 1** is a proof-of-concept study, the olfactory-visual mechanism at stake will be further delineated using a more difficult visual category to isolate, i.e., facelike objects (**Study 3**). Indeed, facelike objects are quite challenging to categorize. They are seen in common objects, from which feature configuration evokes a face (see **Box 2**). Hence the categorization of facelike objects implies to discriminate the face pattern from the canonical configuration of the common object and from preceding and following objects (i.e., in the sequence of stimulation); and to generalize this response despite the high variability of its source. While faces are ecologically learned from social interactions where the entire body, head and shoulders are available and constitute the expected context of a face (part of which is preserved in natural images (e.g., head, neck and shoulder)), facelike objects have no such regular contextual cue which would make the face pattern expectable. Thus, if the odor truly helps categorization, it may be required for the categorization of facelike objects in **Study 3**.

This section corresponds to the article:
Leleu, A.*, Rekow, D.*, Poncet, F.*, Schaal, B., Durand, K., Rossion, B., & J.-Y. Baudouin. (2020) Maternal odor shapes rapid face categorization in the infant brain. *Developmental Science*, 23 (2), e12877. doi:10.1111/desc.12877 *equal contributions

References of this article are added to the general bibliographic section of the dissertation.

Study 1: Maternal odor shapes rapid face categorization in the infant brain

Abstract

To successfully interact with a rich and ambiguous visual environment, the human brain learns to differentiate visual stimuli and to produce the same response to subsets of these stimuli despite their physical difference. Although this visual categorization function is traditionally investigated from a unisensory perspective, its early development is inherently constrained by multisensory inputs. In particular, an early-maturing sensory system such as olfaction is ideally suited to support the immature visual system in infancy by providing stability and familiarity to a rapidly changing visual environment. Here we test the hypothesis that rapid visual categorization of salient visual signals for the young infant brain, human faces, is shaped by another highly relevant human-related input from the olfactory system, the mother's body odor. We observe that a right-hemispheric neural signature of single-glance face categorization from natural images is significantly enhanced in the maternal versus a control odor context in individual 4-month-old infant brains. A lack of difference between odor conditions for the common brain response elicited by both face and non-face images rules out a mere enhancement of arousal or visual attention in the maternal odor context. These observations show that face-selective neural activity in infancy is mediated by the presence of a (maternal) body odor, providing strong support for multisensory inputs driving category acquisition in the developing human brain and having important implications for our understanding of human perceptual development.

1. Introduction

To deal with the flurry of sensory inputs coming from all modalities in the rich environment surrounding us, the brain needs to organize events into distinct categories, that is, stimuli that are treated as equivalent. Without this fundamental categorization function, our nervous systems would be overwhelmed by the sheer diversity of our experience. For this reason, categorization is thought of as a building block for all cognitive functions such as learning, memory and communication (Murphy, 2002; Rosch et al., 1976; Smith and Medin, 1981).

How categories are progressively formed in the human brain during early development remains, however, largely unknown. Classically, perceptual development is studied separately for each sensory modality, under the assumption that the brain first needs to decode modality-specific features for each input to define its category before combining these unimodal categories to form higher-order semantic concepts (Grill-Spector and Weiner, 2014; Lambon Ralph et al., 2017; Mandler, 2004; Mareschal and Quinn, 2001; Piaget, 1952). An alternative view posits that because visual, auditory, tactile, olfactory and gustatory cues co-occur in the environment, multisensory inputs constrain the early organization of categories and further benefit to the development of unisensory perception (Bremner et al., 2012; Gibson, 1969; Lewkowicz, 2010). Supporting this latter view, it is clear that infants easily bind auditory and visual inputs (Lewkowicz, 2000; Lickliter and Bahrick, 2000) and take advantage of intersensory redundancy (Bahrick et al., 2004). For instance, neonates learn better their mother's face or the face of a stranger when it is accompanied by their voice (Guellaï et al., 2011; Sai, 2005).

How categorization in a given modality relies on multisensory inputs depends on the functional onset of the different sensory modalities (Gottlieb, 1971). In the sequence of human sensory development, the olfactory system becomes functional earlier than the visual system (Turkewitz and Devenny, 1993). Human fetuses encode, retain and actively use the odor properties of their environment (Schaal et al., 2000, 1998), and their delivery to infants as isolated stimuli elicits differentiable physiological and behavioral responses (Doucet et al., 2007; Rattaz et al., 2005; Russell, 1976; Soussignan et al., 1997). Odor cues are thus in a position to ease the interpretation of inputs from the later-developing visual system. In addition, contextual odors are more stable in space and time compared with highly variable visual inputs (Schaal and Durand, 2012). Hence, olfaction may support the early development of visual categorization in assisting the brain to detect regularities in the flow of visual information, in assigning relevance and in attributing meaning to visual events based on prior odor knowledge, and in channeling some visual inputs into a common category. Accordingly, recent studies showed that 3-month-olds look longer at a smiling than a disgusted face in a pleasant odor context (Godard et al., 2016), and maternal body odor enhances preferential looking for a face over a car in 4-month-olds (Durand et al., 2013). However, these behavioral effects could be due to reorientation of attention following categorization, and have been observed only during pairwise discriminations with limited stimulus sets. Critically, what is currently missing is direct evidence that nonvisual cues, such as odors, shape visual categorization processes (i.e., discrimination between categories and generalization across variable exemplars from a single category) during early development.

To investigate odor-driven early development of visual categorization in the human brain, we examine here whether a neural correlate of the earliest and most salient form of visual categorization for young infants, human face categorization, is shaped by the concurrent presentation of a relevant odor for infants, maternal body odor. We take advantage of relatively recent evidence for rapid face categorization of natural images over the right occipito-temporal cortex of 4- to 6-month-old infants with frequency-tagging in electroencephalography (EEG) (de

Heering and Rossion, 2015). We extend this observation in a younger age group of eighteen 4-month-old infants with a new set of highly variable face images (Figure S1, Appendix 2) subtending a large area (28°) of the infants' visual field (Figure IV-1). Infants are exposed to two odor conditions: a control odor using an unworn t-shirt and the maternal odor using a t-shirt worn by each mother during three nights preceding testing (Durand et al., 2013). We therefore explore whether the high-level face categorization response in the infant brain is modulated by concurrent odor cues from the maternal body odor.

2. Materials and Methods

a. Participants

Twenty-five full-term 4-month-old infants participated in the study. They were recruited through the local birth registry after mail contact and interested parents were sent the material for collecting the maternal body odor. Before testing, all parents gave written informed consent and none reported their infants suffering from any visual, olfactory, neurologic or psychiatric disorder. Testing was conducted according to the Declaration of Helsinki and approved by the French ethics committee (CPP Sud-Est III - 2016-A02056-45). Data from seven infants were excluded due to unusable EEG data ($N = 2$), less than two valid sequences for one condition ($N = 3$), noncompliance with the procedure for odor collection ($N = 1$), or atypical data compared with the group's mean ($N = 1$). The final sample thus consisted of 18 infants (6 females, mean age = 129 ± 9 (SD) days, range: 120–157 days).

b. Visual stimuli

A large set of images of various objects (animals, plants, man-made objects; $N = 170$) and human adult faces ($N = 66$, 33 females) unsegmented from their natural background and with variable colors, viewpoints and lighting conditions, was used (Figure IV-1A). Images were first cropped to a square and resized to 400 × 400 pixels. Objects and faces were more or less off-centered after cropping to increase their eccentricity and avoid the presence of a clear facial pattern in the mean face image (Figure S1, Appendix 2). Stimuli were presented in the center of a screen at a viewing distance of 57 cm and subtended a large area of the infants' visual field, i.e. roughly 28 × 28° of visual angle (Figure IV-1B). Hence, face size was close to the typical size in infants' everyday social interactions but faces were presented at variable locations, increasing the difficulty for single-glance categorization.

c. Odor stimuli

Infants were exposed to maternal odor cues in contrast with a control odor condition (Durand et al., 2013). Maternal body odor was collected on a white t-shirt (100% cotton) sent to the mother enclosed in a zip-locked hermetic plastic bag one week preceding the experiment. The t-shirt was worn by the mother for the three consecutive nights preceding testing. Night wear improves standardization across participants by attenuating activity-related individual differences.

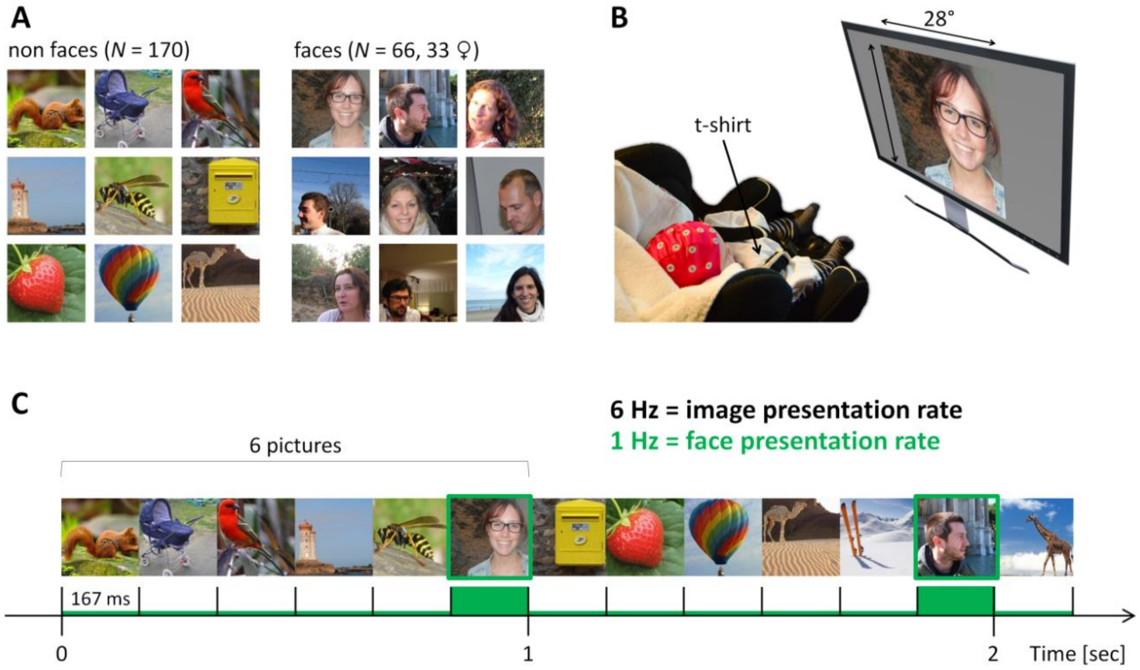


Figure IV-1. A frequency-tagging approach in electroencephalography (EEG) isolating a neural marker of face categorization in an odor context. A. Examples of the unsegmented images of objects and faces used as stimuli. **B.** After EEG-cap placement, infants were installed in a seat facing a computer screen. Two odor conditions were delivered by disposing t-shirts on the infant's chest: a t-shirt worn by the mother (maternal odor) or an unworn identical t-shirt (control odor). Images were presented in the center of the screen with a size of about 28° of visual angle, thus subtending a large area of the infants' visual field. **C**. Example of 2 seconds (/ 32) of fast stimulation with images periodically displayed at a base rate of 6 Hz (i.e., 6 pictures per second) without inter-stimulus interval. At this rapid rate, each stimulus is presented for ≈ 167 ms implying that perception occurs at a glance. Faces are inserted every 6th stimulus, at a lower rate of 1 Hz. Hence, two dissociated brain responses are tagged at two frequencies within the same stimulation sequence and quantified in the EEG frequency spectrum: a common visual response (6 Hz and harmonics, i.e. integer multiples) reflecting the processing of all cues that flicker at the base rate; a face categorization response (1 Hz and harmonics) directly reflecting the discrimination of faces from other objects and their generalization into a single category.

In addition, mothers were asked to refrain from using perfume and odorous soap during the collection period. During the days, they were instructed to store the t-shirt in the hermetic bag that could be left at ambient temperature but far from any heating device. The control condition consisted of an unworn identical t-shirt with equivalent storage procedure. Before sending the t-shirt to the mother, both t-shirts were laundered using hypoallergenic powder detergent (Persavon, France).

d. Procedure

Fast periodic visual stimulation was designed with a frequency-tagging approach to dissociate a common visual response and a face categorization response within the same stimulation sequence (de Heering and Rossion, 2015; Rossion et al., 2015). Using custom software written in Java, stimuli were presented on a 24-inch LED screen (60 Hz refresh rate, resolution: 1920 × 1080 pixels) with a mid-level grey background (128/255 in greyscale) at a 6-Hz base rate (6 images per second) without inter-stimulus interval. At this rate, each stimulus lasts about 167 ms (1 sec/6) implying that perception occurs at a glance. The 6-Hz base frequency of image presentation tags a common visual response reflecting the general visual processing of all presented natural images. In each stimulation sequence, a face stimulus appears every 6 stimuli, with all stimuli randomly selected from their respective sets (Figure IV-1C). Hence, faces are introduced at a rate of 6/6 = 1 Hz in the rapid train of stimuli. Any *differential* response to faces *vs*. non-face stimuli that is reliably (i.e., periodically) generated is reflected at 1 Hz and harmonics (i.e., integer multiples) in the EEG frequency spectrum. This response is thus a direct marker of face categorization, devoid of low-level visual confounds (see de Heering and Rossion, 2015; Rossion et al., 2018, 2015).

After electrode-cap placement, infants were comfortably installed in a baby car seat in front of the screen in a light- and sound-attenuated room. They were continuously monitored using a camera placed on top of the screen. To reduce the presence of olfactory noise, this room was well aired between testing sessions and experimenters did not use, eat or drink any odorous product before testing. During testing, parents were asked to stay far enough (at least 2.5 m) from their infants and to not interact with them except in case of manifest distress. The odor conditions were delivered by disposing the t-shirts on the infants' upper chest, attached with the seat belts, about 5 secs before a sequence began (Figure IV-1B). T-shirts were folded to optimally expose infants to the odorous axillary, breast and neck regions. They were manipulated with two pairs of dedicated disposable nitrile gloves (Schield Scientific, The Netherlands). Each infant was tested in the two odor conditions alternated every two sequences. Their presentation order was counterbalanced across infants.

Each 34.5-sec visual sequence started with a pre-stimulation interval of 0.5 sec of a blank screen, followed by a fade-in of increasing contrast lasting 1.833 secs. Then the stimulation lasted 31.167 secs at full contrast before a 0.833-sec fade-out of decreasing contrast and a blank post-stimulation interval of 0.167 sec. The 66 face images were divided in two sets of 33 faces each being randomly assigned to one sequence during the testing of one odor condition. The 170 non-face images were used in all sequences. Auditory tones were used to reorient infants' attention toward the screen during stimulation. Their non-periodicity avoided any contamination of the frequency-tagged EEG responses by auditory-evoked potentials. A sequence was not considered for further analyses if infants started to cry or manifest distress before it ended. An infant-based criterion was used to stop testing when infants stopped looking at the screen, or were too tired or discomforted to pursue the experiment. Infants performed between 4 and 16 sequences (mean = 8.5 ± 3.31 (SD) sequences), for an overall testing duration per infant between 2 min and 18 secs and 9 min and 12 secs.

e. EEG recording and analysis

EEG was continuously recorded from 32 Ag/AgCl electrodes mounted in a cap (Waveguard, ANT Neuro, The Netherlands) according to the 10-10 classification system (acquisition reference: AFz, electrode impedance < 15 kΩ, sampling rate: 1024 Hz). EEG data were then preprocessed and frequency-domain analysis (Appendix 2A) was performed to isolate and quantify both 6-Hz common visual response and 1-Hz face categorization response and their harmonics (i.e., integer multiples). At a high frequency resolution, frequency-domain representation provides high signal-to-noise ratio (SNR) since the noise spreads to broad frequency ranges while the signal is captured in tiny frequency bins associated with little noise. Frequency resolution was 0.03125 Hz here, allowing noise level estimation from frequency bins surrounding the signal. According to de Heering & Rossion (2015), the face categorization response appears over the right occipito-temporal channel P8 and to a lesser extent over its homologous channel P7 in the left hemisphere. Analysis was thus conducted within right and left regions-of-interest (ROIs; Figure S2, Appendix 2) centered on P8 and P7 and including contiguous channels (O1/2, P3/4, CP5/6). Likewise, since the common visual response is mainly observed over the medial occipital electrode Oz (de Heering and Rossion, 2015), it was analyzed within a ROI (Figure S2, Appendix 2) encompassing Oz and contiguous electrodes (POz, O1, O2). As in previous studies with this approach (e.g., de Heering and Rossion, 2015; Rossion et al., 2015), the significance of each brain response was estimated at both group and individual levels using *Z*-scores (response *vs*. noise amplitude). Odor conditions were then compared over identified channels using *T*-tests (individual noise-corrected amplitudes) and *Z*-scores for every individual odor effect (see Appendix 2A for details).

3. Results

a. Rapid face categorization in the infant brain

For combined odor conditions, visual inspection revealed a face-selective brain response at the predefined 1-Hz rate of face pictures presentation mainly over right posterior regions (Figure 2.A). The face categorization response reached significance over the right occipito-temporal channel P8 ($Z = 4.79$, $p < .001$, one-tailed, signal > noise) and its contiguous electrode CP6 ($Z = 4.26$, $p < .001$) with a noise-corrected amplitude across conditions of 1.14 ± 0.49 (*SEM*) µV and 1.18 ± 0.37 µV, respectively. This response was lower (0.34 ± 0.49 µV) but significant over the left occipito-temporal channel P7 ($Z = 1.91$, $p = .028$). The response was only recorded on the first harmonic (Table S1) and was not driven by a small subset of infants (Figure IV-2B and Table S2, Appendix 2) since 10 infants presented a significant response over CP6 and/or P8 and another 3 infants over at least one other electrode (i.e., O2, P4) within the right-hemispheric ROI. Given that a face-selective response was previously isolated in the infant brain with some infants installed in a car seat and others seated on their mother's lap (de Heering and Rossion, 2015), these observations across odor conditions replicate and extend this finding in a younger age group with a novel, even more challenging, stimulus set. They indicate that, at 4 months of age, the infant brain is already able to categorize at a glance multiple variable faces embedded in their natural background and presented in a fast train of various non-face images.

b. Maternal odor shapes the neural signature of face categorization

Visually, the face-selective response evolves from a parieto-temporal response slightly larger in the right hemisphere in the control odor context to a stronger right-hemispheric response in the maternal odor context (Figure IV-2C). Accordingly, a significant categorization

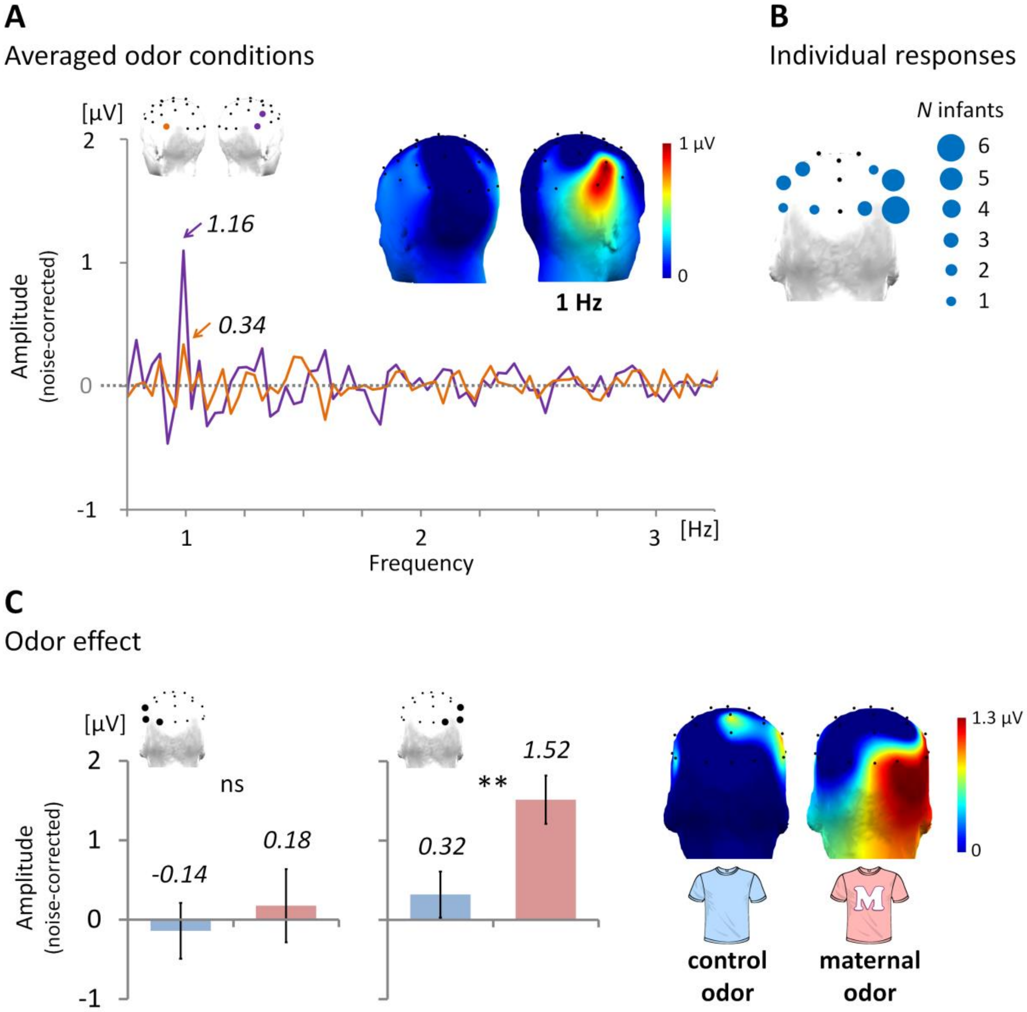


Figure IV-2. Face categorization response over lateral posterior brain regions. A. Noise-corrected amplitude of the EEG frequency spectrum averaged across the two odor conditions over left (orange: P7) and right (purple: averaged across CP6 and P8) posterior channels showing a neural response at the predefined 1-Hz rate of face images presentation. Italic values indicate the amplitude of the response and 3-D topographical head maps illustrate its spatial distribution from left and right posterior views. **B.** Head map (posterior view) depicting the density of significant individual face categorization responses over analyzed lateral posterior channels (i.e., P7/8, O1/2, P3/4, CP5/6). Circle size at each channel reflects the number of infants (out of 18) presenting a significant response here (i.e., $Z > 1.64$, $p < .05$, one-tailed, signal > noise). **C.** Noise-corrected amplitude of the face categorization response over left (averaged across CP5, P7 and O1) and right (averaged across CP6, P8 and O2) posterior channels for the two odor conditions revealing enhanced amplitude of the right-hemispheric response in the maternal odor context (** $p = .004$, ns $p = .57$, error bars represent standard errors of the mean). Color-coded head maps (posterior view) show the spatial distribution of the response.

response to face pictures was found over the right channel CP6 ($Z = 2.15$, $p = .016$) and the left channel P7 ($Z = 2.64$, $p = .004$) in the control odor context, while the right-hemispheric electrodes CP6 ($Z = 2.19$, $p = .014$), P8 ($Z = 3.36$, $p < .001$) and O2 ($Z = 2.71$, $p = .003$) reached significance in the maternal odor context. Pooling the three latter channels (CP6, P8, O2), the neural signature of face categorization was larger in the maternal than the control odor context, with a highly significant odor effect (maternal – control) of +1.20 ± 0.36 µV, $t_{17} = 3.37$, $p = .004$. In contrast, no significant difference was found over the homologous electrodes (CP5, P7, O1) in the left hemisphere (+0.32 ± 0.55 µV, $t_{17} = 0.57$, $p = .57$). The odor effect was strong over O2 (+2.25 ± 0.45 µV, $t_{17} = 5.03$, $p < .001$), while smaller and non-significant over P8

(+0.95 ± 0.75 µV, $t_{17} = 1.27$, $p = .22$) and CP6 (+0.40 ± 0.93 µV; $t_{17} = 0.42$, $p = .68$). It was not significant over P7 (-0.47 ± 1.12 µV; $t_{17} = -0.42$, $p = .68$).

To further highlight the strength of the odor effect over the right posterior region, Figure IV-3A and B depict its magnitude over channel O2 and its topographical pattern for the group and for individual infants. Individual data for electrode O2 revealed that 17 out of 18 infants presented descriptively larger amplitude of the face categorization response in the maternal *vs.* control odor context. When considering the three right channels CP6, P8 and O2, 17 infants showed at least one electrode with a minimum increase of 1.48 µV in the maternal odor context. Individual odor effects estimated from *Z*-scores (Table S3, Appendix 2; $Z > 1.96$ or < -1.96, $p < .05$, two-tailed, maternal ≠ control) indicated that 9 infants presented a significantly larger response in the maternal odor context over at least one electrode within the ROIs. According to one-tailed significance testing of a larger face-selective response for the maternal *vs.* control odor ($Z > 1.64$, $p < .05$), a significant effect was found for 7 infants over O2 and/or P8 and/or CP6, and over at least one other channel within the ROIs for another 5 infants (spatial distribution illustrated in Figure IV-3C).

c. Common visual processes elicited by all images are immune to maternal odor influence

As expected (de Heering and Rossion, 2015), the 6-Hz base rate of fast periodic stimulation elicits a large brain response at exactly the same frequency and its harmonics (e.g., 12 Hz, 18 Hz.) over the medial occipital cortex (Figure IV-4A). This response reflects the brain synchronization to visual cues rapidly changing 6 times per second. It was significant at 6 Hz over

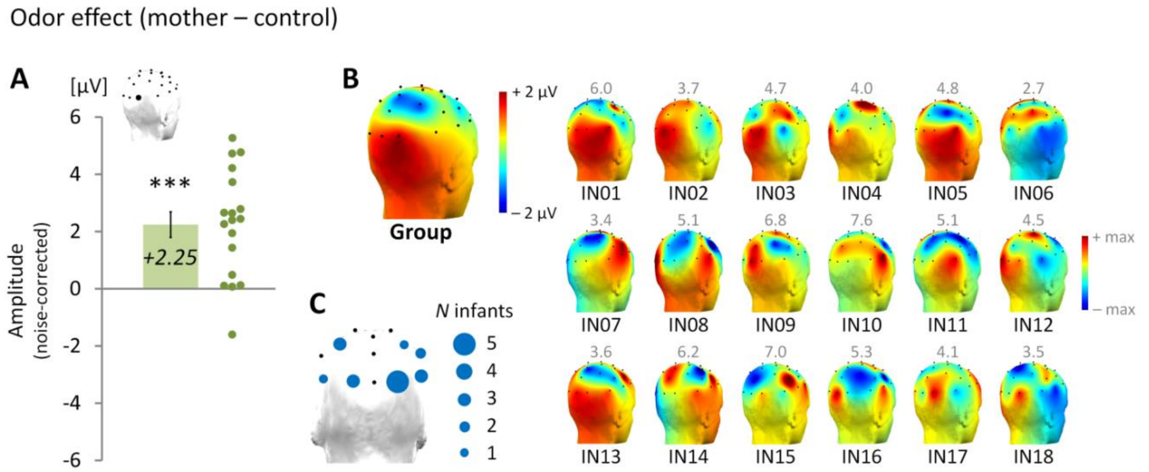


Figure IV-3. Effect of maternal odor cues on the face categorization response recorded in each individual infant brain. A. Odor effect (i.e., maternal odor minus control odor) on the face-selective response plotted over channel O2 for grand-averaged noise-corrected amplitude (*** $p = .0001$, error bar represents standard error of the mean) and every individual infant ($N = 18$). **B.** Color-coded 3-D topographical head maps from a right posterior view revealing the spatial patterns of the effect for both group and individual infants. The effect is centered over channel O2 for the group. It is visible for almost every individual infant brain over at least one right posterior electrode among the three electrodes isolated in grand-averaged data (i.e., CP6, P8 and O2, see text for details). The scale of each individual map ranges from ± its maximum amplitude as indicated by the grey value above each map. **C.** Head map (posterior view) depicting the density of significant individual odor effects over analyzed lateral posterior channels (i.e., P7/8, O1/2, P3/4, CP5/6). Circle size at every channel represents the number of infants (out of 18) with a significant effect here (i.e., $Z > 1.64$, $p < .05$, one-tailed, maternal odor > control odor).

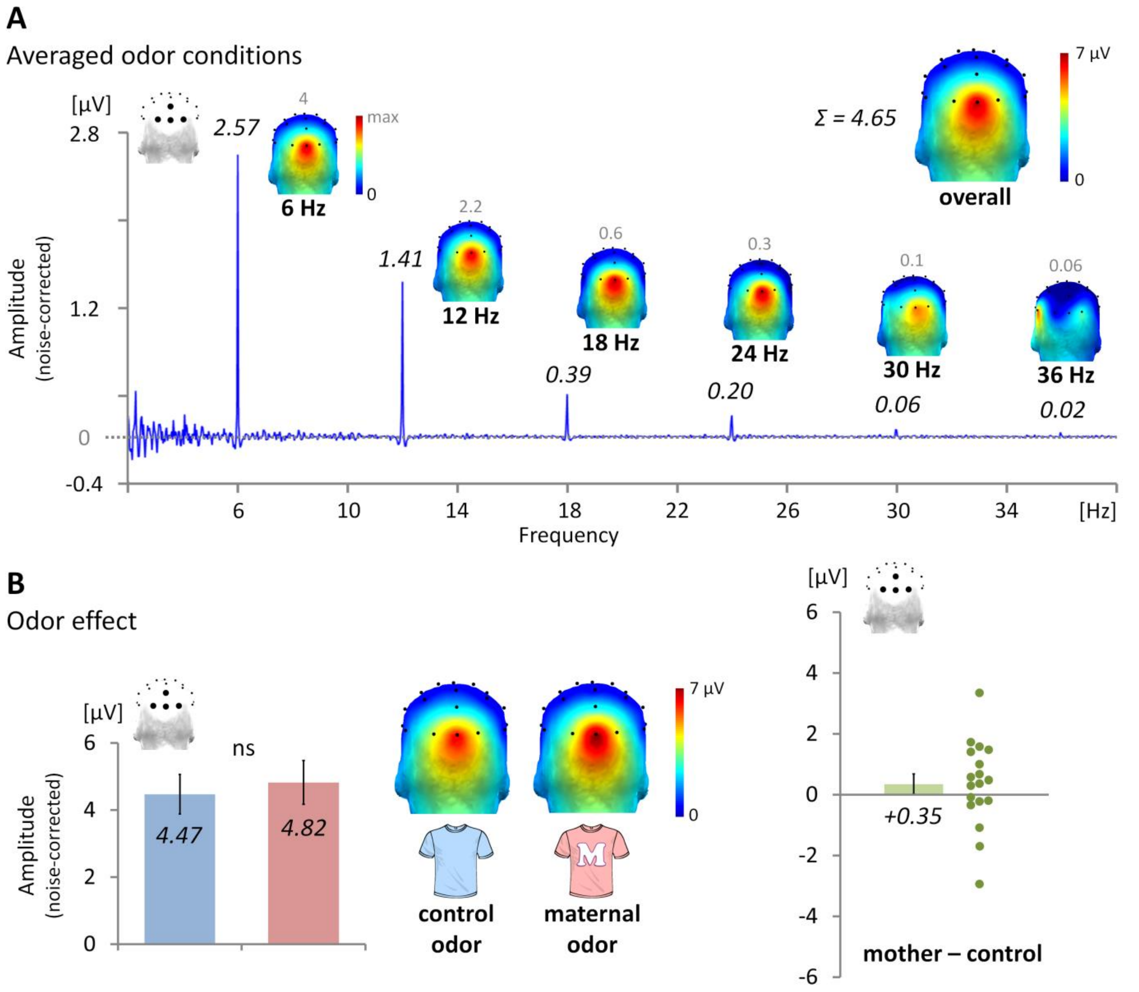


Figure IV-4. Common visual response to the rapid stream of natural images over medial occipital regions. A. Noise-corrected amplitude of the EEG frequency spectrum averaged across the two odor conditions and across four medial occipital channels (Oz, O1, O2, POz) revealing highly identifiable responses at the 6-Hz base rate of stimulation and its harmonics (i.e., integer multiples). Italic values above each harmonic indicate its amplitude and 3-D topographical head maps show their spatial distributions from a posterior view. The scale of each map ranges from 0 µV to its maximum amplitude as indicated by the grey value above each map. Amplitudes are summed across significant harmonics to quantify the overall response in a single value (top right). **B.** Left: the overall common visual response pooled across the four medial occipital channels is non-significantly increased by maternal body odor (ns p = .28, error bars represent standard errors of the mean). Right: the odor effect plotted across the same electrodes for the group and for the eighteen infants.

the four medial occipital channels (Oz, POz, O1, O2) with Z-scores ranging from 2.48 (p = .007) for POz to 17.79 (p < .001) for Oz (Table S4, Appendix 2). The same four electrodes reached significance until the fifth harmonic (30 Hz) and Oz and O2 until the sixth harmonic (36 Hz). The common visual response was thus quantified from the sum of the six first harmonics (Retter and Rossion, 2016). This combined response was significant for the four channels (from Z = 4.42 for POz to Z = 17.39 for Oz, ps < .001). Its noise-corrected amplitude ranged from 2.62 ± 0.74 µV over POz to 7.17 ± 0.88 µV over Oz, for a global magnitude of 4.65 ± 0.60 µV pooled across the four channels. The high reliability of this response is attested by individual data (Table S5, Appendix 2), with a significant response in every infant over channel Oz.

The common visual response was clearly visible in both odor conditions (Figure IV-4B) with a significant response over Oz, O1 and O2 in both conditions (Z-scores ranging from 7.56 to

18.03, *p*s < .001), and over POz only in the maternal odor context ($Z = 6.30$, $p < .001$). A slight non-significant increase was observed for maternal odor *vs.* the control odor (separate four channels: *t*s < 1.68, *p*s > .11, pooled channels: $t_{17} = 1.12$, $p = .28$, maternal – control = +0.35 ± 0.33 µV). Figure IV-4B shows that infants' individual odor effects are homogenously distributed around zero. In brief, the 4-month-old infant brain clearly responds to the rapid 6-Hz stream of widely variable natural images, but this common response to all stimuli is not influenced by concomitant maternal odor cues.

4. Discussion

Taken together, these observations demonstrate that concurrent body odor inputs from the mother actively shape face categorization at 4 months of age by enhancing a face-selective response in individual infant brains, especially over the right occipito-temporal cortex. This result builds upon behavioral observations of specific association between a face and a voice (Guellaï et al., 2011), and is consistent with odor-driven enhancement of 4-month-olds' preference for a face over another object category (Durand et al., 2013). It goes well beyond the latter observation however by providing evidence that the neural basis of a rich and rapid face categorization response (i.e., against many types of biological and non-biological objects, and across widely variable unsegmented pictures of faces) is directly constrained by a concomitant socially relevant odor. In contrast, the medial occipital common response to the rapid 6-Hz stream of face and non-face images is not affected by the presence of the maternal body odor, excluding a general increase in arousal or visual attention that typically leads to larger brain activity in response to periodic visual stimulation (Morgan et al., 1996; Müller et al., 2006; see Norcia et al., 2015 for review).

As a potential mechanism underlying odor-driven tuning of face categorization in the infant brain, the constant maternal odor context could pre-activate neural patterns of face-selective activity in the visual cortex that we tagged at 1 Hz with the periodic visual stimulation. This would be in line with the activation of the fusiform gyrus in response to the sole presentation of body odors in adults (Prehn-Kristensen et al., 2009; Zhou and Chen, 2008). More generally, this suggests that category-selective cortical areas receive direct multisensory inputs constraining categorization, supporting the view that multisensory processing extends into brain regions typically considered as unisensory (Driver and Noesselt, 2008; Ghazanfar and Schroeder, 2006).

Visual categorization is a challenging task for the infant brain. It develops from accumulated sensory experience and goes beyond physical cues to improve discrimination (e.g., faces vs. other objects) and generalization (e.g., across variable face exemplars). In that respect, odors meet key principles for an efficient multisensory support by conveying prior knowledge and reducing the sensory noise induced by physical variability (Ernst and Bülthoff, 2004). Indeed, the early functional onset of olfaction compared with the later-maturing visual system (Turkewitz and Devenny, 1993) favors the use of olfactory experience for the interpretation of scarce or ambiguous visual information. Moreover, the high odor stability in space and time (Schaal and Durand, 2012) induces olfactory stimulation with a low refresh rate (Sela and Sobel, 2010), while visual inputs must be categorized from widely changing exposure conditions (e.g., lighting, viewpoint, movements). Odors are therefore well suited to improve the generalization of variable visual inputs by providing constant related information from another sensory system.

From a developmental perspective, it would be important to determine whether face categorization is already odor-driven in younger infants, and still modulated in children or adults. Using the same kind of frequency-tagging paradigm across age (e.g., Lochy et al., 2019a; Rossion et al., 2015; see Hoehl, 2016), it would be straightforward to test predictions about the developmental course of olfactory-visual processing. For instance, the mother's breast odor triggers eye opening in 3-day-old infants, suggesting an odor-induced aroused state that increases visual attention (Doucet et al., 2007). Hence, at birth, odors may first operate as an undifferentiated stimulation of attention, an effect which would be reflected by an increase of a common brain response to the presentation of all images (i.e., 6 Hz and harmonics). Subsequently, accumulation of experience with co-occurring diagnostic olfactory and visual inputs (i.e., body odors and faces) would progressively lead to more selective odor influence on visual categorization, as observed here in 4-month-olds. However, the neural face categorization response is largely immature at 4 months of age (i.e., smaller and less complex, being limited to one harmonic) compared with 5-year-old children (Lochy et al., 2019a) and adults (Retter and Rossion, 2016; Rossion et al., 2015). Hence, the odor effect may be particularly strong in infancy because face categorization is not fully developed. This effect may progressively decrease during perceptual development until a robust and saturated neural categorization response can be elicited solely from visual stimuli. In this context, it would be interesting to determine whether body odor can influence rapid face categorization in children and adults, especially for degraded, ambiguous, or coarse visual inputs (e.g., low-pass spatial filtered faces), which typically elicit weaker face-selective neural responses (Quek et al., 2018a).

Admittedly, the present study is limited in that it cannot fully determine whether the odor effect is specific to maternal odor or generalizable to any human body odor. Here we used own mothers' body odor since it conveys many relevant cues for human infants compared with the odor of an unworn t-shirt, as a proof of concept. Maternal odor is experienced before birth, enabling transnatal stability and familiarity in the postnatal world replete with sensory novelty (Schaal et al., 2002). Mother's odor is a complex mixture of compounds conveying nested informative cues about conspecifics (e.g., human-, female-, mother-, identity-related) sometimes pertaining to biological status (e.g., lactation-related odor). In that respect, building on the present demonstration, future studies should precisely delineate which odor cues in the familiar maternal body odor support infants in categorizing faces (e.g., does an unfamiliar mother's body odor boost face categorization? Do some cues have a supra-additive effect when combined?). As an indication, we did not find a different odor effect between breast-fed and bottle-fed infants

(Figure S3, Appendix 2) suggesting a weak contribution of lactating status, but further investigation is needed to reach a definitive conclusion.

In sum, the present finding endorses a multisensory account of category learning in the human brain and opens new avenues to investigate olfactory determinants of adaptive neurocognitive development in other sensory modalities. In particular, along with the search for the odor cues triggering the neural tuning of face categorization, future studies should also explore the specific role of olfactory-visual congruency in helping the brain to rapidly categorize some inputs in the flow of visual information. More generally, it will be necessary to evaluate whether olfactory-visual processing only applies to social information, or whether it plays a generic function in organizing how the infant brain apprehends the visual world. Given that much evidence about visual categorization in infancy, and about virtually every neurocognitive process, has been obtained through testing infants seated on their parents' lap, future studies should examine whether and how such parental sensory context, including body odor, mediates infants' processing abilities.

This section corresponds to the article:
Rekow, D., Leleu, A., Poncet, F., Damon, F., Rossion, B, Durand, K., Schaal, B., & Baudouin, J.-Y. Categorization of objects and faces in the infant brain and its sensitivity to maternal odor: further evidence for the role of intersensory congruency in perceptual development. *Cognitive Development, 55C, 10093* doi: 10.1016/j.cogdev.2020.100930

References of this article are added to the general bibliographic section of the dissertation.

Study 2: Categorization of objects and faces in the infant brain and its sensitivity to maternal odor: further evidence for the role of intersensory congruency in perceptual development.

Abstract

According to recent evidence, rapid categorization of natural face images in the infant brain is enhanced by concomitant maternal odor (Leleu et al., 2020). To test whether this effect is selective to faces, we recorded scalp electroencephalogram (EEG) in 4-month-old infants presented with variable exemplars of a nonface visual category - cars - appearing every 6 stimuli in 6-Hz streams of natural object images. At the same time, infants were exposed to the maternal or to a control odor context. A relatively weak neural categorization response to cars (i.e., a differential response to cars that generalizes across exemplars) was observed at 1 Hz over the right occipital cortex in both odor conditions, revealing rapid categorization of an unfamiliar object in the infant brain. However, the car categorization response was not modulated by maternal odor, suggesting that odors selectively prime neural activity in the infant visual cortex to categorize congruent incoming inputs.

1. Introduction

Human infants present with a remarkable ability to categorize their visual environment; i.e., to discriminate visual objects into different categories and generalize their discriminative response across various category exemplars (Mareschal and Quinn, 2001, for review). For instance, when simultaneously displayed with two images depicting a cat and a dog, 3-4 month-old infants previously familiarized with other cat exemplars preferentially look at the dog, indicating that they regard the novel cat exemplar as belonging to the familiar “cat” category (Quinn et al., 1993). Infants can operate such categorization during the course of an experiment, the so-called online category learning, by extracting regularities from unfamiliar visual objects (e.g., giraffes; Eimas and Quinn, 1994). At this age, categorization of facial information is already effective due to everyday exposure to faces: for instance, 3-month-olds spontaneously prefer female faces (Quinn et al., 2002), same-race faces (Kelly et al., 2005), and adult faces (Heron-Delaney et al., 2017) over male, other-race and infant faces, respectively. These observations support the contribution of early experience in the development of visual categories (Oakes et al., 2009; Quinn, 2011, for reviews).

Categorization ability of infants has also been investigated with event-related potentials (ERPs) and tasks derived from familiarization/novelty preference paradigms. In 4- to 7-month-olds, a larger negative component over central brain regions is observed for novel exemplar(s) when contrasting living object categories (Marinović et al., 2014; Quinn et al., 2006) or living vs. non-living object categories (Elsner et al., 2013; Grossmann et al., 2009), suggesting sustained attention to novelty (Reynolds and Richards, 2005). When comparing ERPs between familiarization and test phases, the brain response to the first learned exemplars is equivalent in amplitude to the response to the novel category exemplars at test, while the response to the last learned exemplars is not different from the response to the familiar category at test, providing a neural signature of online category learning (Quinn et al., 2006). The N290 and P400 medial occipital ERP components in response to faces have also been largely investigated in 3- to 12-month-old infants (Halit et al., 2003; Hoehl, 2016, for reviews; Conte et al., 2020, for more recent evidence) and related to the early visual expertise developed for same- over other-species faces (de Haan et al., 2002; Halit et al., 2003), female over male faces (Peykarjou et al., 2016), or more generally for faces over nonface objects (e.g., toys or houses; Conte et al., 2020).

Recently, a fast periodic visual stimulation approach in scalp electroencephalography (FPVS-EEG) was introduced to measure rapid categorization in infants (de Heering and Rossion, 2015; Leleu et al., 2020; Peykarjou et al., 2017; see also Barry-Anwar et al., 2018). By presenting visual stimuli from various categories at a rapid base rate (e.g., 6 Hz) and inserting stimuli from a target category at a lower rate (e.g., 1 Hz; i.e., every 6 stimuli), a direct differential response (i.e., without post-hoc subtraction) to the target category is objectively measured at the predicted frequency (e.g., 1 Hz) in the EEG spectrum if the infant brain discriminates this category from the other(s) for the different category exemplars (i.e., generalizes). Most significantly, contrasting faces with several living and non-living categories using a large set of natural images unsegmented from their background, a neural face categorization response can be isolated over the right occipito-temporal cortex of 4- to 6-month-old infants (de Heering and Rossion, 2015). Importantly, this response is not accounted for by the low-level visual properties contained in the amplitude spectrum of the images (de Heering and Rossion, 2015).

To clarify the developmental origin of this neural face categorization response, Leleu et al., (2020) recently showed that it is substantially enhanced in 4-month-olds by the concomitant presentation of the mother's body odor compared with a control stimulus. These results are in line with previous evidence that odor exposure leads to increased orientation toward congruent visual information at 3 and 4 months (Durand et al., 2013; Godard et al., 2016), suggesting that initial categorization of visual stimuli as faces is shaped by multisensory inputs. More generally, although visual categorization has been mainly investigated from a unisensory perspective, such observations support the view that multisensory inputs promote the development of visual categories (Bremner et al., 2012; Lewkowicz, 2010). After birth, the visual system must apprehend a myriad of rapidly changing novel inputs across variable exposure conditions (e.g. movement, lighting, viewpoint). In this context, olfaction has a specific status from the earliest steps of development which confers the ability to mediate visual perception. The olfactory system is already able to process and encode mother-induced variations of the amniotic environment, shaping long-term memories which can function as familiarity references for the newborn (e.g., Schaal et al., 2000). This transnatal conservation of familiar odor cues do then co-occur with the reception of the first visual events and eventually engage early multisensory integration (Schaal and Durand, 2012, for review). In addition, odor perception is less sensitive to spatial and temporal variations than visual perception (Sela and Sobel, 2010). This property places olfaction in an ideal position to promote the acquisition of visual categories by reducing the sensory noise induced by physical variability and thus adding reliability across visual inputs from a single category. Prior experience of the association between a (maternal) body odor and a face could thus trigger a consistent discrimination response between faces and other categories (i.e., face categorization), leading to greater attention to the former (Durand et al., 2013).

However, an outstanding issue concerns the specificity of the odor-vision association. In particular, one could argue from the observations of Leleu et al. (2020) that the temporal stability of the maternal odor would help infants to detect any visual regularity within the rapidly changing visual stream of images, so that any periodically-presented visual object could be better categorized in the presence of the maternal body odor. The present study aimed at testing this alternative hypothesis. To do so, we first aimed at isolating a neural categorization response to an unfamiliar non-human visual category (i.e., cars) using FPVS-EEG and a large set of natural images, providing evidence of rapid visual categorization across highly variable exemplars. Second, we aimed at determining whether maternal odor enhances the putative car categorization brain response as we previously observed for face categorization (Leleu et al., 2020; see also Durand et al., 2013). Following the same procedure, we exposed each infant to two odor contexts using an unworn t-shirt (control odor) and a t-shirt worn by each mother 3 nights preceding testing (maternal odor) while recording their visual brain responses. Last, we compared our present data with those of Leleu et al. (2020) obtained with faces in a different sample of infants to test for the selectivity of the maternal odor effect.

2. Materials and methods

a. Participants

Twenty-one full-term and healthy 4-month-olds participated in the study. Parents were recruited through the local birth registry. They were fully informed about the purpose and methods of the study before agreeing to participate. They were then sent the material for maternal body odor collecting at home (see details below). Written and informed consent was obtained for all infants, and no parents reported their infant having any visual, olfactory or neurological disorder. The study was conducted in accordance with the Declaration of Helsinki for human experimentation and approved by the French ethics committee (CPP Sud-Est III - 2016-A02056-45). Three infants were discarded from the final sample due to less than two sequences per condition (*N* = 2) retained after preprocessing the data (see EEG recording and preprocessing section for more details) and atypical data compared to the group (*N* = 1; mean corrected amplitude across odor conditions over O2 (8.95 µV) above 2 *SD*s of the group's mean amplitude (1.38 µV, *SD* = 2.62 µV)). The final sample was thus composed of 18 infants (9 females, mean age ± *SD*: 131 ± 5 days, range: 124–140 days). Since no previous study explored whether maternal odor has a modulatory effect on the neural categorization of a nonface object, we estimated sample size by considering that (1) maternal odor elicits a strong effect on neural face categorization (Cohen's d = +1.20 over channel O2) with *N* = 18 infants, leading to maximal power 1-β = 1 (Leleu et al., 2020); (2) even if the odor effect on car categorization would be twice lower (i.e., Cohen's d = +0.60), estimated sample size would remain close (*N* = 17) by considering a significance level α = .05 (one-tailed, maternal > control) and the usual power 1-β = .80. We therefore made sample sizes equal in the two studies.

b. *Visual stimuli*

Natural images (i.e., unsegmented from the original background) of various objects (man-made objects including non-car vehicles, plants and animals; N=170, same stimulus set as in Leleu et al., 2020) and cars (variable models; *N* = 66) were used (Figure IV-5). Pictures of cars were used as the single object category, for several reasons: cars have a canonical orientation, they form a visually homogenous category, and they have multiple parts, just like faces ("internal": lights, radiator grill, window, bumper; "external": mirrors, wheels, etc.). Also, pictures of cars have been used as control stimuli to faces in numerous neuroimaging (e.g., Gauthier et al., 2000; Grill-Spector et al., 2004; Rossion et al., 2012) or electrophysiological studies (e.g., Rossion and Caharel, 2011; Rossion and Curran, 2010) with adults. Finally, pictures of cars were contrasted with those of faces in the first behavioral study showing that infants look longer at a face in the presence of maternal odor (Durand et al., 2013). Here, all the images varied substantially in terms of color, viewpoint and lighting condition, and each depicted only one object. Each image was cropped to a square then resized to 400 × 400 pixels. In addition to their variable shapes, the objects were off-centered to increase their eccentricity so that no object can be identified from the mean image (Figure S1, Appendix 3). Stimuli were presented at the center of a computer screen placed 57 cm in front of the infant's face. They subtended roughly a 24 × 24° of visual angle, representing a large part of the infant's visual field.

c. *Odor stimuli*

Following previous studies (Durand et al., 2013; Leleu et al., 2020), the maternal and control odors were delivered from worn and unworn white t-shirts (100% cotton), respectively.

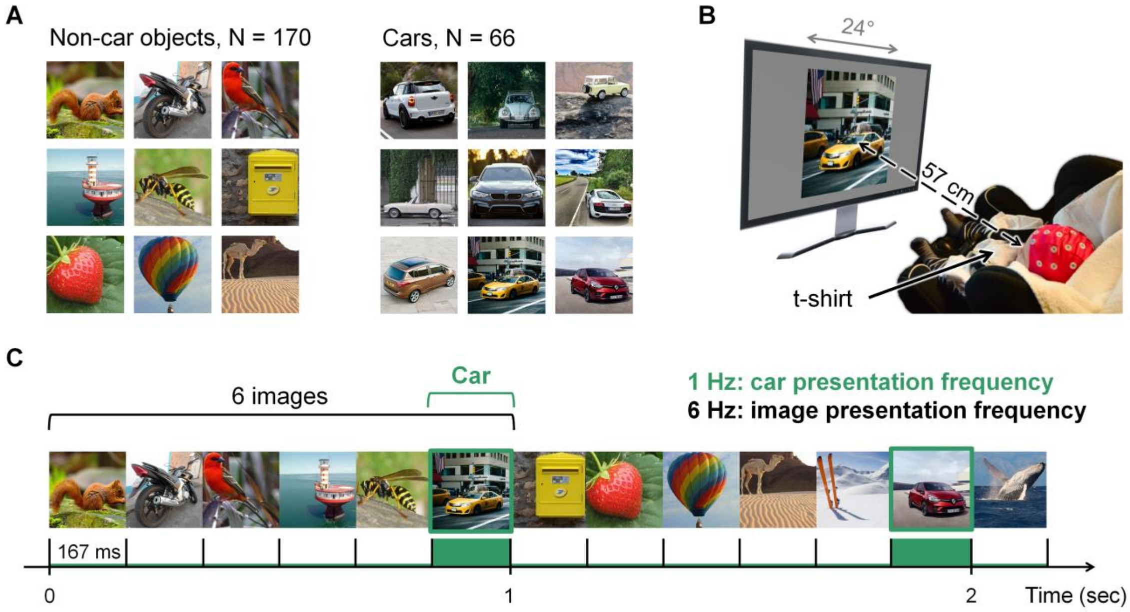


Figure IV-5. An EEG frequency-tagging approach to measure car categorization in odor contexts. A. Example of the stimuli used in the experiment and depicting various non-car objects and cars. **B.** During the experiment, infants were installed in a seat placed at 57 cm from a computer screen and odorous t-shirts (control vs. maternal) were placed on their chest while stimuli appeared rapidly on the screen covering roughly 24 × 24° of visual angle. **C.** Excerpt of 2 sec of fast periodic stimulation (from 32-sec-long sequences) showing 6 images/sec (i.e., 6-Hz base rate) and interspersing images of cars every 6th stimulus (i.e., 1-Hz car-selective rate). Each stimulus lasts 167 ms on screen (i.e., one fixation). This design implies that two dissociable responses are tagged in the EEG frequency spectrum: a general visual response (6 Hz and harmonics) reflecting the common processing of all stimuli and a car categorization response (1 Hz and harmonics) triggered by the discrimination of cars from other objects and the generalization of this selective response across variable exemplars.

Both t-shirts were first laundered using a scentless hypoallergenic powder detergent (Persavon, France). For the collection of the maternal odor, a prewashed t-shirt enclosed in a hermetic zip-lock plastic bag was sent to the mothers one week before the testing day. The t-shirt was worn the three consecutive nights before testing. A written procedure detailing the standardized night-wear instructions (to minimize activity-related individual differences, see Durand et al., 2013) was provided to the mothers. Notably, they were asked to refrain from using odorous soap or perfume before wearing the t-shirt. During the days of the collection period, the t-shirt was stored in the hermetic bag at room temperature but carefully left away from any heating device. The control odor condition consisted of an identical t-shirt, unworn and following equivalent storage procedure.

d. Procedure

A frequency-tagging approach was used to dissociate a general visual response and a car categorization response within the same fast periodic visual stimulation sequence (for review, Rossion et al., 2018). Stimuli were displayed on a 24-inch LED screen (60 Hz refresh rate) with a resolution of 1920 × 1080 pixels on a mid-level gray background (i.e., 128/255 in grayscale). They were presented at a base rate of 6 Hz (i.e., 6 images per second) without inter-stimulus interval. With this rate, each stimulus allows only a single glance, since it only lasts 167 ms (i.e., 1 sec/6) on the screen and is immediately masked by the following stimulus. The 6-Hz frequency gathers the processes common to all stimuli, reflecting a general visual response to the stream of stimulation.

Each stimulation sequence was composed of 5 non-car images alternating with an image of a car placed as 6th stimulus, i.e., introduced at the rate of 6/6 = 1 Hz. All images were randomly picked from their respective sets (objects vs. cars) without repetition within a sequence. This frequency-tagging approach is used to directly quantify and isolate the general visual response (6 Hz and harmonics; i.e., integer multiples) and a car categorization response (1 Hz and harmonics). Moreover, thanks to periodicity, the brain response recorded at 1 Hz is a direct marker of the categorization of car exemplars, reflecting their discrimination from the other objects and their generalization into a single category despite their variability.

The procedure was identical to Leleu et al. (2020). After a size-adjusted electrode cap was placed on the infant's head, infants were seated in a car seat positioned at a 57 cm distance from the computer screen, in a light- and sound-attenuated room. The room was aired between testing sessions and equipped with an air-extractor placed approximately 2 m above the seat which continuously renewed the air with a silent and undetectable air flow. To reduce the olfactory noise, the experimenters did not ingest, inhale or use any odorous product before testing. Experimenters were not blind to the odor context presented to the infant. During stimulation sequences, the infant was tested alone, behind occluding (scentless) blinds in order to minimize distraction. A camera placed on top of the screen monitored the infant continuously. In addition, parents were asked to stay at a relative distance (at least 2.5 m) of their infant and not to interact with them during testing, except in case of manifest distress.

The two odor conditions were constituted by the aforementioned t-shirts, optimally folded to expose the infant to the most odorous areas (axillary, breast and neck regions) and manipulated with dedicated disposable nitrile gloves (Schield Scientific, The Netherlands). Each odor condition was delivered throughout the sequence by placing, a few seconds before a stimulation sequence started, the folded t-shirt on the infant's chest (fixed by the seatbelt). To optimize testing duration and minimize infant manipulation, the two odor conditions were counterbalanced every two sequences for each infant and their initial order was counterbalanced across infants. Between the two odor conditions, a minimum interval of 1 min was introduced (i.e., corresponding to the time needed to switch t-shirts and to aspire surrounding air), while animated shapes were shown on screen.

Each 34.5-sec visual sequence opened with a pre-stimulation interval of 0.5 sec of blank screen, followed by a fade-in of increasing contrast (0 to 100%) lasting 1.833 sec. The full-contrast stimulation lasted 31.167 sec followed by a 0.833-sec-long fade-out of decreasing contrast (100 to 0%) and closed on a blank post-stimulation interval of 0.167 sec. The various objects (*N* = 170) were used for all sequences but the car set was randomly divided into two subsets of *N* = 33 images, each alternatively assigned to one sequence during testing. If needed, auditory tones were used to reorient infant's attention toward the screen. Being non-periodic and sporadic, they did not contaminate the precise frequency-tagged EEG responses of interest with auditory-evoked potentials. Sequences were removed from analysis if aborted because of the infant distress or if parents or experimenters intervened during the presentation. Testing stopped when infants showed manifest disinterest from the screen and/or signs of fatigue or boredom. Infants were included in the final sample if they achieved at least two valid sequences for each odor condition (i.e., 4 valid sequences in total). Infants from the final sample performed between 4 and 16 sequences (mean ± *SD*: 10 ± 3.4 sequences), for an overall testing duration ranging from 2 min 18 sec to 9 min 12 sec per infant.

e. EEG recording and preprocessing

EEG was continuously acquired from a 32 Ag/AgCl electrode cap (Waveguard, ANT Neuro, The Netherlands) according to the 10–10 classification system. During recording, the fronto-central channel AFz was used as reference. Acquisition was made under ASAlab 4.7 (ANT Neuro, The Netherlands) with a sampling rate of 1024 Hz. Electrode impedance was maintained below 15 kΩ. Analyses were then performed using Letswave 6 running on Matlab 2017. Before preprocessing, both mastoid electrodes (M1 and M2) were removed from the montage because they were noisy or artifact-ridden for most infants.

Preprocessing steps were similar to those run in a recent study (Leleu et al., 2020). A 4th-order Butterworth filter was first applied with cutoff values of 0.1–100 Hz, to each individual EEG dataset. After resampling datasets to 200 Hz, each sequence was cropped in 36-second-long segments starting from the beginning of the fade-in. The Artifact Blocking algorithm (Fujioka et al., 2011; Mourad et al., 2007) was applied independently to each segment to reduce artifacts over ± 500 µV. Linear interpolation was used to rebuilt a noisy channel in two infants using neighboring electrodes. Individual dataset were then re-referenced to a common average reference. The 36-sec segments were cropped down into 32-sec epochs starting from the end of fade-in (first image of the full-contrast phase) and encompassing exactly thirty-two 1 Hz cycles.

Two data-driven criteria were calculated for each individual dataset to increase signal-to-noise ratio (SNR) by excluding unusable sequences. First, fast Fourier transform (FFT) was applied and amplitude spectra extracted for all electrodes with a high frequency resolution of 1/32 = 0.03125 Hz. The first criterion rejected epochs which failed to show a general visual response of the visual system to the stream of images at the base rate frequency and its second harmonic (i.e., 6 Hz and 12 Hz), as a neural marker of adequate looking at the stimulation (Barry-Anwar et al., 2018; de Heering and Rossion, 2015; Leleu et al., 2020; Peykarjou et al., 2017). For each channel and each frequency bin, *Z*-scores were calculated as the difference between the signal amplitude and the mean noise amplitude (estimated from the 20 surrounding bins, 10 on each side after exclusion of the two adjacent and the two extreme (i.e., minimum and maximum) bins) divided by the standard deviation of the noise. Sequences were included if at least two *Z*-

scores were greater than 1.64 ($p < .05$, one tailed, signal > noise) or at least one Z-score greater than 2.32 ($p < .01$, one-tailed) over the usually responding middle occipital electrodes (Oz, POz, O1, O2; de Heering and Rossion, 2015; Leleu et al., 2020; Peykarjou et al., 2017). One-tailed testing was used to determine the significance of the neural response because the frequency spectrum is expressed in absolute amplitudes, leading to the a priori hypothesis of signal > noise (Rossion et al., 2020). Thus, a significant neural response means a larger response than surrounding noise, and a negative Z-score is considered non-significant. Nine epochs were excluded in a total of 5 infants. The second criterion was used to further removed epochs with atypical scalp-wide power calculated on the 1-Hz response. Channels were pooled together based on FFT amplitude spectra and amplitude at the 1 Hz frequency was corrected by subtracting the mean noise (baseline-corrected amplitude, BCA), estimated here from the 6 surrounding bins (due to high EEG power in the low-frequency range and non-linear decrease as frequency increases (Fransson et al., 2013), noise is steeper for lower than for higher frequency bins around 1 Hz; considering too many bins would overestimate noise level). Atypical sequences were defined by noise-corrected amplitude at 1 Hz greater or lower than 2 *SD*s of the mean of all sequences (calculated individually) remaining after application of the first criterion, rejecting 5 epochs in a total of 5 infants. Once these two criteria were applied, the final number of sequences was 4 to 15 per infant (mean ± *SD*: 9.2 ± 3.2), with an overall rejection of 14 epochs out of 180. The resulting number of sequences was 84 sequences for the control odor condition (mean ± *SD*: 4.7 ± 1.7) vs. 82 for the maternal odor condition (4.6 ± 1.8).

f. Frequency-domain analysis

For each infant, remaining 32-sec segments were sorted per condition and averaged in the time domain to reduce cerebral activity non phase-locked to the stimuli. FFT was applied and amplitude spectra were extracted for all electrodes. In a first step, we estimated the significance of the brain responses and defined the range of significant harmonics (i.e., integer multiples) to consider for further analysis regardless of the condition. FFT data were averaged across conditions and for each frequency bin and each channel, and amplitude was normalized (i.e., by dividing by the square root of the sum of squared amplitudes of all channels; McCarthy and Wood, 1985). Normalization was used to scale differences between electrodes on the global magnitude of the response across the scalp to identify the electrodes over which the response is the largest and reduce the high amplitude variance in the low-frequency band that may mask significant responses. Individual datasets were then grand-averaged and Z-scores calculated for each electrode. As the first study investigating the categorization brain response to a nonface category in infants, posterior channels (N = 13, Figure S2, Appendix 3) were explored for both the general (6 Hz and harmonics) and the categorization (1 Hz and harmonics) responses, using a threshold of $Z > 2.32$ ($p < .01$, one-tailed, signal > noise). Harmonics were included until Z-scores over one channel were no longer significant. Then, individual normalized amplitudes for each response were summed across harmonics. Final Z-scores were calculated on these summed amplitudes for individual and grand-averaged datasets, estimating the significance of the overall responses for individual infants and the group. Baseline-corrected amplitudes (BCA) were also calculated on non-normalized dataset for each individual infant and each condition, and then summed across significant harmonics to quantify each response in a single value expressed in microvolts. Individual BCAs were averaged across odor conditions and then grand-averaged to illustrate group-level brain responses.

In a second step, the difference between the two odor conditions was analyzed. We first determined significant electrodes for each condition separately to identify any electrode that would be significant in only one odor condition. For each brain response, individual datasets were normalized on the global power previously calculated, harmonics were summed, and *Z*-scores were computed on grand-averaged data. A standard threshold ($Z > 1.64$, $p < .05$, one-tailed, signal > noise) was applied to channels identified at the previous step whereas the significance of other posterior channels was assessed with the more conservative threshold ($Z > 2.32$, $p < .01$, one-tailed). The direct comparison between the two odor conditions was then performed on individual BCA for each significant channel using T-tests (two-tailed) and individual data were grand averaged for illustration purpose. To quantify evidence in support of the null hypothesis for non-significant effects, Bayes factors (BF_{10}) were calculated using JASP (https://jasp-stats.org/) and a standard zero-centered Cauchy prior with effect size scaled at $1/\sqrt{2}$ (Gronau et al., 2020).

In a final step, a complementary analysis was performed on BCA to compare the influence of maternal odor on the neural categorization responses to cars (i.e., the present study) and to faces (Leleu et al., 2020). In both studies, 18 infants were tested. The two groups did not differ in sex ratio, age, and final number of analyzed epochs (all *p*s > .31). To test for a potential subtle effect of maternal odor over the right occipito-temporal cortex regardless of the visual category, we considered the two regions of interest (ROI) where the face categorization response was recorded in Leleu and collaborators' study (2020): right (rOT: CP6, P8, O2) and left (lOT: CP5, P7, O1) occipito-temporal regions. A repeated-measures ANOVA was run with *Hemisphere* (rOT, lOT) and *Odor* (control, maternal) as within-subject factors, and *Category* (faces, cars) as a between-subject factor. Since O2 is the only responding channel for the categorization response to cars (see Results), we also ran an ANOVA for the categorization responses measured over this sole channel with *Odor* as a within-subject factor and *Category* as a between-subject factor. For the general visual response, we ran another ANOVA with *Odor* (control, maternal) as a within-subject factor and *Category* (faces, cars) as a between-subject factor on a single middle occipital ROI (mO) encompassing channels Oz, POz, O1 and O2. Tukey's HSD tests were conducted as post-hoc comparisons whenever effects were significant and effect sizes are reported as partial eta squared (η_p^2).

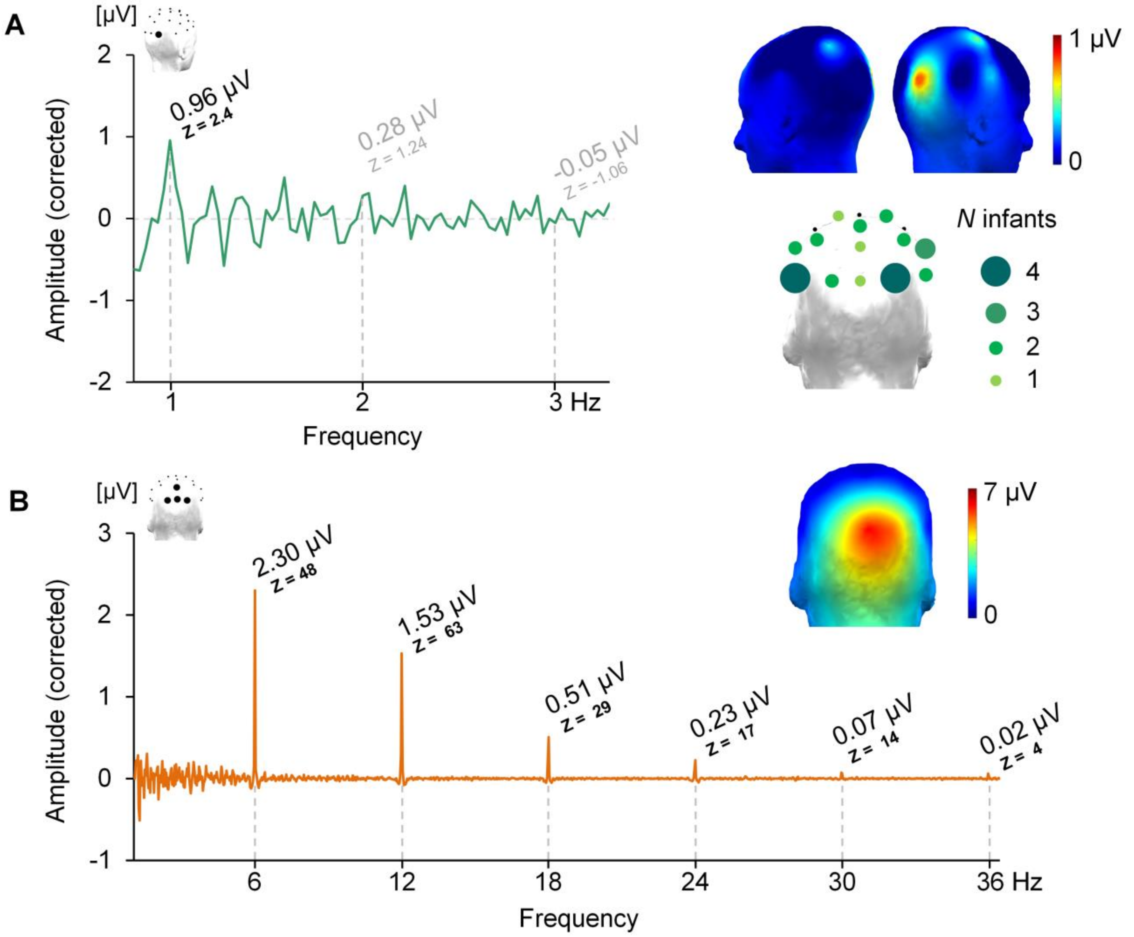


Figure IV-6. (A) Car categorization response and (B) general visual response (*N* = 18). A. (left) Amplitude (noise corrected) of the EEG spectrum recorded over the right occipital channel O2 across odor conditions. Numerical values indicate the amplitude of the response with corresponding *Z*-scores. Only the 1st harmonic is significant (black, $Z > 2.32$, $p < .01$ one tailed, non-significant peaks are indicated in grey). (top-right) 3-D topographical head maps of the car categorization response at 1 Hz over left and right hemispheres. The response is clearly visible over channel O2. (bottom-right) Head map (back view) showing the density of significant individual Z-scores ($Z > 1.64$, $p < .05$, signal > noise) over all 13 posterior channels. Circle size and color illustrate the number of infants with a significant response on the corresponding channel. **B**. Amplitude (noise corrected) of the EEG spectrum recorded over the middle occipital region (O1, Oz, O2 and POz) across odor conditions along with 3-D topographical head maps (back view) of the general visual response summed across significant ($Z > 2.32$, $p < .01$, one tailed) harmonics (i.e., 6 Hz and integer multiples). Numerical values indicate the amplitude of the response with corresponding Z-scores.

3. Results

a. *Car categorization and general visual responses in the 4-month-old infant brain*

For both odor conditions combined, a brain response was found at the predefined 1-Hz rate of car pictures presentation (Figure IV-6A). Exploring posterior channels (see Methods), we found only one significant electrode reaching the threshold of $Z > 2.32$ ($p < .01$, one-tailed, signal > noise): O2 ($Z = 2.44$, $p = .007$). No other electrode reached significance. Over O2, the car categorization response was found only on the 1st harmonic ($Z = 1.24$ and $Z = -1.06$ for the second (i.e., 2 Hz) and third (i.e., 3 Hz) harmonics, respectively), with a magnitude of 0.96 ± 0.46 (*SEM*) µV (Figure IV-6A). This categorization response is robust, since it is not induced by a small subset of infants (T-test against 0: $t_{17} = 2.45$; $p = .025$, one-tailed, signal > noise). Four infants presented a significant response over O2 ($Z > 1.64$, $p < .05$, one tailed), five others over one immediate neighboring electrode (Oz, POz, P4 or P8), six more over at least one other posterior electrode, and the last 3 infants showed a significant 1-Hz response elsewhere over the scalp (Figure IV-6A and Table S1, Appendix 3).

A general brain response to the rapid stream of visual stimuli was recorded at 6 Hz and harmonics (i.e., 12 Hz, 18 Hz, etc.) over the middle occipital cortex (Figure IV-6B). This response represents a mixture of low- (e.g. color) and higher-level (e.g. object identification) processes elicited by all visual stimuli. Across odor conditions, *Z*-scores highlighted a significant response ($Z > 2.32$, $p < .01$, one-tailed, signal > noise) over POz ($Z = 4.95$, $p < .001$), O1 ($Z = 6.15$, $p < .001$), Oz ($Z = 13.09$, $p < .001$) and O2 ($Z = 10.96$, $p < .001$) at 6 Hz. Following harmonics were significant until the 5th harmonic (i.e., 30 Hz) over POz ($Z = 3.85$, $p < .001$) and O1 ($Z = 4.99$, $p < .001$) and until the 6th harmonic (i.e., 36 Hz) over Oz ($Z = 4.52$, $p < .001$) and O2 ($Z = 4.41$, $p < .001$). The general visual response was thus collapsed across 6 harmonics. *Z*-scores for this overall response were significant for all four electrodes (from $Z = 6.95$, $p < .001$ for POz to $Z = 12.09$, $p < .001$ for Oz) with amplitudes ranging from 2.80 ± 0.72 µV over POz, to 6.23 ± 0.83 µV over Oz (4.66 ± 0.65 µV pooled across the four channels). No other posterior electrodes reached significance. The general visual response is significant in every infant for Oz and O2, in 13 infants for O1, and in 10 infants for POz ($Z > 1.64$, $p < .05$, signal > noise; Table S2 and Figure S3, Appendix 3).

b. No effect of maternal odor on both car categorization and general visual responses

When comparing between the two odor conditions, the car categorization response remained clearly visible over the right posterior occipital channel O2 (Figure IV-7A), with a significant response in both odor contexts (control odor: $Z = 2.02$, $p = .022$; maternal odor: $Z = 1.70$, $p = .045$). Again, no other posterior channels showed a significant Z-score in any odor condition. On this particular site, the maternal odor had no effect [maternal – control] on the categorization response to cars. The amplitude of the response recorded over O2 in the control odor condition (1.19 ± 0.54 µV) is barely diminished in the maternal odor context (0.79 ± 0.54 µV), corresponding to a non-significant decrease of -0.40 ± 0.63 µV ($t_{17} = -0.63$, $p = .54$) in support of a null result ($BF_{10} = 0.28$).

As for the car categorization response, the general visual response is observed in both odor conditions (*Z*-scores ranging from 4.18 to 11.60, *p*s < .001). A faint but non-significant decrease in amplitude was found in the maternal odor context (maternal – control: -0.41 ± 0.47 µV; $t_{17} = -0.88$, $p = .40$), probing evidence in favor of the null hypothesis ($BF_{10} = 0.29$). In sum, the 4-month-old brain in sensitive to the rapid stream of stimulation but this robust general visual response appears to be immune to the concomitant presentation of a maternal odor context (Figure IV-7B).

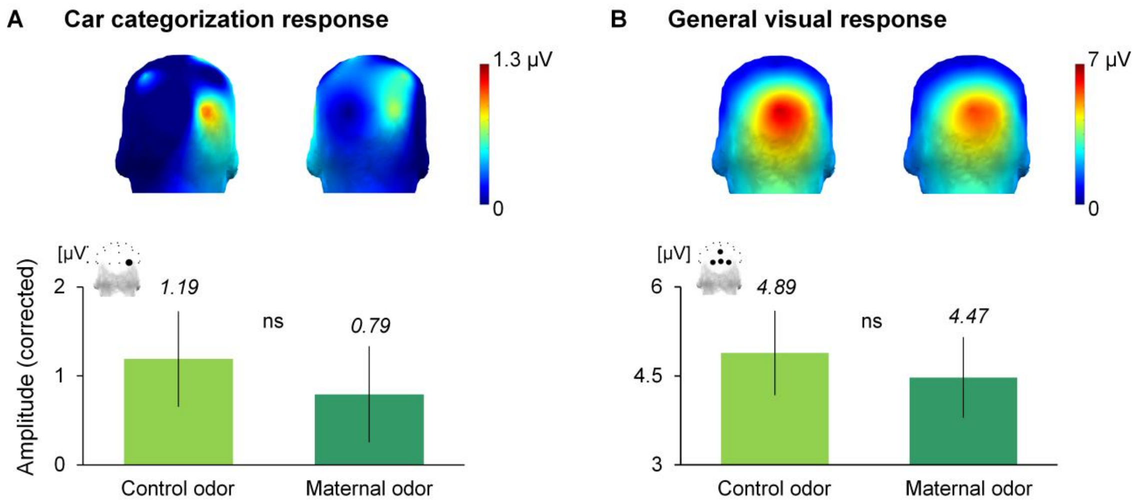


Figure IV-7. Both brain responses are immune to maternal odor. A. Amplitude (noise corrected) of the car categorization response over O2 in the control (left) and maternal (right) odor conditions, showing a slight non-significant decrease of amplitude in the maternal odor condition (-0.40 µV ± 0.63 µV, ns: p = .54). **B.** Amplitude (noise corrected) of the general visual response across 4 middle occipital channels (POz, O1, Oz, O2) in the control (left) and maternal (right) odor conditions, showing a small non-significant decrease of amplitude in the maternal odor condition (-0.41 ± 0.47 µV, ns: p = .40). 3-D topographical head maps (back views) show the spatial distribution of each response. Error bars represent standard errors of the mean.

c. Maternal odor effect on the visual categorization of cars and faces

Using a similar FPVS-EEG approach, we recently showed that maternal odor enhances a neural categorization response to faces over the right occipito-temporal cortex of 4-month-old infants (Leleu et al., 2020), while no maternal odor effect was found over the left occipito-temporal cortex, or for the general visual response over middle occipital scalp regions. To investigate further whether the maternal odor effect is selective to face but not car categorization, we performed a complementary analysis comparing previous data obtained for face stimuli with the present data obtained with car stimuli.

For the categorization response at 1 Hz, we considered two lateral regions-of-interest (ROIs) as defined in Leleu and collaborators' study (2020): right (rOT, pooling channels CP6, P8 and O2) and left (lOT, pooling CP5, P7 and O1) occipito-temporal ROIs, and observed a main effect of *Hemisphere* ($F(1, 34) = 12.54$, $p = .001$, $\eta_p^2 = .27$) with a greater amplitude over rOT (0.65 ± 0.17 µV) than lOT (-0.0043 ± 0.20 µV). More importantly, the *Odor* × *Hemisphere* × *Category* interaction reached significance ($F(1, 34) = 7.06$, $p = .012$, $\eta_p^2 = .17$). A significant *Odor* × *Category* interaction was found over rOT ($F(1, 34) = 15.27$, $p = .0004$, $\eta_p^2 = .31$) but not over lOT ($F < 1$). While the face categorization response is increased by +1.20 ± 0.36 µV ($p = .007$) in the maternal (1.52 ± 0.31 µV) vs. control (0.32 ± 0.29 µV) odor context, the car categorization response is not significantly changed ($p = .19$) despite a decrease of -0.71 ± 0.33 µV (control odor: 0.74 ± 0.32 µV; maternal odor: 0.03 ± 0.23 µV) over the infant right occipito-temporal cortex (Figure IV-8). When considering O2, the only channel with a significant categorization response to cars, the conclusion remains similar with a significant *Odor* × *Category* interaction ($F(1, 34) = 11.7$, $p = .002$, $\eta_p^2 = .26$) explained by an odor effect for faces (+2.25 ±

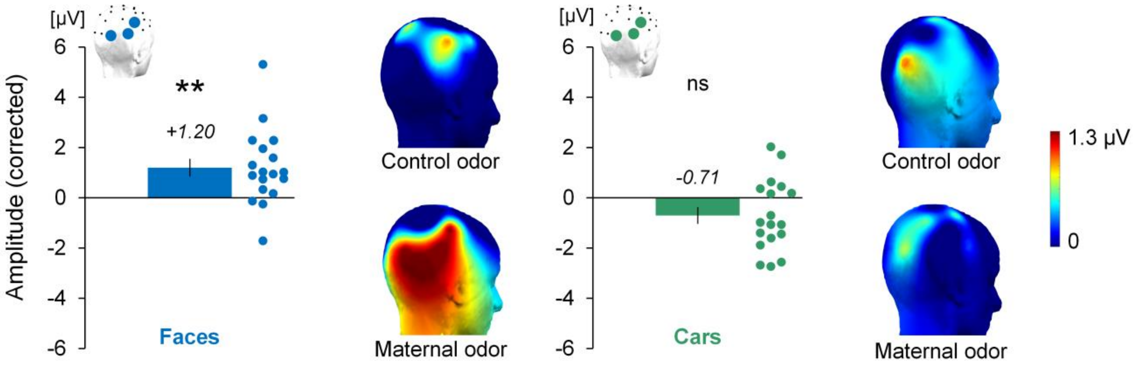


Figure IV-8. Maternal odor effect [maternal – control] for the categorization responses to faces (blue) and cars (green). Maternal odor significantly enhances the response to faces (left, **: p = .007, N = 18) and does not significantly diminish the response to cars (right, ns: p = .19, N = 18) over the right occipito-temporal region (channels CP6, P8 and O2). Individual amplitudes are plotted. 3-D topographical head maps show the spatial distribution of the responses (right lateral view). Error bars represent standard errors of the mean.

0.45 µV, p = .001) but not for cars (-0.40 ± 0.63 µV, p = .89). In contrast, no significant main effects or interactions were found for the general visual response (all Fs < 1.76, all ps > 0.19).

4. Discussion

By isolating a response over the right occipital cortex at the 1-Hz frequency of car pictures presentation, the present study demonstrates the 4-month-old infant brain's ability to rapidly assign a series of highly variable exemplars of cars to a single category, as previously observed for faces with the same FPVS-EEG approach (de Heering and Rossion, 2015; Leleu et al., 2020). However, contrary to the face categorization response identified in Leleu and collaborators' study (2020), which was strongly enhanced in the maternal odor context, no modulation of the neural categorization response to cars was found in the context of maternal odor. The general visual response to the fast train of visual stimuli is also immune to the presence of maternal odor, reflecting a similar level of visual attention or arousal in both odor contexts (Leleu et al., 2020).

The first major result of the present study is the recording of a neural categorization response to variable car images over the right occipital cortex. This extends the visual categorization response with natural images and fast periodic visual stimulation in EEG to a novel category, following studies in adults with faces but also houses and body parts (Jacques et al., 2016a). In infants, this finding indicates that rapid categorization of numerous exemplars is not limited to faces (de Heering and Rossion, 2015; Leleu et al., 2020) but extends to a non-social object that is less familiar than faces in the infant everyday visual environment at 4 months. Infant behavioral studies have already shown categorization abilities for more or less familiar objects using familiarization/novelty preference paradigms in which two simultaneously presented segmented stimuli must be discriminated (see Oakes et al., 2009; and Quinn, 2011 for reviews). Here, our data reveal an ability to discriminate natural views of cars from many other living and non-living categories and to generalize this discrimination across numerous car exemplars. This is not a trivial achievement for the infant visual system since the car exemplars must be categorized at a glance (i.e., 167 ms per stimulus) from forward- and backward-masked natural images implying figure-ground segregation. Despite these high constraints, the car categorization response is reliable, as it is found over posterior scalp regions for a majority of infants. In addition, a complementary analysis revealed that the response tends to increase during the course of the experiment (Supplementary Information and Figure S4, Appendix 3), suggesting that despite a large set of stimuli and a fast presentation mode, 4-month-olds rapidly acquire an unfamiliar category from relatively short exposure (i.e., online category learning; e.g., Eimas and Quinn, 1994; Quinn et al., 2006). Overall, by providing a valid measure of visual categorization including both discrimination and generalization processes thanks to a fair amount of naturalistic stimuli presented in a few minutes, FPVS-EEG brings interesting perspectives for the study of category formation in infancy (see Rakison and Yermolayeva, 2010 for a discussion), where the constraint of short infants' attentional span usually restricts the use of numerous stimuli in a single group of infants.

Interestingly, this response is, overall, not different in amplitude than the response to faces presented in the same context, but is however restricted to a single lateral occipital channel (compared to a face response extending more anteriorly to the temporal cortex). This suggests that car categorization is less robust than face categorization at this age and, as in adults for categorization responses to houses and body parts, is generated by different brain regions (Jacques et al., 2016a). Note that it could be argued that cars are relatively homogeneous visual exemplars that could be categorized solely from systematic differences in basic structural properties (e.g., elongated shapes) or low-level cues (e.g., uniformity of color). For instance, the car and its typical background (frequently showing a road) could lead to a higher proportion of obvious convergence lines than other objects. Nonetheless, the high variability of models, viewpoints and relative positions of the car in each image, as well as the use of control objects that share some basic properties with cars (e.g., bikes, trolley and motorcycles also have wheels and a distinctive metallic texture) reduces the potential contribution of these physical cues, especially with such a fast presentation mode that only allows one fixation per stimulus.

The second main observation is that contrary to the face categorization response isolated in Leleu and collaborators' study (2020), the car categorization response is not at all enhanced by the maternal body odor, neither when considering the single responding electrode O2, nor the broader right occipito-temporal region where the face categorization response is measured. This reveals that maternal odor does not merely facilitate the detection of any regular (i.e., periodic) visual category, but selectively improves the categorization of faces, according to the view that early perceptual development takes advantage of intersensory congruency across simultaneous inputs from different sensory modalities (Bahrick and Lickliter, 2000). Hence, we suggest that maternal odor acts as a prime to socially relevant inputs by pre-selecting dedicated neural substrates in the ventral visual pathway. This would lead to a larger or broader activation of face-selective cortical regions when a face appears in the visual environment. This interpretation is supported by findings from adult studies. Even in the absence of faces, body odors activate face-selective neural responses in the human lateral fusiform gyrus (Prehn-Kristensen et al., 2009; Zheng et al., 2018; Zhou and Chen, 2008). Since multisensory integration is considered as a key aspect of (social-)cognitive development (e.g., Bremner et al., 2012; Schaal and Durand, 2012 for review), and that mounting evidence orients toward multimodal building of knowledge in the brain (Lewkowicz and Ghazanfar, 2009; Mattioni et al., 2020; von Kriegstein et al., 2005; see Ghazanfar and Schroeder, 2006), the categorization of social information could develop from multisensory experience with conspecifics. In this perspective, repeated exposure to co-occurring social inputs from the different senses could progressively strengthen the connectivity between underlying cortical areas through reentrant signaling (Edelman, 1993), so that a body odor would become rapidly able to mediate face-selective activity in the developing visual system.

One may wonder whether the selective effect of maternal odor on face categorization relies on a general matching mechanism between congruent multisensory information, or whether it is specific to social information. In our view, both interpretations are not mutually exclusive. In adults, a large body of research indeed indicates that olfactory-visual congruency applies to nonsocial categories (Lundström et al., 2019; Seigneuric et al., 2010; Zhou et al., 2010). However, social objects are arguably the most familiar objects for young infants, with prominent exposure to faces in the first year of life, followed by gradual experience with other body parts, especially hands, in the second year (Fausey et al., 2016). This may lead to progressive changes in congruency effects between social odors and visual categories that could be further addressed throughout development. Besides, although future studies could also evaluate to which extent the observed effect of odors applies to more familiar nonsocial objects (e.g., toys) to exclude any mere contribution of familiarity, it can be argued that familiar objects are necessarily associated with social situations in infancy and can thus acquire a "social meaning". Given that Admittedly, since the comparison of data obtained for the neural categorization of cars was conducted with previously published data for the categorization of faces, it is noteworthy that these observations should be reinforced and replicated in a novel, and certainly larger, sample to provide more stringent evidence for the selective influence of maternal odor on face categorization. This could be done, for instance, by comparing faces with another social category, in order to test the social origin of the odor effect on visual categorization.

Regardless of the inherent neural mechanisms subtending this specific modulatory effect, our results are in line with studies showing that maternal odor mediates infants' visual behavior toward faces (Durand et al., 2020, 2013), and neural responses to facial expressions (Jessen, 2020). It is interesting to note that these studies did not all use the body odor of the own mother but also of a stranger mother (Durand et al., 2020; Jessen, 2020). A maternal odor, as a body odor, represents a mixture of several cues conveying a wealth of information about the person (e.g., identity, sex, age) and her internal states (e.g., physiology, emotion, health; de Groot et al., 2017 for review) and constitutes the most effective olfactory signal for human neonates and infants (Schaal et al., 2002). Hence, the own mother's body odor was used in the present study because it is arguably the most powerful chemosignal that is reliably associated with an infant's social context. However, future studies should determine whether any mother's (and even human) body odor is able to enhance the visual categorization of human faces, and how long this association is maintained across development. In particular, for that latter point, the facilitating effect of maternal odor may progressively fade as the sole visual system becomes able to readily categorize faces (e.g., see Lochy et al., 2019a for a discussion of the development of the face categorization response through childhood and adulthood). In that case, it would be relevant to evaluate whether the odor effect re-emerges in children or adults when the visual input is less identifiable (e.g., blurry, or presented for very brief durations), leading to reduced face categorization responses (e.g., Quek et al., 2018a; Retter et al., 2020).

In sum, our study highlights an innovative neural marker of rapid visual categorization of a non-social and unfamiliar object for human infants (i.e., cars). Thanks to a fast stimulation stream of natural images and the periodic appearance of car stimuli, this brain signature reflects a rich and complex categorization process, that is, a direct differential response to variable exemplars of cars against many other living and non-living objects. Critically, while a neural marker of face categorization characterized with the same approach is strongly enhanced by the presence of the maternal body odor vs. a control odor (Leleu et al., 2020), the car categorization response is insensitive to odor context. Overall, these results indicate that young infants can rapidly categorize various objects from their visual environment, and concurs with the view that perceptual development integrates congruent information across the senses for efficient category acquisition, with early-maturing systems, such as olfaction, providing assistance to later-developing systems, such as vision.

This section corresponds to the article:
Rekow, D., Baudouin, J.-Y., Poncet, F., Damon, F., Durand, K., Schaal, B., Rossion, B. & Leleu, A. Smells like real faces: Odor-driven categorization of illusory faces in the infant brain *(in revision)*

References of this article are added to the general bibliographic section of the dissertation.

Study 3: Smells like real faces: Odor-driven categorization of illusory faces in the infant brain

Abstract

Understanding how the young infant brain starts to organize the flurry of ambiguous sensory inputs coming in from its complex surrounding environment into distinct categories is of primary scientific interest. Here we test the outstanding hypothesis that senses other than vision play a key role in initiating complex visual categorizations in twenty 4-month-old infants exposed to a baseline odor or to their mother's odor while their electroencephalogram (EEG) is recorded. Various natural images of objects are presented at a 6-Hz rate (6 images/second), with facelike object configurations of the same object categories (i.e., face pareidolia) interleaved every 6th stimulus (i.e., 1 Hz). In the baseline odor context, a weak neural categorization response to facelike stimuli appears at 1 Hz in the EEG frequency spectrum over bilateral occipito-temporal regions. Critically, this facelike-selective response is magnified and becomes right-lateralized in the presence of maternal body odor. This reveals that non-visual cues systematically associated with human faces in the infant's experience shape the interpretation of facelike object configurations as faces in the right hemisphere, dominant for face categorization. At the individual level, this intersensory influence appears to be particularly effective when there is no trace of facelike categorization in the baseline odor context. These observations provide evidence for the early tuning of face(like)-selective activity from multisensory inputs in the developing brain, suggesting that perceptual development integrates information across the senses for efficient category acquisition, with early-maturing systems such as olfaction driving the acquisition of categories in later-developing systems, such as vision.

1. Introduction

From the very first moments of life, the human infant brain has to deal with a complex multisensory environment. To avoid being overwhelmed by responding to each object, person and event as completely unique, sensory inputs are grouped into categories. Although this key function, Categorization, has been the topic of much interest in cognitive science (Smith and Medin, 1981), its emergence and development remain largely unknown and much debated (Oakes et al., 2009; Quinn, 2011). In general, the development of categorization is studied separately for each sensory modality, the rationale being that unisensory categories are formed before being combined into more abstract conceptual categories (Mandler, 2004). However, experience is replete with cues coming concurrently from all sensory modalities, each maturing at a specific rate during early development (Lecanuet and Schaal, 1996). An outstanding hypothesis is that categories in early-maturing senses, such as smell, play a decisive role in initiating categories in more slowly-maturing senses, such as vision. Here we address this issue by testing whether maternal body odor, a non-visual cue repeatedly associated with a human face in the infant's experience, can initiate a category-selective neural response to visual stimuli hardly categorized as faces by the young infant brain (i.e., face pareidolia; Figure IV-9).

As complex and highly familiar stimuli categorized at multiple levels (e.g., emotional expression, sex, identity), faces are ideal to study categorization in vision. The most basic and yet challenging categorization of a visual stimulus as a face has been of interest to cognitive (neuro)scientists and researchers in artificial intelligence for decades (Grill-Spector et al., 2018 for review). The human adult brain is particularly impressive at automatically categorizing faces in a single fixation (Crouzet et al., 2010; Rossion et al., 2015), this rapid categorization being subtended by a distributed network of face-selective regions in the occipito-temporal cortex, with a right-hemispheric advantage (e.g., Jonas et al., 2016).

By contrast, the development of face categorization is much less understood and therefore more contentious. At birth, human infants already prefer looking at facelike stimuli (Goren et al., 1975; Johnson et al., 1991), but the origin of this neonatal ability has been debated (for review Simion and Di Giorgio, 2015). The ability to rapidly gaze at human faces embedded in naturalistic displays improves during the first year, markedly after 6 months of age (Kelly et al., 2019; Leppänen, 2016 for review). At the neural level, distinct activity for faces vs. other meaningful or meaningless stimuli has been recorded after at least 3-4 months with electroencephalography (EEG, e.g., Conte et al., 2020; Kouider et al., 2013; Peykarjou and Hoehl, 2013; de Haan et al., 2003 for review). Yet, it is fair to say that these neural responses are generally weak and dominated by a middle occipital activity, likely reflecting a strong contribution of low-level visual cues.

In recent years, a neural categorization response to natural face images has been found as early as 4 months of age using EEG frequency-tagging (de Heering and Rossion, 2015; Leleu et al., 2020). This response is a direct differential response to faces vs. other objects that generalizes across many individual faces, is not accounted for by low-level image statistics, and is mainly recorded over right occipito-temporal sites. Importantly, this face-selective response was found to be increased when infants were simultaneously presented with their mother's body odor compared to a baseline odor (Leleu et al., 2020). This observation was taken as evidence that, early in life, maternal odor boosts face-selective regions in the right occipito-temporal cortex, leading to a larger response to faces. This is in line with behavioral (Durand et al., 2020, 2013; Godard et al., 2016; Guellaï et al., 2011; Sai, 2005) and neural evidence (Bristow et al., 2008;

Jessen, 2020) that intersensory associations mediate how infants process facial information, supporting the view that the weaving of inputs from different modalities favors knowledge acquisition (Lewkowicz, 2010 for review).

However, critically, whether non-visual inputs systematically associated with the presence of a face in the infant's experience can be at the origin of, i.e., initiate, face-selective activity in the infant brain has yet to be demonstrated. This hypothesis is tested in the present study by using nonface objects categorized as faces by neurotypical adults (i.e., face pareidolia, Figure 1A), but which, to our knowledge, have not been associated with face-selective neural activity in infants. In line with our most recent investigation (Leleu et al., 2020), we rely on concurrent maternal odors to trigger face-selective neural responses. Olfaction is indeed ideal for this purpose since it functions earlier than vision, enabling olfaction to vision intersensory transfer of knowledge (Schaal et al., 2020). Moreover, due to a slow refresh rate induced by breathing, odors are perceived as more stable in space and time than visual information (Sela and Sobel, 2010), a functional property that can help to reduce the visual noise by adding reliability to variable inputs of the same category.

To test our hypothesis that a concurrent maternal odor can initiate neural face categorization within the immature visual system of infants, we record scalp EEG in 4-month-olds within two odor contexts (maternal vs. baseline). By contrasting natural images of objects resembling faces from other nonface objects every 6 images in fast streams of 6 images per second (i.e., 6-Hz base rate), we tag a facelike categorization response at 1 Hz in the EEG frequency spectrum (Figure IV-9C). Critically, facelike and nonface stimulus sets depict the same object categories (Figure IV-9A). Hence, a facelike-selective neural response would emerge only if exemplars from different categories elicit similar neural responses according to their facelikeness, and exemplars from the same categories (i.e., facelike and nonface stimuli) elicit dissimilar neural responses.

2. Materials and methods

a. Participants

Twenty clinically-normal full-term 4-month-olds participated in the study (9 females, mean age ± SD: 132 ± 7 days, range: 119 – 145 days). One additional infant was tested but not included in the final sample due to an insufficient number of trials. All parents gave written informed consent and none reported their infant suffering from any sensory (olfactory, visual), neurological or psychiatric disorder. Testing was conducted according to the Declaration of Helsinki and approved by the French ethics committee (Comité de protection des personnes Sud-Est III - 2016-A02056-45).

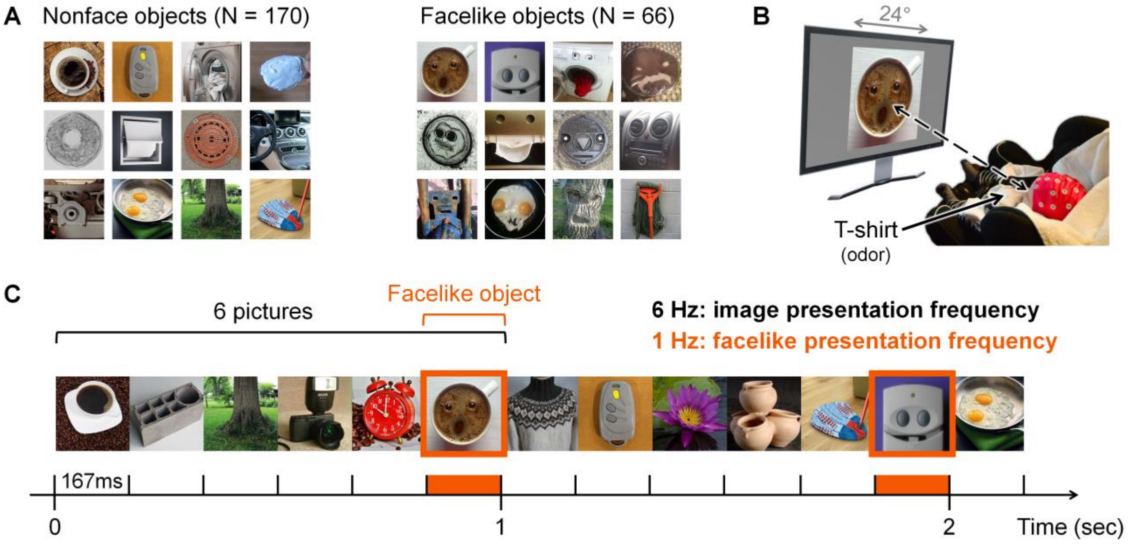


Figure IV-9. An EEG frequency-tagging approach to measure face pareidolia in odor contexts. A. Natural images embedded in their original background were used as stimuli. The set comprised many visual object categories, common to nonface and facelike objects. **B.** After EEG cap placement, infants were installed in a car seat in front of a monitor where stimuli sustained 24° of visual angle. Odors were delivered using T-shirts (unworn or worn by the mother) disposed on the infant's upper chest and maintained by the seat belts during visual stimulation. **C.** Excerpt of a 2-second clip of fast periodic visual stimulation where images are presented at a 6-Hz rate (6 images / s, i.e., each lasting 167 ms) and facelike images interspersed every 6th stimulus (i.e., at a 1-Hz rate). This frequency-tagging approach allows the identification of two distinct responses in the EEG spectrum: a general visual response results from the 6-Hz image presentation frequency, and a facelike categorization response emerges at 1 Hz if the facelike objects are reliably discriminated from the nonface objects.

b. *Visual stimuli*

The full stimulus set consisted of 236 natural images of various objects (animals, plants and man-made objects). They each depicted one single object unsegmented from its background, varying in color, viewpoint and lighting condition. A subset of these images (N = 66) depicted an illusory face (i.e., face pareidolia), based on the same categories than the remaining objects (examples in Figure IV-9A). All images were cropped to a square (400 × 400 pixels) to increase the variability of the item (size, viewpoint) but still covering a large part of the image. They were displayed on a 60-Hz 24-inch LED screen (1920 × 1080 pixels resolution) and subtended approximately 24° of visual angle (Figure IV-9B).

c. *Odor stimuli*

Infants were alternatively presented with the maternal odor and a baseline odor T-shirt, corresponding to the two odor conditions. Odor collection followed a standardized procedure (e.g., Durand et al., 2013) using a white T-shirt (100% cotton). Both T-shirts were washed using a hypoallergenic fragrance-free powder detergent (Persavon, France). One T-shirt was sent to the mother with instructions for night-wear to improve standardization across participants. It was worn directly on the skin during the three consecutive nights immediately preceding the experiment. During the days, it was preserved in a zip-locked hermetic plastic bag, and stored away from any heating device. Mothers were also asked to avoid the use of scented products (e.g., cosmetics, soaps) during the collection period, especially on the breast and axillary areas.

The baseline odor condition consisted in an identical, yet unworn, T-shirt, stored in our premises following the same procedure.

d. Design and procedure

To isolate and quantify both a facelike categorization response and a general visual response within the same stimulation sequence, we used a design similar to previous face categorization studies using FPVS coupled with EEG frequency-tagging (de Heering and Rossion, 2015; Leleu et al., 2020). We presented 34.5-s long sequences showing 207 images on a mid-level grey background (i.e., 128/255 in greyscale) at a base rate of 6 Hz (i.e., 6 images per second). At this rate, each image lasts 167 ms. Sequences were composed of the following segments: an initial blank pre-stimulation interval of 0.5 second followed by a fade-in of 1.833 seconds where contrast modulation ramped up from 0% to 100%, then the full-contrast stimulation of 31.167 s was followed by a fade-out of 0.833 s during which the contrast ramped down to 0% and closing on a final blank post-stimulation interval of 0.167 s.

Within the sequence, facelike images were interleaved as every 6th stimulus, corresponding to a periodic rate of 1 Hz (i.e., 6 Hz/6). Recording periodic responses at 1 Hz and harmonics (i.e., integer multiples) in the EEG frequency spectrum reflects a direct differential response to the facelike stimuli, as opposed to the response to other objects of the same categories displayed in the sequence. Using this frequency-tagging approach, the fast presentation of images at 6 Hz also triggers a general visual response in the EEG spectrum at 6 Hz and harmonics, reflecting the visual processing common to both nonface and facelike stimuli (e.g., luminance, contrast, etc.).

An adjusted EEG-cap was placed on the infants' head before installing them in a baby car seat. Infants were seated at a 57 cm distance from the screen in the light- and sound-attenuated Babylab of Dijon (FR). The lab is equipped with an air-extractor vent which continuously renewed the air in the room during the experiment with a silent and subtle air flow. To additionally reduce olfactory noise, the room was aired between consecutive sessions and experimenters avoided the use or consumption of odorous products (e.g., perfume, soap, coffee, tobacco) before testing. To minimize distraction, the experimental area was enclosed in odor-free occluding blinds, and the infant was continuously monitored via a webcam placed above the screen. Parents stayed on the experimenters' side and were thus distant from their infant with whom they were asked to interact only in case of manifest distress. Using dedicated disposable nitrile gloves, one odorous T-shirt was folded in order to optimally expose the infant to the most odorous areas (axillary, breast and neck regions), placed on the infant chest underneath the seatbelts a few seconds before a trial started. Each odor condition was thus delivered throughout the sequence, and T-shirts alternated every two sequences observing a minimum 1-min interval.

The 66 facelike stimuli were randomly divided into two 33-stimulus sets, each being assigned to one out of the two consecutive sequences for each odor condition. The 170 other objects were drawn randomly at each sequence. Sporadic and non-periodic sounds could be used as attention-getter (e.g., if the infant got distracted from the screen) without contaminating the frequency-tagged EEG responses of interest with auditory-evoked potentials. A sequence could be aborted and thus removed from analysis if the infant expressed distress or if a parent intervened during trial. The experimenter stopped testing on an infant-based criterion, i.e., at parental demand, when the infant showed no more interest toward the screen and/or tiredness or discomfort. The mean total number of sequences performed per infant was of 9 (range: 6–12) for an overall testing duration comprised between 3 min 27 s and 6 min 54 s per infant.

e. *EEG recording and analysis*

Continuous EEG acquisition ran on ASAlab 4.7 (ANT, The Netherlands) using a 32 Ag/AgCl electrode cap (Waveguard, ANT, The Netherlands) according to the 10–10 configuration system (acquisition reference: fronto-central channel AFz, sampling rate: 1024 Hz, electrode impedance < 15 kΩ). EEG data were preprocessed and a frequency-domain analysis (SI Materials and Methods) was conducted to isolate and quantify both the facelike categorization response (1 Hz and harmonics) and the general visual response (6 Hz and harmonics). Statistical analyses were then performed by identifying responsive channels using Z-scores (i.e., signal vs. surrounding noise) and comparing the neural responses across odor conditions using repeated-measures ANOVAs on the noise-corrected amplitude at identified channels. The lateralization of the facelike-selective response was also investigated with a lateralization index, and the relationship between the facelike categorization response recorded in the baseline odor context and the maternal odor effect was estimated to determine whether the odor effect is mainly driven by infants without a response in the baseline context (see Appendix 4 : Supporting Materials and Methods for details).

3. Results

a. *Facelike categorization in the infant brain: a matter of smell?*

To determine whether the 4-month-old infant brain can categorize a large set of naturalistic facelike stimuli in each odor context, we first considered the occipito-temporal channels showing a significant category-selective response to natural photographs of faces in previous infant studies (i.e., CP6, P7/8 and O2, de Heering and Rossion, 2015; Leleu et al., 2020) Figure S1, Appendix 4), and identified whether they also present a significant categorization response to facelike stimuli ($Z > 1.64$, $p < .05$, one-tailed, signal > noise). The mean facelike categorization response measured at 1 Hz is significantly above noise level over both the left (P7, $Z = 1.76$) and right hemisphere (P8, $Z = 2.75$) in the baseline odor context, but significant only over the right hemisphere (channels P8, $Z = 1.88$ and CP6, $Z = 2.05$) in the maternal odor context. We also explored contiguous electrodes (Figure S1, Appendix 4) with a more conservative threshold ($Z > 2.32$, $p < .01$), revealing only one additional right-hemispheric electrode, T8, only in the maternal odor context ($Z = 2.33$). No other electrodes reached significance in any odor context (Appendix 4, Table S1). As for the neural categorization response

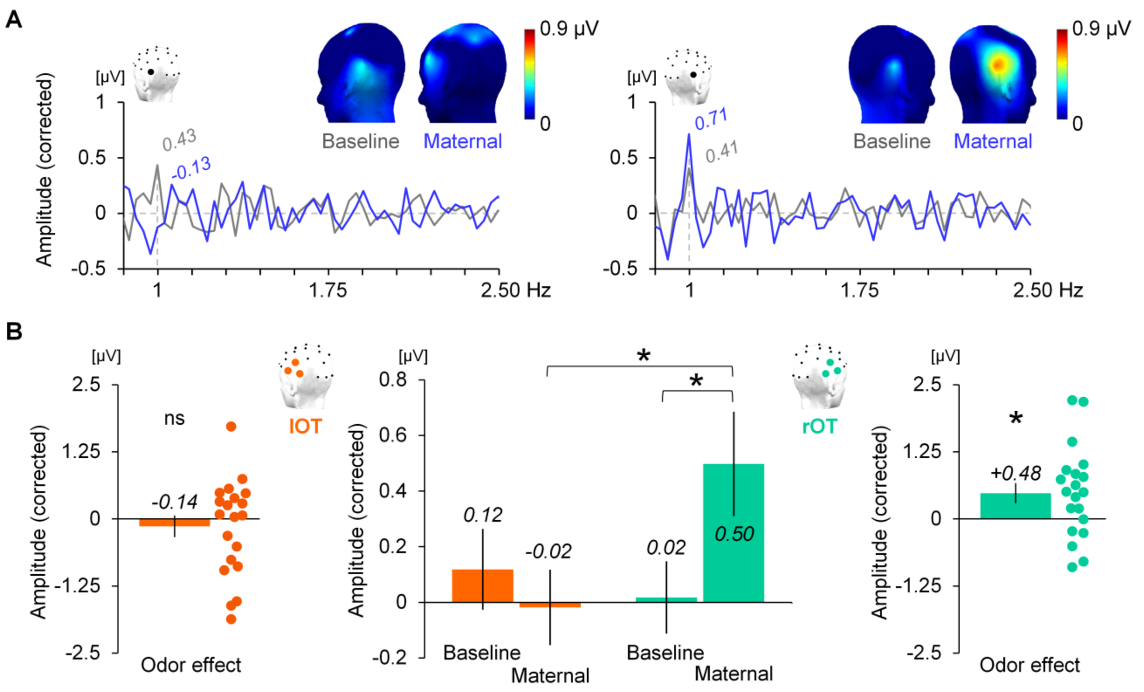


Figure IV-10. The facelike categorization response is shaped by maternal odor. A. Amplitude spectra (noise-corrected) showing the facelike categorization response at 1 Hz over the left channel P7 and the right channel P8 with corresponding 3-D head maps (lateral back view) for the baseline (grey) and maternal (blue) odor contexts. **B.** The amplitude of the facelike-selective response over the left (lOT, orange) and right (rOT, green) regions-of-interest (each encompassing three channels: P7/8, CP5/6, T7/8) and for each odor condition (middle panel) shows that maternal odor enhances the response only over the right hemisphere, leading to a difference between hemispheres in the maternal odor condition but not in the baseline odor condition. On the left and right panels, the odor effect [maternal minus baseline] in each hemisphere is depicted together with individual data (dots). Error bars represent the standard errors of the mean. (*: $p < .05$, ns: $p > .05$)

to human faces in infants (de Heering and Rossion, 2015; Leleu et al., 2020), the facelike-selective response is restricted to the 1st harmonic (i.e., integer multiple), since no identified channel was significant on the 2nd harmonic (i.e., 2 Hz, all Zs < 1.10, Appendix 4, Table S1).

Visual inspection of the noise-corrected amplitude spectra and scalp topographies (Figure IV-10A) confirms a weak, focal, and bilateral facelike-selective response over P7 and P8 in the baseline odor context that shifts toward a larger and spatially more extensive right-hemispheric response in the maternal odor context. Therefore, we considered the three channels identified over the right occipito-temporal cortex (rOT: P8, CP6, T8) and their homologous channels in the left hemisphere (lOT: P7, CP5, T7) using a repeated-measures ANOVA on amplitude variation with Odor (baseline, maternal), Hemisphere (left, right) and Electrode (T7/8, CP5/6, P7/8) as within-subject factors. Only the Odor × Hemisphere interaction reached significance ($F(1, 19) = 5.76$, $p = .027$, $\eta_p^2 = .23$; all other Fs < 2.28, all other ps > .15) due to a significantly larger facelike-selective response in the maternal than in the baseline odor context over the right (maternal minus baseline: +0.48 ± 0.19 (SEM) µV, $t_{19} = 2.56$, $p = .019$), but not over the left hemisphere (-0.13 ± 0.20 µV, $t_{19} = 0.67$, $p = .51$). Hence, the response is comparable between both hemispheres in the baseline odor condition (0.12 ± 0.15 µV vs. -0.02 ± 0.14 µV for the left vs. right hemisphere, respectively, $t_{19} = 0.65$, $p = .53$), but larger over the right (0.50 ± 0.19 µV)

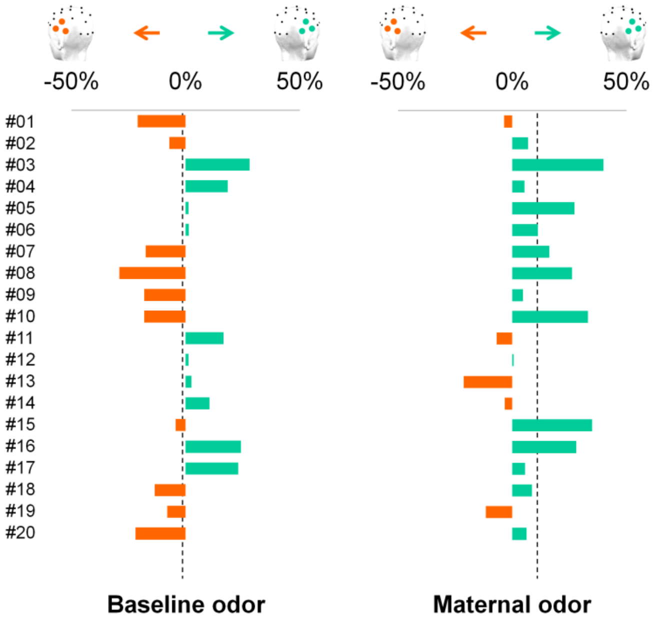


Figure IV-11. The facelike-selective response becomes right-lateralized in the maternal odor context. The facelike-selective response does not differ between hemispheres in the baseline odor context (mean lateralization index = -1.6%, dotted line) whereas it is significantly right lateralized in the maternal odor context (mean index = +10.4%). Individual facelike-selective responses are equally (N = 10) left- (orange) and right-lateralized (green) in the baseline odor context. Conversely, in the maternal odor context, there are 5 vs. 15 left- and right-lateralized responses, respectively.

than the left (-0.02 ± 0.14 µV) hemisphere in the maternal odor condition (t_{19} = 2.42, p = .026) (Figure IV-10B).

b. *Maternal odor initiates the right-hemispheric advantage for facelike categorization*

We further investigated the lateralization of the facelike-selective response in each odor context by computing a lateralization index that estimates the size of hemispheric asymmetry reported to the overall response across both hemispheres (positive and negative values indicate a right and left lateralization, respectively). The facelike-selective response does not differ across hemispheres in the baseline odor context (mean lateralization index: -1.6 ± 3.9%; t_{19} = -0.41, p = .68), while it is right lateralized in the maternal odor context (+10.4 ± 3.7%; t_{19} = 2.79, p = .012), leading to a significant difference between the two odor conditions (t_{19} = 2.28, p = .034). In the baseline odor context, the number of left- and right-lateralized infants does not differ (i.e., 10 infants, Figure IV-11). The magnitude of the lateralization index is close between left- (mean index: -15.9 ± 2.4%, maximum: -29%) and right-lateralized infants (mean: +12.7 ± 3.4%, maximum: +28%). By contrast, in the maternal odor condition, only 5 infants show a left-lateralized response and 15 infants a right-lateralized response, their mean indexes being -9.4 ± 3.4% (maximum: -21%) and +17 ± 3.4% (maximum: +40%), respectively. The presence of maternal odor thus elicits the right-hemispheric lateralization of the facelike categorization response.

c. Odor-driven categorization of face pareidolia in infants without a baseline response

To assess the ability of maternal odor to initiate the categorization of facelike objects, we first explored whether infants with the lowest facelike-selective response in the baseline odor context (baseline response) display the largest increase of the response in the maternal odor context (odor effect) over the right hemisphere. We considered channel P8 over which the baseline response is significant for the group and performed a *Spearman's* correlation between individual baseline responses and odor effects. This yielded a highly significant negative relationship (r = -0.71, R^2 = 0.51, p < .001), showing that infants with low baseline responses also exhibit strong odor effects (Figure IV-12A). Therefore, we directly examined whether the facelike-selective response emerges with the maternal odor in infants without a baseline response over P8. We estimated the significance of individual responses (Appendix 4, Table S2) and found 6 out of the 20 infants with a significant baseline odor response over P8. After removing these

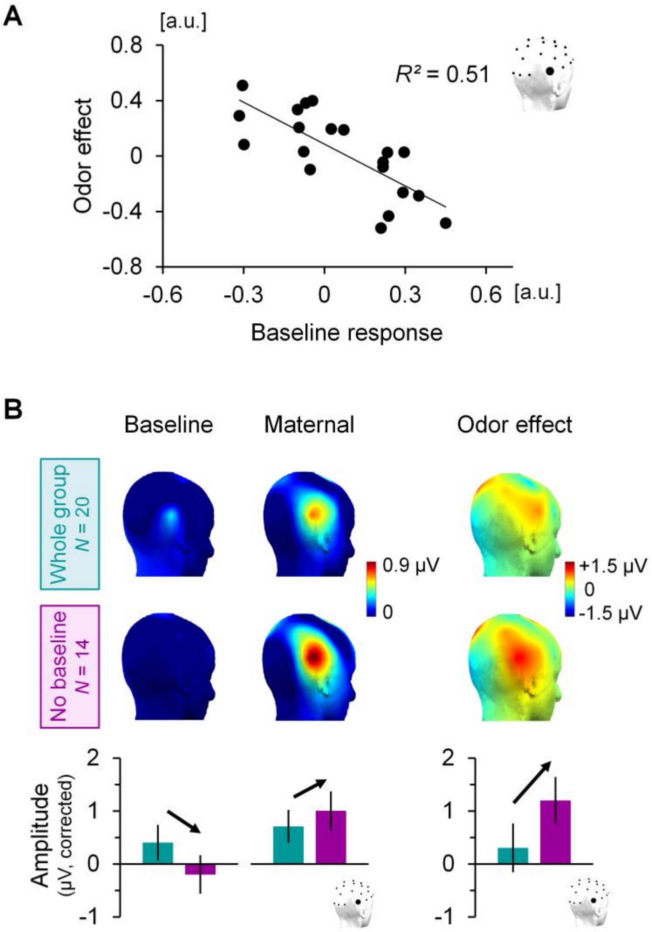


Figure IV-12. Facelike categorization emerges with maternal odor. A. The amplitude of the facelike-selective response recorded in the baseline odor context (baseline response) and the strength of the odor effect (maternal minus control, both expressed in normalized noise-corrected amplitudes, au: arbitrary unit) are negatively correlated over P8, meaning that the infants with the lowest baseline responses have the strongest odor effects. **B.** Amplitude (noise-corrected) of the facelike-selective response in the baseline and maternal odor contexts and their difference (odor effect) for the whole group (N = 20) or after removing the 6 infants with a significant baseline response over P8 ("No baseline" group, N = 14). Right lateral 3-D head maps (top) and histograms (bottom) show the modulation of the response in the baseline and maternal odor contexts and corresponding odor effects depending on the group. Error bars represent the standard errors of the mean.

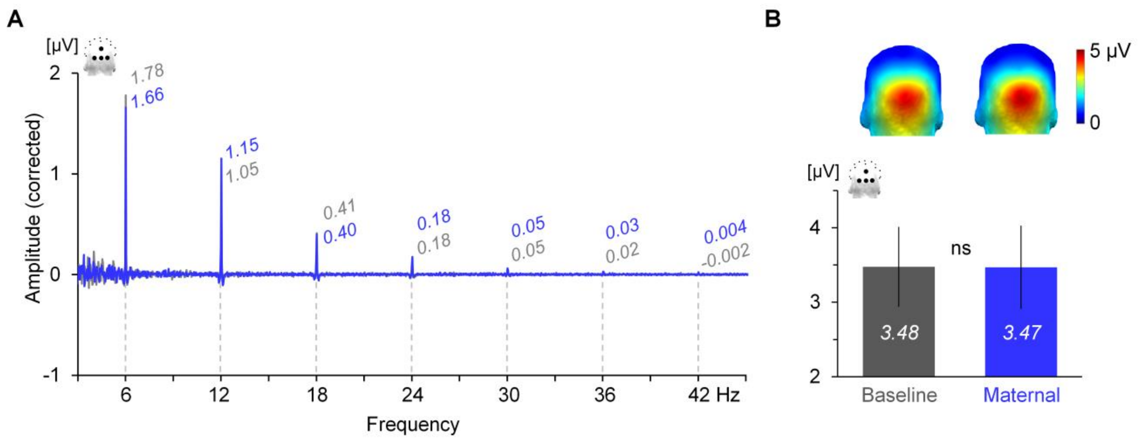


Figure IV-13 The general visual response. A. Amplitude spectra (noise-corrected) showing the general visual response recorded over middle occipital electrodes (O1/2, POz, Oz) at the frequency of stimulation (6 Hz) and its harmonics (i.e., integer multiples, up to 42 Hz) for the baseline (grey) and the maternal (blue) odor contexts. **B.** 3-D head maps (back view) of the overall response summed across 7 harmonics (top) and its mean amplitude (noise-corrected) across the 4 middle occipital channels (bottom) for each odor condition. No effect of maternal odor is noted for this response (*ns*: $p = .98$). Error bars represent the standard errors of the mean.

infants, the mean baseline response across the 14 remaining infants becomes non-significant over P8 ($Z = -0.56$, $p = .71$ *vs.* $Z = 2.75$, $p = .003$ for the whole group), with a noise-corrected amplitude of -0.19 ± 0.36 µV (whole group: 0.41 ± 0.33 µV). By contrast, the facelike-selective response measured in the maternal odor context increases to 1.01 ± 0.37 µV (whole group: 0.71 ± 0.31 µV). Hence, while the odor effect is not significant over P8 for the whole group (+0.31 ± 0.46 µV, $t_{19} = 0.66$, $p = .51$), it is strongly enhanced and gets significant (+1.20 ± 0.44 µV, $t_{13} = 2.72$, $p = .017$) for the 14 infants without a baseline response (Figure IV-12B). These conclusions remain unchanged when channel P7, over which the baseline odor response is also significant for the whole group, is added to the analysis (Appendix 4, Figure S2). Overall, this demonstrates that maternal odor initiates the categorization of illusory faces for infants who do not respond differentially to facelike *vs.* nonface objects in the baseline odor context.

d. No maternal odor influence on the general visual cortical response

By using 6-Hz streams of visual stimulation, we also measured a general visual response corresponding to the periodic brain activity elicited by the fast train of natural images and reflecting both the low- and high-level processing of the stimuli. The general visual response is centered over the middle occipital cortex (Figure IV-13), with 4 channels (POz, Oz, O1, O2) showing a significant response ($Z > 1.64$, $p < .05$, one-tailed, signal > noise) at 6 Hz, as observed in previous EEG infant studies (de Heering and Rossion, 2015; Leleu et al., 2020). *Z*-scores range from 3.44 for POz to 16.54 for Oz in the baseline odor condition, and from 1.77 for POz to 15.02 for Oz in the maternal odor condition. The response is significant over these 4 channels until the 7th harmonic (i.e., 42 Hz, Figure IV-13A). Summed across harmonics, the overall general visual response corresponds to an amplitude of 3.48 ± 0.53 (*SEM*) µV in the baseline odor context ($Z = 24.07$) and 3.47 ± 0.56 µV in the maternal odor context ($Z = 16.21$, Figure IV-13B). The repeated-measures ANOVA run with *Odor* (maternal, control) and *Electrode* (POz, Oz, O1, O2) as within-subject factors did not reveal a main effect of *Odor* nor an *Odor* ×

Electrode interaction (all *F*s < 1). Only a main effect of *Electrode* reached significance (F (2.24, 42.69) = 13.11, ε = .75, p < .001, η_p^2 = .41), highlighting a lower response over POz (1.70 ± 0.35 µV) than over any other middle occipital electrode (O1: 3.42 ± 0.61 µV, Oz: 4.77 ± 0.71 µV, O2: 3.99 ± 0.69 µV, all *t*s > 3.04, all *p*s < 0.01) along with a greater response over Oz than the other electrodes (all *t*s > 2.29, all *p*s < .05).

4. Discussion

Using EEG frequency-tagging, we hereby demonstrate the 4-month-old infant brain's ability to categorize facelike stimuli at a glance in the form of an occipital-temporal response recorded over "face-responsive" scalp regions (de Heering and Rossion, 2015; Leleu et al., 2020). While the facelike-selective response is weak and bilateral in the baseline odor context, adding maternal body odor boosts and shifts the response over the right hemisphere. Critically, this intersensory integration of information is particularly effective when there is no sign of facelike categorization for the sole visual system, revealing the ability of a non-visual input to initiate a category-selective response in the infant visual cortex. In addition, no odor effect is observed on the general response to the fast train of visual stimuli, ruling out a higher level of visual attention or arousal when exposed to maternal odor, in line with previous studies (Leleu et al., 2020; Rekow et al., 2020b).

A selective response to face pareidolia in the infant brain

Here we identify a neural response elicited by the periodic occurrence of facelike objects among nonface objects over regions typically responding to natural faces (i.e., occipital-temporal locations) as identified in previous studies using the same approach in infants (de Heering and Rossion, 2015; Leleu et al., 2020), children (Lochy et al., 2019a), and adults (Rossion et al., 2015). This response therefore indicates that the 4-month-old infant brain is able to categorize as faces a variety of objects presented in rapid streams of forward- and backward-masked natural images. Compared to the categorization response to human faces (Leleu et al., 2020), the amplitude of the facelike-selective response is about three times lower, likely reflecting greater difficulty. Indeed, considering that we used a large set of facelike and nonface objects, both depicting the same categories, the infant brain must overcome this deceptive information to discriminate stimuli depicting the same object categories, and generalize this discrimination across stimuli depicting different object categories according to facelikeness. As far as we know, no previous study did find such complex categorization response to face pareidolia at this early age (see e.g., Kobayashi et al., 2012). Thus, in the case of challenging perceptual abilities for young infants, the frequency-tagging approach offers a sensitive measurement to isolate a robust category-selective visual response.

Maternal odor tunes the categorization of facelike objects in the right hemisphere

Strikingly, we found that the facelike-selective response evolves from a weak, focal, and bilateral neural activity in the baseline odor context, to a larger, spatially more extensive, and strictly right-hemispheric response when adding maternal odor. The implications of this finding are twofold. First, it reveals that maternal odor does not only facilitate the categorization of human faces (Leleu et al., 2020), but also of a wide variety of nonhuman objects on the shared basis that they can be interpreted as faces. In that respect, one may wonder which nonhuman visual cues are perceived as facelike in the presence of maternal odor. Facelike stimuli all have salient "eyelike features" (e.g., Figure IV-9A), the eyes being considered the most important features to identify an illusory face in adults (Omer et al., 2019), and corresponding to the most explored face region when infants are exposed to maternal odor (Durand et al., 2013). However, since we used the same object categories for both facelike and nonface objects, eyelike features (e.g., egg yolks) were present in both stimulus sets (Figure IV-9A) and had to be integrated in a configuration to be perceived as facelike. Maternal odor might thus trigger the perception of facial attributes from the spatial arrangement between parts rather than from isolated features. This interpretation is supported by the localization of the odor effect over the right hemisphere, in line with its role in the perception of a facelike configuration in adults (Caharel et al., 2013; Rossion et al., 2011).

Second, this right lateralization of the facelike-selective response with maternal odor is relevant to the long-standing debate about the emergence of the right hemisphere advantage for face categorization during development (for review: Behrmann and Plaut, 2020). While clearly established in adults (e.g., Jonas et al., 2016), the right-hemispheric dominance for faces has been inconsistently observed in children and infants (Cantlon et al., 2011; Conte et al., 2020; de Heering and Rossion, 2015; Lochy et al., 2019a; Peykarjou and Hoehl, 2013). This led to suggest that the right hemisphere advantage depends on the acquisition of literacy and the progressive tuning of the left occipito-temporal cortex for word recognition (Dehaene et al., 2015; Dundas et al., 2013). However, the present finding, indicates that maternal odor elicits a strong right lateralization of face(like)-selective responses in the infant brain. Given that infants are often tested on their parents' lap, maternal body odor, and more generally any parental multisensory cue, may constitute a potent yet neglected factor of hemispheric lateralization in infancy. While this issue deserves further investigation and while learning to read may still later contribute to strengthen hemispheric asymmetry, our observation reveals that the origin of the right hemisphere advantage for faces has to be sought in early infancy, well before the onset of literacy.

Visual categorization can emerge with the help of a non-visual cue

A key finding of the present study is that the weakest individual responses in the baseline odor condition lead to the strongest odor effects, such that the facelike-selective response arises with maternal odor in infants without a response in the baseline odor context. This finding relates to the inverse effectiveness principle, whereby the efficiency of multisensory integration increases as the responsiveness to unisensory stimuli decreases (Regenbogen et al., 2016). Hence, the more the input is ambiguous for a given infant, the more maternal odor cues could strengthen, and even initiate, facelike categorization to counteract the difficulty of this task for their immature visual system. More generally, this supports the view that co-occuring multisensory inputs actively organize and shape infants' knowledge of the environment (Lewkowicz, 2010). Interestingly, while co-occurrence means that spatiotemporal relationships between events from the different senses are critical, odor perception is strongly insensitive to variations in space and time (Sela and Sobel, 2010). In addition, olfaction is an early-maturing sense, ideally suited to assist the development of later-maturing senses such as vision (Schaal et al., 2020). These two properties make olfaction a critical sensory modality for the acquisition of visual categories in the developing human brain.

Along this line, one could wonder whether the odor effect, observed here in 4-month-olds and for complex facelike stimuli, would be maintained at a later age after maturation of the visual system. The detection of human faces in naturalistic scenes strongly improves during the first 6 months of postnatal life (Kelly et al., 2019; Leppänen, 2016 for review) following sustained exposure to faces (Fausey et al., 2016). Similarly, the face-selective response tagged in EEG develops quantitatively and qualitatively from infancy to adulthood (de Heering and Rossion, 2015; Lochy et al., 2019a; Rossion et al., 2015). Future studies should thus pursue this investigation in different age groups to delineate olfactory-visual integration as a function of the relative maturity of the sensory systems. According to our observations across individual infants, we suggest that the odor effect progressively declines as the sole visual system becomes able to readily categorize stimuli as faces.

Which neural mechanisms could subtend the odor effect?

In line with the role of intersensory congruency in perceptual development (Bahrick and Lickliter, 2000), the repeated co-occurrence of odor and visual cues in the social niche of the developing infant could increase the likelihood of a face in the visual environment when the infant smells a (maternal) body odor. At the neural level, this would be reflected by a strengthened connectivity between the olfactory and visual systems through reentrant signaling (Edelman, 1993), such that maternal odor would be able to pre-activate face-selective regions in the ventral visual pathway, thereby tuning their responsiveness when a face(like) visual input appears. This interpretation is consistent with findings in adults showing that body odors alone activate the lateral fusiform gyrus (Zhou and Chen, 2008), a well-known category-selective visual region, and downstream recipient of the primary olfactory cortex (Zhou et al., 2019). This is more broadly in line with a large-scale connectivity between distinct "unisensory" brain regions dedicated to the same semantic domain (Mahon and Caramazza, 2011). Interestingly, it has been recently shown that the functional layout of the category-selective occipito-temporal cortex can be constrained by auditory inputs in people who are born blind (Mattioni et al., 2020). In this context, we are tempted to speculate that this mechanism also applies in infancy because face-selective regions are too immature to readily categorize face(like) stimuli from the sole visual input. Despite the difficulty of setting neuroimaging studies with young infants, recent advances in this endeavor (Deen et al., 2017; Kamps et al., 2020) offer a promising avenue for the future investigation of the mechanisms at stake in odor-driven category-selective neural responses.

It is worth noting that intersensory effects in the infant brain are not limited to social information (Werchan et al., 2018), and evidence obtained in adults shows that non-social odor cues actively modulate visual perception (Hörberg et al., 2020; Seigneuric et al., 2010; Zhou et al., 2010). However, social stimuli are arguably the most relevant and familiar cues in early development, in both visual (Fausey et al., 2016) and olfactory (Schaal et al., 2020) domains. This makes social information the best candidate to evidence potent intersensory effects during the first months of life, and, more generally, to demonstrate that the developing brain takes advantage of multisensory inputs for category acquisition. In this regard, one could inquire whether body odors that do not belong to the infant's own mother would be able to shape face(like) categorization. Body odors are mixtures of cues conveying nested information about people and their internal states (de Groot et al., 2017), and which influence on the perception of congruent facial information has been described in adults (Kamiloğlu et al., 2018; Wudarczyk et al., 2016). However, previous infant studies investigating this question have used maternal odors for their powerful effectiveness on infant behavior and cognition (Durand et al., 2020, 2013; Jessen, 2020; Leleu et al., 2020; Rekow et al., 2020b). Whether and how different "social chemosignals" interact with face perception in infancy is yet to be explored.

Moving to adulthood

Altogether, these three studies have first confirmed the impressive ability of infants to rapidly process information in order to categorize objects independently of their viewpoint, exposure, stimulus-driven specificities. Importantly, we have also described to what extent maternal odor influences visual categorization in early infancy: in the form of a congruent intersensory association, particularly effective when visual processing appears challenging. Indeed, maternal odor, a reliable and almost omnipresent cue in the sensory bubble of the young infant (Schaal and Durand, 2012), embodies a powerful role in bonding early in life (Schaal et al., 2020), and previous studies have evidenced its apparent effect on visual behavior in neonates (Doucet et al., 2007) and young infants (Durand et al., 2020, 2013). We here reveal the maternal odor effect on visual categorization in individual infant brains, shaping the categorization of visual information provided it bears congruency, here the social dimension brought by the face – admittedly one of the most relevant visual object for infants.

These observations take root in a broader mechanism of multisensory integration, whereby concurrent sensory inputs contribute to a common representation (Ernst and Bülthoff, 2004), and are thus not limited to social (face) categories associated with (maternal) body odor, selected for their relevance in early stages of development. Moreover, by revealing that the odor effect was the strongest when the baseline response was the lowest at the individual level, our findings strongly suggest an inverse effectiveness mechanism on perceptual abilities, at stake in early stages of cognitive development (Bahrick and Lickliter, 2012; Holmes, 2007).

Considering that face knowledge and abilities is rapidly growing during the first months, that adults are reputed *face experts*, but that literature still report several cases in which odor effects on adult visual perception is observable, how could body odor effect over face categorization manifest with development?

On the "short term" of cognitive development, we predict that maternal odor will gradually loose its effect along with 1) the maturation of the visual system and the development of face perception abilities in the visual realm; 2) motor development bringing forth a new relationship to other individuals (more distal and less oriented toward the face, e.g., Fausey et al., 2016) and 3) the fading of the physiological changes characterizing the "maternal" quality of the mother's body odor. These elements will be further discussed in the perspective section (part VIII), supported by preliminary data from older infants (4-to-12-month-olds).

In adults, the rationale is that odors could have an effect on visual categorization provided the neural response is not saturated. If it were, the odor effect would become measurable by increasing the difficulty of the task, i.e., ensuring the neural response can be enhanced. A proposition on tackling this issue is presented in **Study 4**, corresponding to chapter two.

Chapter two

Chapter two

V. Odors still exert a tuning function on visual categorization for the adult visual system

In adults, scientific knowledge about visual categorization is much advanced as compared to that of infants, especially using the FPVS-(i)EEG approach. In addition to faces, the neural signature to houses (scalp: Jacques et al., 2016a; iEEG: Hagen et al., 2020), body parts (Jacques et al., 2016a) and facelike objects (Rekow et al., in prep., Appendix 5), were also isolated and quantified.

This last study combines the three infant studies into one, with some adaptations. Instead of maternal odor, we used adult body odor, sampled from unfamiliar individuals (i.e., axillary sweat, see Methods and Appendix 6: Supporting information of Study 4, for more details). It was implicitly diffused alternatively with another odorant (i.e., gasoline) and a baseline odor (i.e., scentless mineral oil) during the visual stimulation, which consisted in all three visual categories (faces, cars, facelikes, same material as in Study 1 to 3), alternated across sequences. How can odor help in categorizing these categories, considering that the typical adult visual system is extremely efficient?

Interestingly, adults are not equal at face pareidolia and individual differences are often reported. This is due to the intrinsic ambiguity of the illusory face to be perceived from a common object. It represents an interesting challenge for the visual system, since the source of the illusion is a proper object, and face pareidolia corresponds to a dominant face bias. Therefore, the facelike category can be described as *ambiguous* and could thus constitute an interesting category to investigate the odor effect in adults, since face pareidolia is not systematic despite a mature and typically efficient visual system.

This section corresponds to the article:
Rekow, D., Baudouin, J.-Y., Durand, K. & Leleu, A. Smell what you hardly see: Odors assist categorization in the human visual cortex *(in preparation)*

References of this article are added to the general bibliographic section of the dissertation.

Study 4: Smell what you hardly see: Odors assist categorization in the human visual cortex

Abstract

Visual categorization is the brain ability to rapidly and automatically respond to visual information in a category-selective manner (i.e., different responses between categories and similar responses within categories) despite widely variable sensory inputs. Whether such category-selective neural responses are purely visual or can be influenced by other sensory modalities remains unclear. Here, we test whether odors modulate visual categorization, expecting that odors facilitate the neural categorization of congruent visual objects, especially when the visual category is ambiguous. Scalp electroencephalogram (EEG) was recorded while natural images depicting various objects were displayed in rapid 12-Hz streams (i.e., 12 images / second) and variable exemplars of a target category (either human faces, cars, or facelike objects in dedicated sequences) were interleaved every 9th stimulus to tag category-selective responses at 12/9 = 1.33 Hz in the EEG frequency spectrum. During visual stimulation, participants (N = 26) were implicitly exposed to odor contexts (either body, gasoline or baseline odors). We identified clear category-selective responses to every category over the occipito-temporal cortex, with the largest response for human faces and the lowest for facelike objects. Critically, body odors boost the response to the ambiguous facelike objects (i.e., either perceived as nonface objects or faces) over the right hemisphere, especially for participants who noticed their presence in the stimulation sequence. By contrast, odors do not significantly modulate other category-selective responses, nor the general visual response recorded at 12 Hz, revealing a specific influence on the categorization of ambiguous stimuli. Overall, these findings support the view that the brain actively uses cues from the different senses to readily categorize visual inputs, and that olfaction, which is generally considered as poorly functional in humans, is well placed to disambiguate visual information.

1. Introduction

Vision is commonly considered the dominant sense in humans. This is illustrated by its representation in scientific papers, or by the fact that nearly 3 out of 4 persons are more afraid of blindness than of any other sensory deprivation (Hutmacher, 2019). In particular, no one report anosmia as the most scaring deprivation (Hutmacher, 2019), in line with the depreciation of the human sense of smell for centuries. The function of olfaction has long been confined to alertness (Herrick, 1933), as most of our chemical environment remains unnoticed (Sela and Sobel, 2010), and we are consistently better at detecting than identifying an odor (Cain, 1979; Yeshurun and Sobel, 2010). In fact, odor recognition appears rather undetermined and flexible (Barwich, 2019; Cain, 1979), and is largely influenced by contextual cues, such as colors (Morrot et al., 2001; Österbauer et al., 2005; Zellner et al., 1991) or verbal labels (Herz and von Clef, 2001). As a result, olfactory-visual interactions have often been investigated through the lens of visual information modulating odor perception (Amsellem et al., 2018; Demattè et al., 2009; Gottfried and Dolan, 2003; Jadauji et al., 2012; Manesse et al., 2020; Porada et al., 2019).

Over the last decades, it has yet been progressively established that humans possess a keen sense of smell (McGann, 2017; Schaal and Porter, 1991), and mounting evidence reveals how olfaction influences other sensory modalities, in particular vision. Odors indeed attenuate the attentional blink for congruent visual objects (Robinson et al., 2013), help color recognition if odors and colors were previously paired (Demattè et al., 2006), improve congruent object detection in visual scenes (Seigneuric et al., 2010; Seo et al., 2010), and bias perception towards the congruent object during binocular rivalry (Zhou et al., 2010). At the neural level, odor (in)congruency modulates the scalp electroencephalographic (EEG) activity elicited by a visual stimulus (Ohla et al., 2018), or by an auditory cue that follows paired odor and visual stimuli and signals that the visual stimulus must be explicitly categorized (Hörberg et al., 2020). Olfactory-visual integration activates a broad neural network (Ripp et al., 2018), including the lingual and fusiform gyri (traditionally considered as visual brain regions), which respond as a function of the reported congruency between a visual object and an odor (Lundström et al., 2019).

The influence of odors on vision has also been extensively described for one of the most important objects of the human visual environment, i.e., faces. Odors facilitate face memory (Cecchetto et al., 2020; Steinberg et al., 2012) and orient judgments of face attractiveness (Demattè et al., 2007; Parma et al., 2012; Rikowski and Grammer, 1999), face sex (Kovács et al., 2004), or face-evoked personality traits (Cook et al., 2015, 2017, 2018; Dalton et al., 2013; Li et al., 2007). Emotional body odors (i.e., collected in anxiogenic or happy contexts) elicit (in)congruency effects on the perception of facial expressions (Kamiloğlu et al., 2018; Mujica-Parodi et al., 2009; Rocha et al., 2018; Wudarczyk et al., 2016; Zernecke et al., 2011; Zhou and Chen, 2009), which is also biased by hedonically-contrasted non-body odors (Cook et al., 2017; Leleu et al., 2015a; Leppänen and Hietanen, 2003; Seubert et al., 2010; Syrjänen et al., 2017, 2018). The neural underpinnings of the interactions between odors and facial information have been explored, revealing various patterns of modulations in "visual" brain regions (Cecchetto et al., 2020; Wudarczyk et al., 2016; Novak et al., 2015; Seubert et al., 2010), or in the EEG activity elicited by the face stimulus (Adolph et al., 2013; Cook et al., 2017; Forscher and Li, 2012; Leleu et al., 2015b; Poncet et al., 2021; Rubin et al., 2012; Syrjänen et al., 2018). Interestingly, given the high relevance of the sense of smell at the beginning of life (Schaal et al., 2020, for review) compared to the relative immaturity of the visual system (Braddick and Atkinson, 2011), odors strongly influence how infants look at faces (Durand et al., 2020, 2013), or how their brain responds to facial information (Jessen, 2020; Leleu et al., 2020; Rekow et al., 2020b, in revision).

Despite consensual evidence that odors influence visual perception, several important questions remain unanswered. *First*, whether odors are truly able to influence neural visual categorization is unclear. Visual categorization is the ability of the brain to rapidly (i.e., at a single glance) and automatically (i.e., without volitional control) respond to a certain class of visual objects (e.g., Bugatus et al., 2017; Thorpe et al., 1996), relying on a set of category-selective regions in the ventral occipito-temporal cortex (VOTC). These regions go beyond the sensory input and generate categorical responses, that is, distinct responses to different categories (i.e., between-category discrimination) and common responses to different instances of one category despite their physical variability (i.e., within-category generalization, Bracci and Op de Beeck, 2016; Hagen et al., 2020; Jacques et al., 2016b). While well-known category-selective regions (e.g., the fusiform gyrus) have been associated with the effect of odors on vision in the previously reviewed neuroimaging studies (Cecchetto et al., 2020; Lundström et al., 2019; Seubert et al., 2010; Wudarczyk et al., 2016), their neural activity was often considered for contrasts between different behavioral responses rather than contrasts between different visual categories irrespective of the behavioral output. Similarly, in EEG studies, odor influence has been rarely explored for selective responses to a variety of inputs from a given category contrasted to many other object categories (e.g., only a few individual faces for each emotion in the numerous studies investigating the effect of odors on the perception of facial expressions) and sometimes measured at late latencies over parietal and frontal regions (e.g., Hörberg et al., 2020; Ohla et al., 2018), contrary to occipito-temporal category-selective EEG responses (e.g., Jacques et al., 2016a). To our knowledge, the only EEG studies measuring how odors modulate a category-selective visual response have been conducted in 4-month-old infants (Leleu et al., 2020; Rekow et al., 2020b, in revision). Whether odors affect automatic visual categorization in the adult brain is still to be established.

Second, since both faces and body odors convey a wealth of information about our conspecifics (e.g., identity, sex, age) and their internal states (e.g., emotion, health), prior interest for odor-face integration was focused on this specific person-related information. However, for faces, before categorizing fine-grained information such as identity or facial expression, the initial categorization level is the mere categorization of a visual object as a face (Quek et al., 2020). As far as we know, no study has addressed whether body odors may tune this generic face categorization function in adults. In infants, maternal body odor orients the infant's gaze more and longer towards a face when it is paired with a car (Durand et al., 2013), and a face-selective neural response is strongly enhanced in the presence of maternal body odor over the right occipito-temporal cortex at 4 months of age (Leleu et al., 2020). This effect is selective to the generic categorization of a visual stimulus as a face, as no such effect was found for a nonface category (i.e., cars: Rekow et al., 2020b), except for nonface objects perceived as faces (i.e., face pareidolia; Rekow et al., in revision). Hence, whether this olfactory-visual interaction for generic face categorization is maintained in adulthood must be examined.

Third and finally, considering that the adult visual system readily categorizes faces and other visual objects from the sole visual input in typical conditions, whether the putative odor influence on category-selective responses in the adult brain depends on the ambiguity of the visual input has to be delineated. Indeed, the odor effects on category-selective neural responses in 4-month-old infants (Leleu et al., 2020; Rekow et al., 2020b, in revision) have been observed when the visual system is still immature and visual experience is poor compared to that of adults. In addition, the less efficient visual categorization is for a given infant, the strongest their odor effect is (Rekow et al., in revision), in line with the inverse effectiveness principle of multisensory integration (Regenbogen et al., 2016; Stein and Meredith, 1993). Similarly, numerous adult studies found the largest odor effects on facial expression recognition for ambiguous stimuli (Forscher and Li, 2012; Leleu et al., 2015a; Mujica-Parodi et al., 2009; Novak et al., 2015; Rubin et al., 2012; Zernecke et al., 2011; Zhou and Chen, 2009). In this context, whether congruent odors act as disambiguating cues on category-selective visual responses in the adult brain (i.e., the so-called disambiguation function of multisensory integration; Ernst and Bülthoff, 2004) has to be explored.

Here we address these issues using a fast periodic visual stimulation and an EEG frequency-tagging approach (FPVS-EEG). We focus on the visual categorization of human faces, nonface objects resembling faces (i.e., facelike objects), and cars contrasted to a variety of other living and non-living objects. Natural images were displayed at a fast rate of 12 Hz (i.e., 12 images / s) and the target category (i.e., human faces, facelike objects or cars in different sequences) was inserted every 9th stimulus (i.e., at 1.33 Hz) in 24-second-long sequences while participants performed an orthogonal cross-detection task. FPVS-EEG thus allows to isolate a general visual response common to all stimuli at 12 Hz and harmonics (i.e., integer multiples) in the EEG frequency spectrum, and, most importantly, a category-selective response at 1.33 Hz and harmonics (Jacques et al., 2016a; Rossion et al., 2015; Norcia et al., 2015 for review). The latter response is a direct differential response to the target category (i.e., reflecting its discrimination from the other categories displayed in the sequence and which generalizes across the various exemplars of the target category) generated by category-selective regions in the VOTC (Gao et al., 2018; Hagen et al., 2020; Jonas et al., 2016). Thanks to the fast rate of stimulation and the orthogonal behavioral task, the category-selective response measures single-glance and automatic visual categorization. During visual stimulation, participants were alternatively and blindly exposed to a body, a gasoline or a baseline (i.e., mineral oil) odor context, the two formers being chosen for their expected congruency with face(like) and car stimuli, respectively. Following previous studies in infants (Leleu et al., 2020; Rekow et al., 2020b, in revision), and since faces and cars are readily categorized in the adult brain whereas facelike objects are more ambiguous (i.e., they elicit a lower response than genuine human faces and are reported by only a fraction of participants in such a rapid and implicit mode of visual stimulation; Rekow et al., in prep.), we hypothesized that the congruent body odor context mainly enhances the visual categorization of facelike objects, this effect depending on the reported awareness of facelike objects after testing.

2. Material and methods

a. *Participants*

Twenty-six participants (14 females, 4 left-handed, mean age ± SD: 25 ± 4.5 years old) were recruited from the university campus and were compensated for their participation. All were healthy at the time of the study. They reported normal or corrected-to-normal vision and no history of allergy, sensory impairment, psychiatric or neurological disorder. They provided written informed consent prior to beginning and testing was conducted in accordance with the Declaration of Helsinki. A full debriefing after the experiment explained the whys and whereabouts of the study and revealed they have been exposed to implicit olfactory stimulation during testing. An additional consent was thus obtained after full disclosure.

b. *Visual stimuli*

We used a total of 368 natural images of objects unsegmented from their background (examples in Figure V-1A) divided in 4 subsets: 66 human faces (33 females), 66 cars, 66 facelike stimuli (i.e., nonface objects configured as faces) and 170 base objects of numerous living and non-living categories (e.g., plants, vegetables, animals, man-made objects). These stimuli have been used in previous experiments using an analogous FPVS-EEG approach in infants (Leleu et al., 2020; Rekow et al., 2020b, in revision) and adults (e.g., Quek et al., 2018a; Rekow et al., in prep.). Each image contained a single item, depicted off-centered in the image to increase physical variability across category exemplars. In addition, items varied in size, viewpoint, lighting condition and background. After being cropped to a square, they were resized to 300 × 300 pixels. Displayed on a screen at a distance of 57 cm, they roughly covered 8.3° of visual angle.

c. *Odor stimuli*

Three odor contexts were used: a generic human body odor (i.e., pooled across 8 donors), a gasoline odor, and a baseline odor (i.e., mineral oil). The two formers were chosen for their congruency with the visual categories (i.e., face(like)s and cars) and the latter as a control odor condition. Pilot experiments were conducted to characterize the sensory properties of body odors and match them with those of the gasoline odor (see Appendix 6, Supplementary Methods for details).

The body odor consisted in axillary sweat samples on cotton pads. They were collected from 16 independent non-smokers donors (8 females, mean age ± SD: 25 ± 4 years old). All donors followed a 24-hour hygiene procedure (see Appendix 6, Supplementary Methods for details). Two pools of 8 individuals each (4 females) were created by matching sampling duration and age across pools (see Appendix 6, Table S1) and were used for a pilot odor evaluation (see Appendix 6, Tables S2, S3 and Supplementary Methods) and the main EEG experiment (see below). The gasoline odor consisted in 1 mL of 10^{-3} gasoline oil diluted in mineral oil and disposed on a volume of cotton pads equivalent as for the body odor condition (i.e., 1 cotton pad, cut in 16 units). The odorless baseline odor consisted in a cotton pad impregnated with 1 mL of mineral oil and cut in 16 units. Odors for each participant were prepared 1 hour before testing in a separate room. Units of cotton pads containing body odors, gasoline or mineral oil were put in dedicated 60 mL sealed glass flasks and left at room temperature (+20°C).

d. Procedure

EEG was recorded in a sound and light-attenuated cabin equipped with an air-vacuum. To reduce additional olfactory noise, the non-smoker experimenter used scentless soap and avoided consuming coffee, tea, or any odorant product prior to testing. In the cabin, participants were seated at a 57-cm distance from the screen with their head on a chinrest. The screen (24-inch LED) displayed images with a refresh rate of 60 Hz and a resolution of 1920 × 1080 pixels on a uniform grey background (i.e., 128/255 in greyscale). To diffuse the odorants, we used an odor-delivering device adapted from previous studies (Leleu et al., 2015b; Poncet et al., 2021). The three odor flasks were connected to a device delivering a constant flow of scentless air originating from a tank of pressured air purified by charcoal filters and set at room temperature. The airflow was delivered at an undetectable pressure (i.e., 0.5 bar) to avoid the mechanical sensation of air on the skin and to ensure unawareness of olfactory stimulation throughout the experiment. The airflow was directed to one of the three flasks by a hand-activated valve from where a tube was connected to the chinrest to diffuse odors directly under the nose of the participants in the cabin. The flasks and the odor diffusing system were hidden from the participants.

We used a fast periodic visual stimulation (FPVS) coupled with an EEG frequency-tagging approach (Norcia et al., 2015) to measure rapid (i.e., single glance) and automatic (i.e., without explicit intention) visual categorization in the brain. The design was adapted from previous studies which successfully isolated visual categorization responses at different levels of brain organization in adults (e.g., Gao et al., 2018; Hagen et al., 2020; Jacques et al., 2016a), and infants (de Heering and Rossion, 2015; Leleu et al., 2020; Rekow et al., 2020b, in revision). Base objects were presented without inter-stimulus interval at a rapid 12-Hz base rate (i.e., 12 images / second, ≈ 83 ms per image, Figure V-1B) and images of either human faces, cars, or facelike objects (one target category per sequence) were periodically interspersed every 9th stimulus, corresponding to a category-selective rate of 1.33 Hz (i.e., 12 / 9; 750 ms between each category exemplar). Thanks to this frequency-tagging approach, we isolate two distinct brain responses in the EEG frequency spectrum: (1) a general visual response at 12 Hz and harmonics (i.e., integer multiples) elicited by the information rapidly changing 12 times per second (e.g., local contrast) and (2) a category-selective response at 1.33 Hz and harmonics reflecting the visual

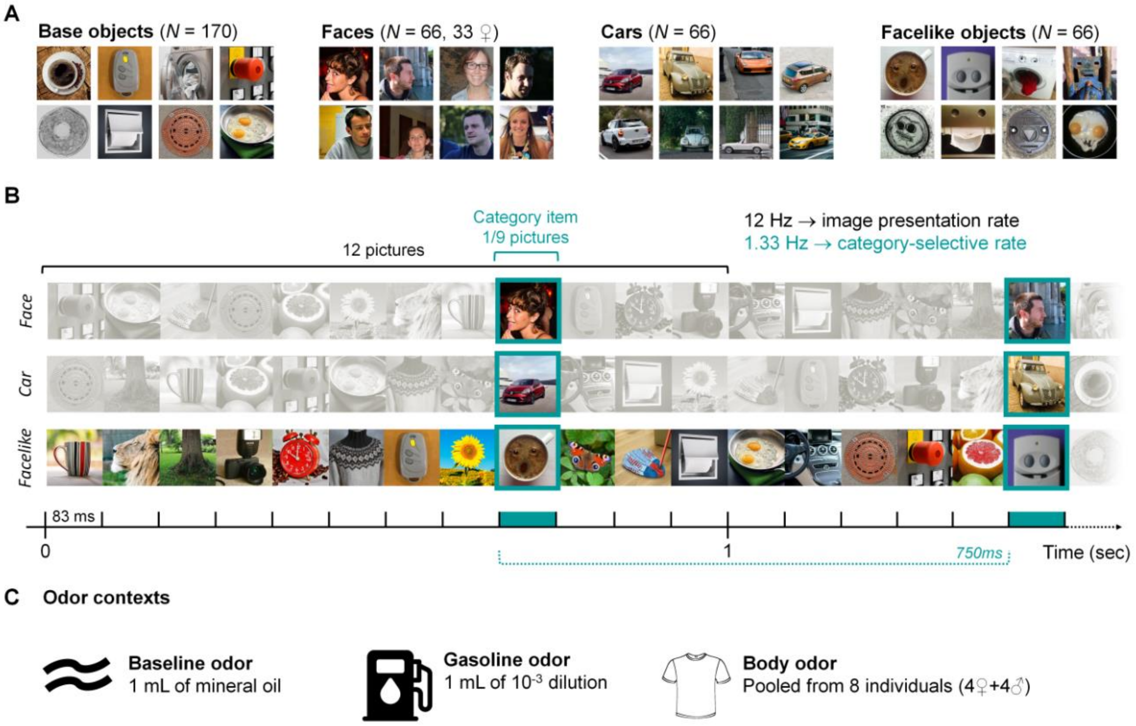


Figure V-1. Stimuli and experimental paradigm. A. Examples of variable unsegmented images used as stimuli and depicting base objects (*N* = 170), human faces (*N* = 66, 33 females), cars (*N* = 66) and facelike objects (*N* = 66). **B.** Excerpt of ≈ 1.5s (out of 27) of fast periodic visual stimulation (FPVS) at a 12-Hz base rate (i.e., 12 images per second, 83 ms per image). Base objects are presented while faces, cars or facelike objects (in different sequences) are inserted every 9th stimulus (i.e., at 1.33 Hz, 750 ms between two exemplars). As a result, two brain responses can be isolated in the EEG frequency spectrum: a general visual response at 12 Hz and harmonics (i.e., integer multiples), which captures the overall response to the information rapidly changing at 12 Hz (e.g., contrast), and a category-selective response at 1.33 Hz and harmonics, reflecting the visual categorization of faces, cars or facelike objects (i.e., discrimination from base objects that generalizes across exemplars). **C.** Odor contexts (baseline, gasoline and body odor) are presented throughout each FPVS sequence (one odor per sequence).

categorization of the target category. The latter response is elicited by populations of neurons that selectively respond to this category in the VOTC (Gao et al., 2018; Hagen et al., 2020; Jonas et al., 2016).

The visual stimulation sequences consisted in 27-second sequences. After a fixed interval of 1.5 seconds, a fade-in ramping from 0 to 100% contrast depth lasted 1.417 s before 23.333 s of full-contrast stimulation. A 0.667-s fade-out of decreasing contrast followed and the sequence closed on a 0.083 s of post-stimulation interval of grey background. For the target categories, each set of 66 images was randomly divided into two 33 stimuli sets, each set being used in a single sequence. All base objects were used in every sequence. During each sequence, stimuli were randomly selected from their respective sets. For the body odor, each participant was exposed to only one body odor pool (see Appendix 6, Supplementary Methods). Given the high volatility of the gasoline odor, two 1 mL samples were presented each for one half of the experiment. The nine experimental conditions were presented 4 times each: 3 odor contexts (body, gasoline, baseline) × 3 visual categories (human faces, facelike objects, cars) × 4 repetitions (2 subsets of stimuli presented twice). Each participant was thus tested for 36 sequences organized in 12 blocks of 3 sequences. In each block, odor conditions were paired each with one visual category, such that every odor and visual conditions were presented once within a block. These odor-visual associations were alternated between blocks.

After ensuring the participant was still and ready, the experimenter started odor diffusion and launched visual sequences. Odor diffusion started 5 seconds before each visual sequence and remains for the whole sequence. A minimum interval of 25 seconds was introduced between visual sequences and during which the baseline odor was diffused. In other words, at the end of each visual sequence, the experimenter immediately replaced the odor stimulation by the baseline odor if necessary, and waited 25 seconds before asking the participant if they were ready for the next sequence.

To ensure that participants stayed focus on the visual stimulation, they performed an orthogonal behavioral task during the sequences. The task consisted in the detection of a 250 × 250 pixel-large white cross (3-pixel thick, 200 ms duration) which superimposed with the images at the center of the screen. The cross appeared randomly six times per sequence, with a 2-second-minimum interval between appearances. Participants were instructed to press the spacebar simultaneously with both index fingers the most rapidly as possible and as soon as they detected the cross. An ANOVA was run on accuracy and response times for correct detections, ensuring no effect of *Category* (face, car, facelike) and *Odor* (body, gasoline, baseline), or *Category* × *Odor* interaction was found for the orthogonal task (all *F*s < 0.94, all *p*s > 0.40). The mean accuracy was near ceiling (97.7 ± 0.3 (*SD*) %) with a mean response time of 396 ± 28 (*SD*) ms.

After the EEG experiment, participants were asked to fill a questionnaire intended to document (1) the non-detection of odors during the experiment and their evaluation, (2) naivety regarding the frequency-tagging approach and the tagged categories, and (3) whether they perceived the facelike stimuli (see Appendix 5: Rekow et al., in prep., for details). No participants declared having noticed the presence of the airflow and the diffusion of odors during the experiment, nor the periodicity of the presentation, or the dissociation of sequences based on target categories. A total of 9 participants (i.e., 35%) declared having perceived the facelike stimuli on the course of the experiment; they will be henceforth designated as "aware" participants vs. "unaware" participants for those who did not notice the facelike objects (i.e., the 17 remaining participants). After the experimenter disclosed the diffusion of odors, participants were asked to rate the odorants (see Appendix 6, Supplementary Methods, Tables S2 and S3). Gasoline and body odors did not differ in perceived pleasantness, intensity and familiarity (all *t*s < 1.95, all *p*s > .06).

e. EEG recording and preprocessing

Scalp electroencephalogram (EEG) recording started once the participant was installed in the cabin. It was continuously acquired until the end of the experiment. A 64-channel Biosemi Active-Two amplifier system was used, with Ag/AgCl electrodes disposed according to the 10–10 classification montage (BioSemi, The Netherlands) and sampled at 1024 Hz. Reference and ground were constituted by the active electrode CMS (Common Mode Sense) and the passive electrode DRL (Driven Right Leg), respectively. Electrode offset was set below ± 15 µV for all electrodes.

Following EEG analyses were run on Letswave 6 (https://www.letswave.org/) implemented on Matlab 2017 (MathWorks, USA). Continuous individual datasets were first highpass filtered at 0.1 Hz using a 4th-order Butterworth filter, then resampled to 200 Hz. Epochs were segmented from the start of the fade-in until 0.583 ms after the end of fade-out (i.e., for 26 s) resulting in 36 segments per participant. To identify eye-blinks and additional high artifacts over frontal or temporal electrodes, an Independent Component Analysis (ICA) using a square mixing matrix was computed for each epoch and participant. The mean ± SD number of ICs removed was 4 ± 2 (range: 1–8). Additional artifact-ridden electrodes were linearly interpolated from 3 to 5 (depending on edge/central locations) immediately neighboring channels, for an average of 2 ± 2 interpolations per participant (range: 0–7). Epochs were then re-referenced to the average of the 64 channels.

f. EEG frequency-domain analysis

EEG data analysis was largely similar to previous FPVS-EEG studies on visual categorization (Jacques et al., 2016a; Rekow et al., in prep.; see Retter and Rossion, 2016 for a discussion). Epochs were precisely segmented to comprise an exact number of category-selective 1.33-Hz cycles, i.e., into 24-s-long epochs, starting from the end of the fade-in (i.e., first target category exemplar) to the end of the fade-out, for a total of 32 cycles. To reduce neural activity non phase-locked to the presentation of the target stimuli, epochs were then individually averaged for the 4 repetitions of each condition, resulting in 9 epochs of 24 s per participant (i.e., 1 per experimental condition). A fast Fourier transform (FFT) was applied to every epoch and amplitude spectra were extracted for all channels with a high frequency resolution of 1/24 = 0.0417 Hz.

Next, we evaluated the number of harmonics to retain for having a thorough estimation of each brain response. To consider an identical number of harmonics across experimental conditions, individual data were grand-averaged across odor contexts and visual categories, and channels were pooled together. *Z*-scores were computed on amplitude spectra as the difference between each frequency bin and the mean surrounding noise estimated from the 20 adjacent bins (10 on each side) excluding the most extreme (minimum and maximum) and immediately adjacent bins, divided by the standard deviation of the noise. Harmonics were considered until *Z*-scores ceased to be consecutively significant ($Z > 1.64$, $p < .05$, one-tailed, signal > noise). For the category-selective response, harmonics were significant until the 14th harmonic (i.e., 18.67 Hz). For the general visual response, harmonics were significant the 4th harmonic (i.e., 48 Hz; harmonics above the 50-Hz response elicited by AC power were not considered). To provide a summary representation of both responses, they were compiled by summing significant harmonics (excluding the 12-Hz harmonic (i.e., general response) for the category-selective response) for each condition, channel and participant. In the following sections, mentions of both responses will refer to these overall responses summed across harmonics.

The magnitude of each brain response was quantified in a value expressed in microvolt (µV) by subtracting the mean background noise from the raw amplitudes (baseline-corrected amplitudes), based on the same noise estimation as defined above. Considering that each visual category may recruit different neural populations, we estimated regions of interest (ROIs, Figure S1) separately for each category from group-level data. Baseline-corrected amplitudes at each electrode were ranked from highest to lowest (Appendix 6, Tables S4 and S5). For the three category-selective responses, the six best electrodes were P10, PO8, P8, P9, PO7 and P7 (different order for each visual category; Appendix 6, Table S4). Two ROIs were thus considered over the right occipito-temporal cortex (rOT) and the left occipito-temporal cortex (lOT) to account for putative hemispheric asymmetries. For all three visual categories, a single ROI was built for the general visual response over the middle occipital cortex (4 best channels: O1/2, Oz, Iz). For both brain responses, ROIs were used for statistical analyses. Signal-to-noise ratios (SNR) were also computed to estimate the strength of each brain response for grand-averaged data, by dividing uncorrected summed amplitudes by the mean surrounding noise.

Statistical analyses were computed separately for each brain response. The significance of each brain response at both group and individual levels was estimated using *Z*-scores (see above) calculated on uncorrected amplitudes. Repeated-measures ANOVA were also run on individual baseline-corrected amplitudes. For the category-selective response, *Odor* (body, gasoline, baseline), *Category* (faces, cars, facelike objects) and *Hemisphere* (rOT, lOT) were used as within-subject factors, and *Group* (aware, unaware) as a between-subject factor. For the general visual response, the same factors were considered without the factor *Hemisphere* (only one ROI). Mauchly's test for sphericity violation was computed and Greenhouse-Geisser correction (ε) for degrees of freedom was applied whenever sphericity was violated. Effect sizes are reported with partial eta squared ($\eta_p{}^2$). For significant *Odor* effects, orthogonal contrasts were calculated to qualify the effects. Since the amplitude of the category-selective response can be highly different between visual categories (Jacques et al., 2016a; see Appendix 5: Rekow et al., in prep. for the difference between the face- and facelike-selective responses), the *Odor* effect on the weakest category-selective response might be masked by the largest responses in the omnibus ANOVA. Hence, we also ran a repeated-measures ANOVA after having normalized each category-selective response by its overall amplitude over the scalp (McCarthy and Wood, 1985). A significant *Odor* effect for a given visual category was then further explored by directly conducting a repeated-measures ANOVA on the difference between odor conditions (expressed in non-normalized baseline-corrected amplitudes) for this specific category, and *Z*-scores (see above) were calculated to estimate the significance of the effect at both group and individual levels.

3. Results

a. *Neural categorization of human faces, cars and facelike objects across odor contexts*

Despite the high constraints put on the visual system to categorize human faces, cars, and facelike objects at a glance within rapid streams of numerous living and non-living objects, the three visual categories elicit a clear selective response (i.e., a direct differential response that generalizes across category exemplars) distributed on several harmonics (i.e., 1.33 Hz and integer multiples) in the EEG frequency spectrum, especially over the occipito-temporal cortex (Figure V-2A). Summed across harmonics and averaged across hemispheres, every response is highly significant (*Z* = 21.1, 11.3, and 2.13 respectively for the face-, car-, and facelike-selective responses, all *p*s < .017). After noise correction, the face-selective response appears as the largest (mean amplitude across hemispheres ± *SEM*: 2.56 ± 0.21 µV), followed by the car-selective response (1.38 ± 0.12 µV, 54% of the face-selective response) and the facelike-selective response (0.29 ± 0.05 µV, 21% of the car-selective response, 12% of the face-selective response), as revealed by a strong main effect of *Category* (*F*(1.6, 39.8) = 71.1, *ε* = 0.80,

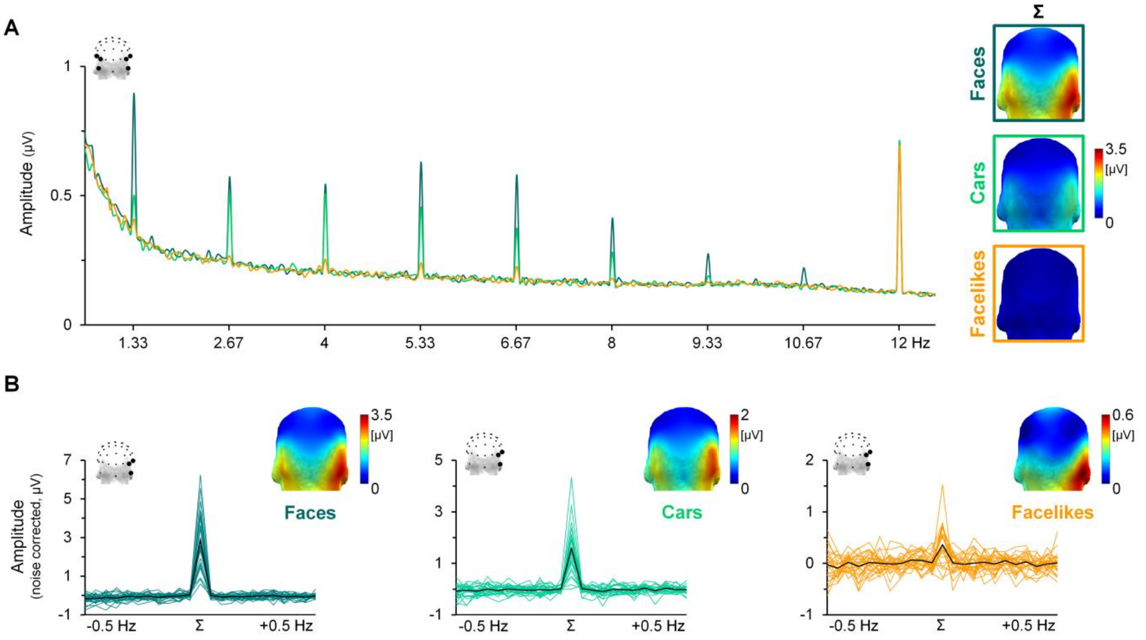


Figure V-2. EEG frequency spectrum averaged across odor contexts for each visual category. A. Left: Grand-averaged FFT amplitude spectra (uncorrected) recorded for sequences presenting human faces (dark green), cars (light green) and facelike objects (orange) among other objects. All types of sequences elicit clear responses (larger than surrounding frequencies) at the 12-Hz frequency of stimulation and at the 1.33-Hz category-selective frequency and its harmonics (i.e., integer multiples, here displayed from 2.67 Hz to 10.67 Hz) over bilateral occipito-temporal channels (P9/10, PO7/8 and P7/8). **Right:** 3D headmaps (back view, same scale) showing the topography and the magnitude (in baseline-corrected amplitude) of each category-selective response summed across harmonics (Σ). **B.** Baseline-corrected amplitude of the category-selective responses summed across significant harmonics (Σ) compared to surrounding frequencies (± 0.5 Hz, baseline-corrected amplitude ≈ 0, signal ≈ noise) over the right occipito-temporal region (rOT). The black line depicts the mean of the group and colored lines represent individual spectra. Adjusted-scale 3D headmaps (back view) are shown for each category.

$p < .001$, $\eta_p{}^2 = .74$). Accordingly, while every participant presents with a significant (i.e., $Z > 1.64$) face-selective response over at least one hemisphere, and 25 participants out of 26 with a significant car-selective response, the facelike-selective response is significant in only 14 participants out of 26. In addition, the three responses are larger over the right hemisphere (rOT > lOT, main effect of *Hemisphere*: $F(1, 25) = 9.39$, $p = .005$, $\eta_p{}^2 = .27$; Figure V-2B), especially the facelike-selective response (0.36 ± 0.08 µV vs. 0.23 ± 0.05 µV, i.e. +59% over rOT; faces: 2.88 ± 0.29 µV vs. 2.25 ± 0.22 µV, +28% over rOT; cars: 1.61 ± 0.19 µV vs. 1.16 ± 0.09 µV, +39% over rOT).

b. *Category-selective responses as a function of odor contexts*

Visual inspection suggests that, compared to the other odor contexts, the body odor context increases the facelike-selective response, whereas both the face- and car-selective responses seem identical across odors (Figure V-3). However, given the very low amplitude of the facelike-selective response compared to the two other responses, the omnibus ANOVA did not reveal any significant interaction involving the *Category* and *Odor* factors (all Fs < 1.35, all ps $> .26$). We therefore conducted another ANOVA with the same factors after having normalized the responses by their whole-scalp amplitude (McCarthy and Wood, 1985) to equate their magnitude, and found a significant *Category* × *Odor* interaction ($F(2.3, 55.8) = 4.47$, $\varepsilon = 0.58$, $p = .012$, $\eta_p{}^2 = .16$). As suggested by visual inspection, the *Odor* effect is significant for the facelike-selective response ($F(2, 48) = 5.12$, $p = .009$, $\eta_p{}^2 = .18$), while non-significant for both the face-selective and car-selective responses (all Fs < 1). For the facelike-selective response, a significant difference between the body odor context and the two other contexts ($F(1, 24) = 9.58$, $p = .005$, $\eta_p{}^2 = .29$) explains 70% of the effect. The remaining difference between the baseline and gasoline odors is not significant ($F(1, 24) = 2.48$, $p = .13$, $\eta_p{}^2 = .09$).

Descriptively, the facelike-selective response (Figure V-3, right panel) is particularly increased by the body odor context over the right hemisphere (rOT), with a ≈ 54% larger amplitude in this odor context than in the two other contexts (0.47 ± 0.09 µV vs. 0.27 ± 0.09 and

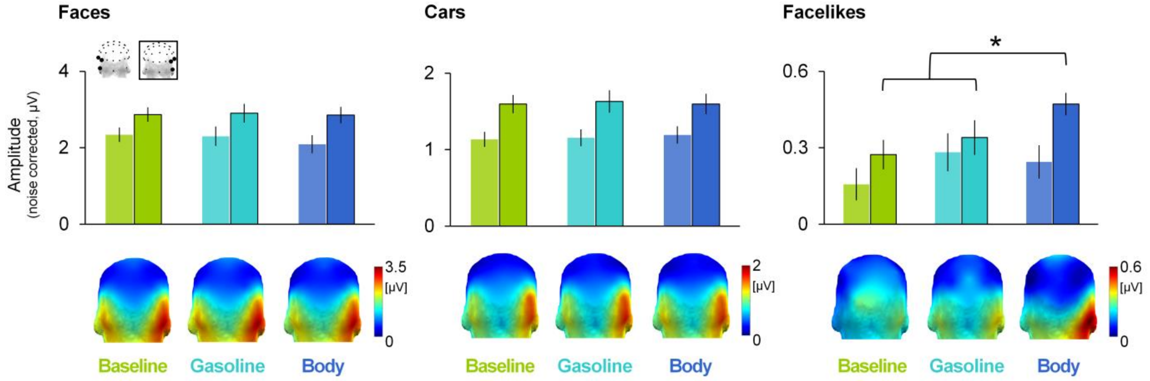


Figure V-3. Category-selective responses according to each odor context. Summed baseline-corrected amplitudes of the category-selective responses for each visual category (left: human faces, middle: cars, right: facelike objects), odor context (green: baseline odor, light blue: gasoline odor, dark blue: body odor) and hemisphere (lOT and rOT, delineated) together with corresponding 3D head-maps (back view, adjusted scales). Error bars represent standard errors of the mean; *: $p < .05$.

0.34 ± 0.11 µV for the baseline and gasoline odors, respectively). In contrast, this response is less variable over lOT, its amplitude ranging from 0.16 ± 0.06 to 0.28 ± 0.07 µV, the latter being observed for the gasoline odor context. As a result, despite a non-significant *Odor* × *Hemisphere* interaction ($F(2, 48) = 1.27$, $p = .29$, $\eta_p^2 = .05$), we dissociated the *Odor* effect as a function of the hemisphere and found a significant *Odor* effect over rOT ($F(2, 48) = 3.71$, $p = .032$, $\eta_p^2 = .13$), but not lOT ($F(2, 48) = 1.32$, $p = .28$, $\eta_p^2 = .05$). The effect over rOT is almost entirely driven (97%) by the difference between the body odor and the two other odor contexts ($F(1, 24) = 11.4$, $p = .003$, $\eta_p^2 = .32$). Moreover, individual *Z*-scores over rOT revealed that the facelike-selective response is significant for 10 participants out of 26 in the baseline and gasoline odor contexts, increasing up to 17 participants in the body odor context. Over lOT, significant individual responses are observed for only 4 (baseline), 6 (body), and 7 (gasoline) participants out of 26.

For the face-selective response (Figure V-3, left panel), amplitude varies between 2.86 ± 0.29 and 2.91 ± 0.32 µV across odor contexts over rOT. Over lOT, the response is of 2.35 ± 0.19 and 2.30 ± 0.25 µV in the baseline and gasoline odor contexts, respectively, while slightly lower in the body odor context (2.09 ± 0.24 µV), as indicated by a marginal *Odor* × *Hemisphere* interaction ($F(2, 48) = 2.49$, $p = .093$, $\eta_p^2 = .09$). The car-selective response (Figure V-3, middle panel) is even more stable across odor contexts, its amplitude varying between 1.60 ± 0.18 and 1.63 ± 0.21 µV over rOT, and between 1.13 ± 0.10 and 1.19 ± 0.11 µV over lOT.

c. *Body odor effect on the facelike-selective response according to reported face pareidolia*

Figure V-4 depicts the facelike-selective response differentiated between participants according to their reported awareness of facelike objects after the experiment. Interestingly, the body odor effect previously described over the right hemisphere for the whole group of participants appears more clearly visible for aware than unaware participants. Albeit slightly increased by the body odor, the amplitude of the facelike-selective response is close in the three odor contexts for unaware participants (body: 0.39 ± 0.11 µV, gasoline: 0.33 ± 0.14 µV, baseline: 0.34 ± 0.12 µV), while more strongly increased by body odor for aware participants (body: 0.62 ± 0.13 µV, gasoline: 0.35 ± 0.18 µV, baseline: 0.14 ± 0.11 µV; about 153% larger amplitude in the body odor context; Figure V-4A).

Hence, to further investigate the difference between the body odor context and the two other contexts (i.e., body odor effect) on the facelike-selective response for both groups of participants, we calculated the amplitude difference between the body odor and the mean of the two other odors (Figure V-4B) and conducted another ANOVA using *Hemisphere* (rOT, lOT) as a within-subject factor and *Group* (aware, unaware) as a between-subject factor. We observed a non-significant effect of *Group* ($F(1, 24) = 1.59$, $p = .22$, $\eta_p^2 = .06$) and a marginal effect of *Hemisphere* ($F(1, 24) = 4.15$, $p = .053$, $\eta_p^2 = .15$), qualified by a significant *Hemisphere* × *Group*

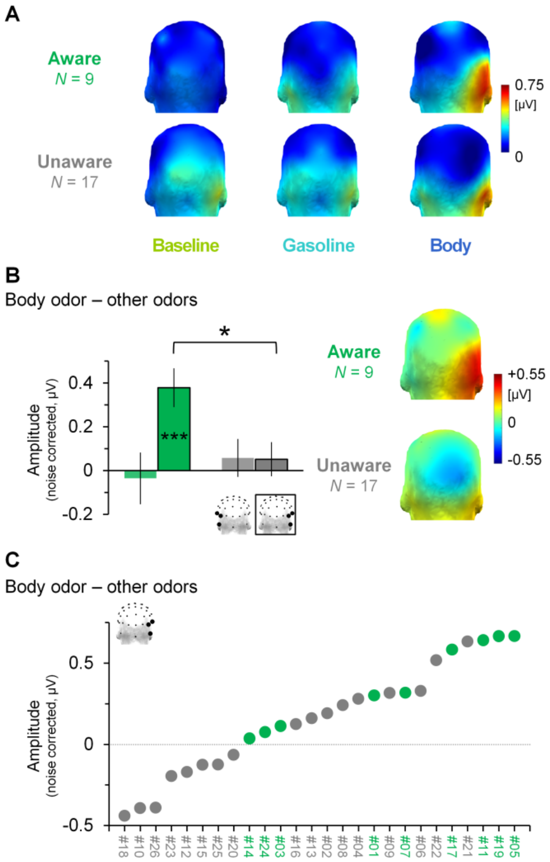


Figure V-4. Body odor effect on the facelike-selective response according to reported awareness of facelike objects. A. Summed baseline-corrected amplitudes of the facelike-selective response for each group of participants (aware and unaware) and odor context (green: baseline odor, light blue: gasoline odor, dark blue: body odor) together with corresponding 3D head-maps (back view). **B.** Body odor effect (body – other odors) for each group of participants (aware: green, unaware: grey) and hemisphere with corresponding 3D head-maps (back view). Error bars represent standard errors of the mean, *: $p < .05$; ***: $p < .001$. **C.** Ranking of individual body odor effects.

interaction ($F(1, 24) = 4.38$, $p = .047$, $\eta_p^2 = .15$). The body odor effect is larger for aware than unaware participants in the right hemisphere (aware: +0.38 ± 0.09 µV vs. unaware: +0.05 ± 0.08 µV; $F(1, 24) = 6.81$, $p = .015$, $\eta_p^2 = .22$), but not in the left (aware: -0.04 ± 0.12 µV vs. unaware: +0.06 ± 0.09 µV; $F < 1$). Therefore, the body odor effect is larger in the right than the left hemisphere only for aware participants ($F(1, 24) = 6.52$, $p = .017$, $\eta_p^2 = .21$; unaware: $F < 1$). Z-scores calculated on the mean body odor effect for each group of participants additionally showed that the effect is significant only for aware participants in the right hemisphere (rOT: $Z = 3.81$, $p < .001$ vs. lOT: $Z = -0.25$, $p = .60$; unaware participants: rOT and lOT: $Z = 0.58$ and 0.51 respectively, all ps >.28).

Finally, individual responses are markedly different according to participants' awareness of facelike objects. Individual body odor effects over rOT indicate that every aware participant has a positive body odor effect (i.e., larger response in the body odor context than the two others) compared to 9 (53%) unaware participants (Figure V-4C). Individual Z-scores calculated for each odor context revealed that only 3 out of 9 aware participants (i.e., 33%) have a significant facelike-selective response in the baseline and gasoline odor contexts, compared to 8 participants (89%) in the body odor context. By contrast, the number of unaware participants

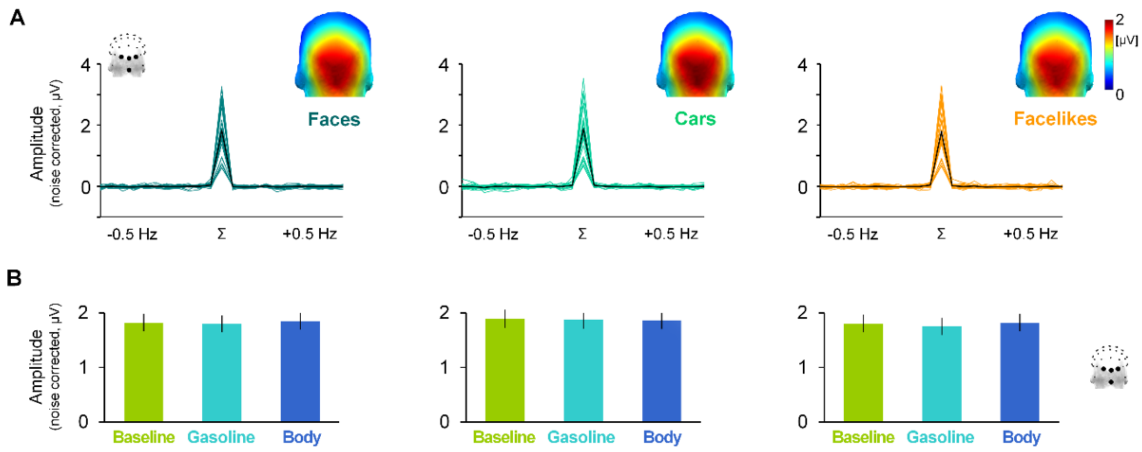


Figure V-5. General response to the rapid visual stream. Summed baseline-corrected amplitude of the general visual response over the middle occipital ROI (O1, Oz, O2, Iz) for each category averaged across odor contexts for EEG spectra (**A**). Individual spectra are depicted by colored lines and the mean amplitude is in black, together with corresponding 3D head-maps (back view). These summed amplitudes are further dissociated by odor context for bar plots (green: baseline odor, light blue: gasoline odor, dark blue: body odor; **B**) under each corresponding visual category. Error bars represent standard errors of the mean.

with a significant response only slightly increases from 7 out of 17 (41%) in both baseline and gasoline contexts to reach 9 (53%) in the body odor context. In addition, 7 (78%) aware participants have their highest *Z*-score across odors in the body odor context compared to only 5 (29%) unaware participants.

d. General visual response

The 12-Hz streams of images elicit a clear neural activity at the same frequency and harmonics over the middle occipital cortex, reflecting the general visual response to all cues rapidly changing 12 times per second (e.g., local contrast). Summed across significant harmonics (Figure V-5), the response has a mean baseline-corrected amplitude of 1.83 ± 0.16 µV, and is very robust, with every single participant having a significant response over the middle-occipital ROI (*Z*-scores ranging from 28 to 228 when collapsing all nine conditions, all *p*s < .001). The general visual response does not differ as a function of the visual category displayed at 1.33 Hz, the odor context or the reported awareness of facelike objects after testing (all *F*s < 2.07, all *p*s > .13), revealing that participants paid similar attention to the visual stimulation throughout the experiment.

4. Discussion

By using a fast periodic visual stimulation and an EEG frequency-tagging approach (FPVS-EEG) to track categorical occipito-temporal responses to faces, cars and facelike objects, and by implicitly exposing participants to body, gasoline and baseline odor contexts, we provide evidence for the influence of congruent, but not incongruent, odors over rapid and automatic visual categorization at both group and individual levels. This olfactory-visual interaction is effective only when the target category is ambiguous, i.e., body odor selectively facilitates the neural categorization of a variety of facelike objects as faces, especially for participants who reported their presence. No odor effect was observed on the middle occipital response elicited by the fast train of stimuli, or on the behavioral response to the cross-detection task, ruling out any general influence of the mere presence of odors. The present study thus specifically reveals a facilitating effect of congruent odors on neural visual categorization when the interpretation of the visual input is equivocal, in line with the disambiguating function of multisensory integration (Ernst and Bülthoff, 2004).

Following prior studies using FPVS-EEG (e.g., Jacques et al., 2016a; Rossion et al., 2015), we provide a direct measure of neural visual categorization in the form of category-selective responses (i.e., differential responses to the target categories relatively to numerous and diversified other living and non-living objects) that generalize across various category exemplars. Importantly, these responses reflect rapid (i.e., each image appears for 83 ms) and automatic categorization (i.e., visual stimuli were irrelevant to the explicit cross-detection task). The two unambiguous categories (i.e., faces and cars) elicit a robust selective response at the predefined 1.33-Hz frequency and harmonics, clearly visible in the amplitude spectrum and highly reliable across individuals. The facelike-selective response is also clearly isolated in the EEG frequency spectrum, albeit less reliable across participants. The magnitude of the category-selective responses differs across categories, with the largest response for human faces and the lowest response for facelike objects, corroborating previous studies (Hagen et al., 2020; Jacques et al., 2016a; Rekow et al., in prep.). Every category-selective response is mostly distributed over the occipito-temporal cortex with a right hemisphere advantage, in line with the critical role of this region in automatic visual categorization (Bugatus et al., 2017; Gao et al., 2018; Hagen et al., 2020; Jacques et al., 2016b).

Most importantly for our purpose, we found that the selective response to facelike objects over the right hemisphere is about two times larger in the presence of body odor. This observation accords well with previous studies showing that congruent odors modulate visual object perception at both behavioral (e.g., Robinson et al., 2013; Seigneuric et al., 2010; Seo et al., 2010; Zhou et al., 2010) and neural (e.g., Ohla et al., 2018) levels. In addition, this indicates that body odors, as powerful "social chemosignals" conveying much information about our conspecifics (de Groot et al., 2017 for review), do not only influence the perception of fine-grained facial information (e.g., facial expression; Adolph et al., 2013; Mujica-Parodi et al., 2009; Rubin et al., 2012; Wudarczyk et al., 2016; Zernecke et al., 2011; Zhou and Chen, 2009), but also improve the generic categorization of a visual stimulus as a face. It is worth noting that neither a facilitating nor an inhibiting odor effect was observed for incongruent associations (i.e., gasoline effect for face/facelike stimuli or body odor effect for cars), contrary to a recent report of incongruent odors interfering with visual categorization (Hörberg et al., 2020). However, in that latter study, interference was observed on explicit behavior and late (i.e., 300-900 ms) frontal and parietal EEG responses to a delayed auditory cue signaling that the visual stimulus must be categorized. Thus, odors could have not interfered with the automatic visual categorization of the stimulus at its onset, but rather with the controlled and delayed decision on that stimulus.

Our study reveals that odors are specifically prone to facilitate the visual categorization of congruent inputs when their perceptual interpretation is not straightforward, i.e., for facelike objects. Indeed, genuine human faces are unambiguously categorized from the sole visual input even under high stimulation constraints. At brief durations (i.e., 83 ms as in the present study; Retter et al., 2020), or with degraded inputs (i.e., low-pass filtered stimuli; Quek et al., 2018a), all participants report having seen faces and the face-selective response measured with FPVS-EEG is already saturated (and remains stable when presentation conditions become less constraining). By contrast, even with full-spectrum stimuli presented for a longer duration (i.e., 167 ms), not all participants notice facelike objects, which elicit a lower category-selective response than human faces (Rekow et al., in prep.). This is likely due to the fact that facelike stimuli represent various objects similar to the other objects displayed in the stimulation sequence. Therefore, the visual system must go beyond this similarity to produce a differential response to facelike vs. other objects and generalize this response across widely variable facelike objects. In this situation, inputs from other sensory systems are ideal to resolve ambiguity according to prior multisensory experience (Ernst and Bülthoff, 2004). Because body odors are often associated with faces and heighten attention to person-related cues (Cecchetto et al., 2019), they are well-suited to tilt the balance towards the "face" interpretation. This is consistent with previous studies showing that odors provide such disambiguating effects on facial expression perception (Forscher and Li, 2012; Leleu et al., 2015a; Mujica-Parodi et al., 2009; Novak et al., 2015; Rubin et al., 2012; Zernecke et al., 2011; Zhou and Chen, 2009), and more broadly with the inverse effectiveness principle, whereby multisensory integration is particularly effective when the response to unisensory stimuli is scarce (e.g., Stein and Meredith, 1993; Regenbogen et al., 2016). Such inverse relationship between olfactory-visual integration and the strength of the sole visual response has already been observed for facelike categorization in infants (Rekow et al., in revision). At the neural level, the disambiguating effect of odors suggests effective connectivity between the olfactory and the visual systems, in line with body odors activating the lateral fusiform gyrus (Prehn-Kristensen et al., 2009; Zheng et al., 2018; Zhou and Chen, 2009), a category-selective visual region that hosts face-selective areas. It was also observed that the sole presentation of odors activates another typical visual area, the right occipital cortex (Djordjevic et al., 2005; Royet et al., 2001, 1999; Zatorre et al., 2000), suggesting that odors alone can trigger visual imagery (Parma et al., 2017 for review). In sum, odors could function as a prime to improve the detection of congruent inputs in other sensory modalities, e.g., body odors alerting to the potential presence of a person, thus in the present case, favoring the categorization of a face in common objects configured as faces.

Regarding hemispheric asymmetry, the body odor effect on facelike categorization is confined to the right hemisphere, and there is a non-significant decrease of the face-selective response with body odor over the left hemisphere. In fact, these observations relate to previously reported modulations of both face- and facelike-selective neural responses in infants exposed to maternal body odor (Leleu et al., 2020; Rekow et al., 2020b, in revision). This indicates that body odor reinforces the well-known dominance of the right hemisphere for face categorization (Behrmann and Plaut, 2020; Grill-Spector et al., 2017; Hagen et al., 2020; Jonas et al., 2016). This right-hemispheric dominance has been related to holistic perception, the ability to perceive the whole face configuration at a glance (Caharel et al., 2013; Rossion et al., 2011). Hence, we can speculate that body odors, by evoking the presence of a person, favor the perception of a whole face pattern from a single fixation at a stimulus interpretable as facelike. In addition, systematic reviews on the hemispheric lateralization of the neural responses to odors proposed that the right hemisphere is more involved than the left in the recognition of the odor source (Brand et al., 2001; Royet, 2004). Therefore, the right hemisphere is a good candidate for integrating information across the senses to facilitate the categorization of (multi)sensory inputs, putatively relying on large-scale connectivity between distant brain regions dedicated to the same semantic domain (Mahon and Caramazza, 2011).

Strikingly, the body odor effect on facelike categorization is mainly observed in aware participants, i.e., participants who reported face pareidolia after testing. One may thus suggest that body odor, by enhancing facelike-selective neural activity in the visual cortex, triggers the subjective experience of a face in facelike objects. Admittedly, awareness status was defined after the experiment based on a single declarative report. It is thus unclear whether body odor made some participants become aware of the facelike objects, or whether the odor effect is observed because participants were already aware of the facelike objects. However, two elements lead us to favor the first interpretation. First, the magnitude of category-selective responses measured with FPVS-EEG has been previously related to participants' awareness of the visual category (facelike objects: Rekow et al., in prep.; human faces: Retter et al., 2020), with larger amplitudes when participants explicitly report perception. By contrast, here, the facelike-selective response is of close amplitude for aware and unaware participants in the baseline and gasoline odor contexts (and even slightly lower for aware participants in the baseline context). This suggests that aware participants were not more generally prone to face pareidolia than unaware participants, but specifically more sensitive to facelikeness when exposed to body odor. Second, in a side experiment, we tested another 26 participants for their ability to report face pareidolia after being presented with similar 12-Hz visual streams of facelike vs. nonface objects without any odor context (see Supplementary Information for details). Only 4 participants (15%) noticed the presence of facelike objects, which is significantly lower than the 9 aware participants (35%) in the main experiment. This observation thus converges with the interpretation that exposition to body odor elicits awareness of facelike objects in some participants. Future studies should obviously elaborate on this issue by directly manipulating awareness in a single group of participants.

In conclusion, we show that neural visual categorization - i.e., the ability of category-selective regions in the VOTC to rapidly and automatically respond to a given visual category - is shaped by concurrent odor inputs, provided they are congruent (i.e., semantically-related) with the visual stimulus and can facilitate its interpretation (disambiguation). It is worth noting that while our results indicate a specific association between body odor and facelike categorization, we cannot exclude the same type of association for other categories, including cars. Actually, we rather consider that the influence of odors on visual categorization is a general phenomenon when the visual information is ambiguous, odors orienting perception towards the most probable visual category (Ernst and Bülthoff, 2004). Here we used a large set of facelike objects as ambiguous faces, without any equivalent for cars. Indeed, face pareidolia is ubiquitous in humans and pareidolia more barely occur for nonface visual categories, reflecting the high saliency of the “face” category for our species. Future studies should thus evaluate the generalizability of our findings to various visual categories by using degraded stimuli or challenging stimulation parameters that hamper visual categorization.

General discussion

VI. Summary: Multisensory integration is particularly useful in (the development of) visual categorization

From the review of literature, we learned that intersensory associations between odors and congruent visual information exist in humans. It was illustrated with body odors and person-related information, focusing particularly on face perception and their role in socio-cognitive functions. However, this review had left us with a couple of unanswered questions. First, most of these investigations were conducted in adults, but determining if knowledge is either acquired through senses separately at first (Piaget, 1952) or from the understanding of inputs as a result of multisensory experience (Gibson, 2000) remains an ongoing debate (Bremner et al., 2012). It is true that olfactory-visual integration may differ between infant and adult brains, whose sensory maturation, neural connectivity, cognitive functions and accumulated experience are not alike; however, determining if intersensory congruency help young infant to understand their environment would strongly contribute to this discussion. Second, interestingly, intersensory congruency can be derived from the perceived quality of the odor instead of its ecological property: for instance, facial expressions are faster recognized in odor contexts of congruent hedonic valence (e.g., a pleasant strawberry odor helps perceiving happy faces only, Leleu et al., 2015a). It was thus unclear whether body odor, to which we are ecologically exposed during social interactions, would promote generic face categorization and in a selective way. Finally, studies in adults revealed that the odor could be particularly helpful if the visual information is ambiguous (Forscher and Li, 2012; Leleu et al., 2015a; Mujica-Parodi et al., 2009; Novak et al., 2015; Rubin et al., 2012; Zernecke et al., 2011; Zhou and Chen, 2009), illustrating the inverse effectiveness rule of multisensory integration (IER; Stein and Meredith, 1993). Therefore, it was suggested that odor could have a disambiguating effect on congruent categorization when the visual input is ambiguous or in developmental stages when the visual system is still immature and visual experience is still poor.

To solve these issues, we conducted four studies based on the general hypothesis that congruent odors help visual categorization, more precisely that 1) body odor selectively facilitates the processing of faces and facelike objects (for their depiction of a face pattern), so that 2) no body odor effect was expected on the visual categorization of nonface objects (i.e., cars) and the incongruent odors (i.e., gasoline) was not expected to modulate the categorization of faces or facelike objects. In addition, according to the inverse effectiveness rule of multisensory integration, we particularly expected 3) the strongest odor effects when the visual response is the lowest, i.e., corresponding to a challenging categorization (due to the young immature visual system and/or stimulus ambiguity).

A. Main results: a synthesis

By declining the same fast periodic visual stimulation coupled with scalp EEG recordings, we tested the categorization of human faces, cars and facelike objects in infants and adults using the same visual stimuli across ages. Odors were presented as contexts: we exposed infants to a baseline odor or their mother’s odor through an unworn vs. worn t-shirt, respectively (Studies 1 to 3, chapter one); and implicitly diffused odorants (body odors, gasoline or mineral oil) to adult participants (Study 4, chapter two).

In chapter one, we described the selectivity of maternal body odors on generic face categorization in 4 month-old infants as characterized by a strong enhancement of the face(like)-selective response over the right hemisphere. By contrast, while we recorded a significant categorization response to cars (i.e., the nonface category), maternal odor did not exert any influence on car categorization. In addition, maternal odor shifted the neural response to facelike objects from a bilateral response to a right-lateralized response and we further showed that the odor initiated the facelike categorization response in some individual infants who did not categorize facelike objects in the absence of maternal odor.

Further investigating these effects in healthy adults, we observed in chapter two that the (body) odor effect was still observed under certain circumstances. Indeed, the sole odor effect we found was characterized by its congruency between olfactory and visual input and the ambiguity of the visual input (i.e., body odor enhanced the facelike categorization response). Finally, we also detailed in this last study that the body odor effect was stronger in individuals who reported face pareidolia during the experiment, suggesting that the odor may have increased their awareness of a face in these ambiguous stimuli.

Aside these findings, a number of observations were repeatedly reported in the four studies independently; they are synthesized and briefly discussed below.

B. Other noticeable and recurrent observations: common patterns across development

1. Consistently null effects

a. No effect of feeding behavior

In our infant studies, no effects of feeding status were observed (all ts > 1.40; all ps < .18). Previous studies showed that breastfeeding had a direct influence in attachment quality (Gibbs et al., 2018) and in the processing of emotional social stimuli (fearful faces, Jessen, 2020; eyes, Krol et al., 2015a, body expression, 2015b), effects which were linked to the fact that breastfeeding practice is associated with a longer time with the mother (Smith and Forrester, 2017). Yet the length of breastfeeding exposure was not shown to draw particular effect from learning an odorant associated with this reinforcing experience (Delaunay-El Allam et al., 2010) and other studies have reported a null effect of feeding status in preferential looking time during face perception tasks (Durand et al., 2020, 2013). In sum, breastfeeding may bear an emotional quality that does not modulate every aspect of visual processing: further investigations are needed to delineate the impact of feeding behavior on olfactory-visual integration for effective perception.

b. No effect of sex

While a female processing advantage has been reported on several occasions for visual (Lübke et al., 2012; Proverbio et al., 2008) or olfactory stimuli (Koelega and Köster, 1974; Pause et al., 2010), no sex effect was found across the four studies presented here (all *t*s < 1.5; all *p*s > .15). It has been suggested that the female advantage in olfactory perception would come from verbal abilities, which could explain the difference obtained in previous studies, where explicit tasks and odor diffusions were used, compared to our implicit paradigm requiring no verbal representation.

c. The general visual response is immune to changes in odor or category

Across all four studies, no odor effect was found on the general visual response (6 or 12 Hz and harmonics), nor a difference across odor and visual conditions (see below for a comparison between the 3 infant studies). This confirms that the general visual response is dissociated from the category-selective response despite being elicited simultaneously by the same stream of periodic visual stimulation. While responses to the behavioral task in adults also reveal the absence of difference across conditions, this corroborates the fact that both infants and adults paid similar attention to all conditions and that the presentation of odors does not elicit a general effect (i.e., arousal or attention) on the visual responses.

One may have noticed that the amplitude of the 6 Hz response is not identical across the three studies of chapter one, in particular that it seems diminished in Study 3 (mO: 3.5 ± 0.5 µV) vs. in Study 1 and 2 (mO: 4.6 ± 0.5 vs. 4.7 ± 0.6 µV respectively). Albeit non-significant (Anova run with mO averaged across odor conditions, compared between studies: $F < 1.5$, $p = 0.25$), this difference may be caused by different control objects added to the base object stimuli in Study 3 (i.e., 2 to 3 exemplars of each common objects from which a facelike was perceivable at 1 Hz) which had been left identical between Study 1 and 2.

2. The general visual response differs between infants and adults

A second observation can be reported on the general visual response: the response recorded in adults is lower than in infants. It seems reasonable to speculate that (neural) anatomical development is mainly responsible for this difference. Indeed, a first parameter to account for this difference is intrinsic to infant EEG signal. The infants' skulls take times to form especially on the fontanel, a soft spot on the top of the head which closes on average around 14 months (Duc and Largo, 1986) and the background EEG natural activity is of higher amplitude in infants than adults (Bell and Wolfe, 2008) which altogether result in a larger electrical activity recorded by the electrodes. In addition, the adult study uses a 12 Hz base stimulation frequency, and by reducing the duration of all stimuli, thus the interval between two images, it induces a greater proportion of processing overlap manifested by a reduced neural activation. As an illustration, in Rekow et al. (in preparation, Appendix 5: Complementary study), the mean general visual response recorded from sequences presented at 6 Hz is of 3.34 ± 0.57 µV, whereas it is reduced to 1.5 ± 0.36 µV at 12 Hz reflecting that the amplitude of the mean general response decreases as stimulation frequency increases.

3. Hemispheric asymmetry in the odor effect

When an odor effect was found, it was repeatedly observed in the form of a positive odor effect over the right hemisphere. This increase in the neural activation was associated with a nonsignificant decrease of the response over the left hemisphere in infants (Study 1: faces and 3: facelike objects), and in adults while no positive effect over the right hemisphere was observed for the same visual category (Study 4: faces). As measures were obtained in scalp EEG with limited electrode density (i.e., 30 and 64 channels in infants and adults, respectively) capturing only the current spreading over the surface of the scalp, we can only venture about the potential underlying structures and the following hypotheses are thus speculative.

The face network dominantly recruits right-lateralized areas, but bilateral structures contribute to the face response. More precisely, in the architecture of the ventral occipital-temporal cortex (VOTC), the largest part dedicated to face processing belongs to the right hemisphere (Grill-Spector et al., 2017; Grill-Spector and Weiner, 2014). As hemispheric asymmetries (right or left-lateralized) were reported in a number of face perception abilities, models tend to assign different functions to each hemisphere. For instance, the ability to process faces as a whole, namely, holistic processing, refers to the spatial arrangement between face parts and is generally attributed to the right hemisphere (Campbell et al., 1986; Haxby et al., 2000), whereas the left hemisphere would be recruited to process more feature-based aspects of the face (e.g., eyes or mouth, Hillger and Koenig, 1991). Thus, considering that we repeatedly found (body/maternal) odor effects over rOT, we hereby suggest that body odor tunes the detection of facial attributes, e.g., the spatial arrangement between facial features, resulting in a greater categorization response. While the cause of the right hemispheric dominance for face perception is still debated and usually linked to the development of reading abilities (Behrmann and Plaut, 2020) but brings forth inconsistent results (see section II. A. 2.), we propose that a multisensory approach needs to be considered to further investigate (and maybe resolve) this question. Admittedly, as what we measure in this set of experiments is the odor influence *on the* *visual neural response*, it may be that odor reinforces a preexisting right hemispheric dominance in the visual response to faces.

In addition, olfactory processing has rarely been described in terms of hemispheric dominance, yet asymmetries were repeatedly observed (Brand et al., 2001; Royet, 2004 for reviews), notably the right hemisphere would be more involved than the left hemisphere in the recognition of the odor source. This particular aspect might be a key element in understanding such olfactory-visual integrations, and should be precisely addressed in future studies, notably to precisely uncover cortical activations.

C. Odor is most effective for challenging visual inputs

Following the inverse effectiveness rule of multisensory integration (IER; Stein and Meredith, 1993), which describes that the effectiveness of multisensory integration depends on how informative each sensory input is by itself, we had hypothesized that the odor effect would be particularly observed when visual processing appears challenging, i.e., when the sole visual input is hard to interpret by itself. This was mostly expected as a general phenomenon in infancy considering that the visual system is largely immature before the first birthday.

Accordingly, in Study 3, we revealed that the maternal odor initiated the categorization as the odor effect is particularly significant in infants who did not present with a significant response in the baseline condition ($Z < 1.64$, $p > .05$). This was further supported by a negative correlation (Figure VI-1A) showing a linear relation between the strength of the baseline response and the strength of the odor effect, as predicted by the IER. Interestingly, by conducting retrospectively the same analysis on the data of Study 1 using human faces, we find a similar significant effect for the 3 electrodes of the ROI separately (all ps $< .01$) and pooled together ($p < .001$) (Figure VI-1B), showing that the strength of the odor effect is predicted by the strength of the sole visual response. It thus strongly suggests that even in the case of genuine human faces, the multisensory integration manifests as a function of unisensory performance. This contributes to the understanding of how knowledge might be acquired in early visual development, i.e., by stemming from multisensory information. To further confirm the mechanisms at stake, the preliminary results of a fifth study are briefly presented below to explore this general facilitative effect of odors in the development of face categorization, with the underlying prediction that the influence of maternal odor decreases as the visual system develops, i.e., as a function of age (see section VIII. A).

To go further, the correlation was also performed in the adult study exploring the body odor effect in the case of the facelike categorization response. In this case of ambiguous facelike objects, the correlation shows a significant negative relation between the response in the baseline odor context and the body odor effect ($p = .006$; Figure VI-1C), which constitutes evidence that

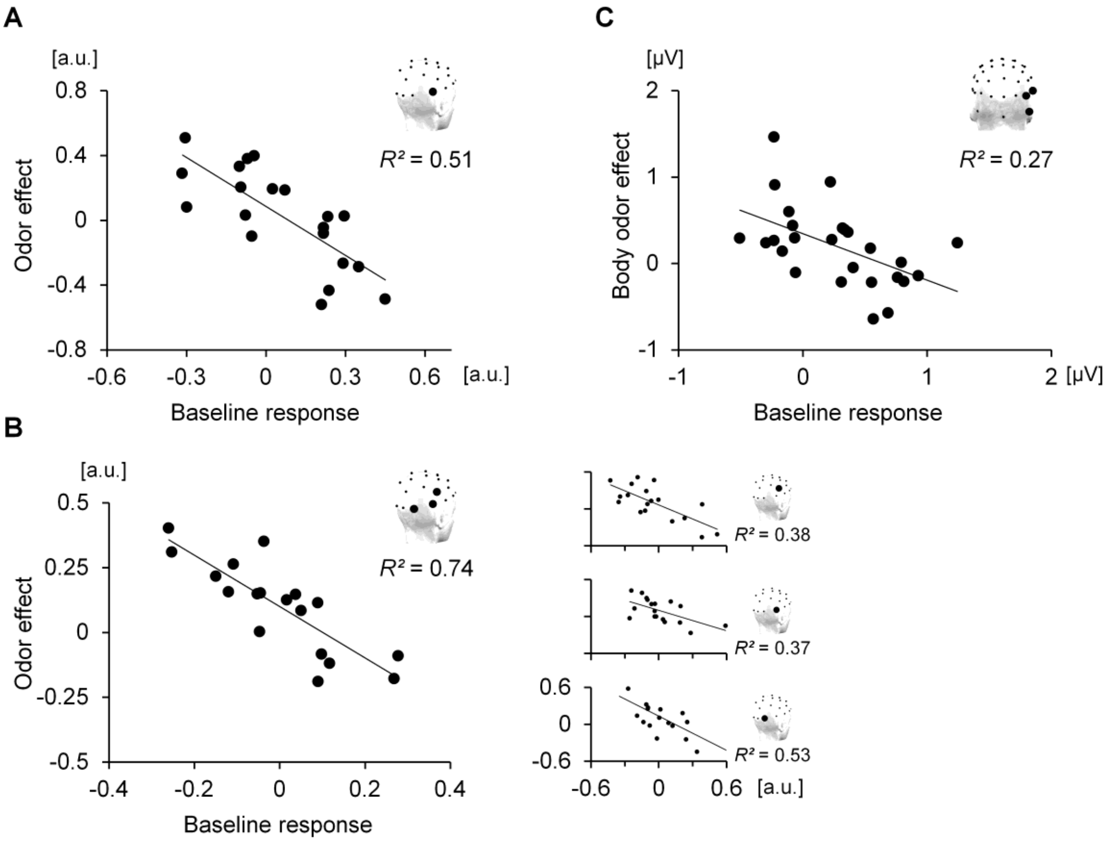


Figure VI-1. The inverse effectiveness across studies. Negative correlations computed on normalized amplitude for the *N* = 20 infants from Study 3 **(A)** and *N* = 18 infants from Study 1 **(B)**, and on the baseline corrected amplitudes of the *N* = 26 adults from Study 4 **(C)**. All correlations are significant and illustrates that the individuals with the lowest baseline responses (in the control odor condition) benefit the most from the odor effect (maternal or body – baseline).

the effect is not confined to early stages of visual development but can be found in the mature visual system as well. Altogether, these complementary analyses add evidence to a line of studies in animal as well as human models (Helfer, 1998; Holmes, 2009, 2007; Meredith and Stein, 1983; Stein et al., 1988; Stevenson et al., 2012; Stevenson and James, 2009), mostly conducted in audio-visual integration for their accurate temporal synchrony. We thus demonstrate that the IER of multisensory integration can also occur with contextual olfactory stimulation.

In the following paragraphs, we will relate our findings to existing models of multisensory perception and neural integration. The present set of studies had focused on body-odor-driven influences on face categorization, which will thus be more thoroughly discussed, keeping in mind that the subtending mechanisms probably reflect more general principles.

VII. Continuing our multisensory journey

A. Why and how odors influence visual categorization

1. An exclusive intersensory selectivity

a. Social congruency

Across our studies, we observed body odor effects selectively on the category-selective response, and only in the case of the congruent visual category, namely for faces and facelike objects. This supports the idea that such intersensory associations are not incidental and that body odor does not promote the detection of any periodic visual category on the basis of its regularity. In fact, while this appears rather intuitive, it had not been previously addressed.

This intersensory association is in line with principles of intersensory congruency, the idea that information channeled by different senses are combined if they complete one another (Bahrick and Lickliter, 2012; Ernst and Bülthoff, 2004). Interestingly, no inhibitory effect was found (e.g., impaired cars categorization with body odors), which is probably harder to measure in our design presenting streams of stimuli (i.e., the body odor is not more incongruent with cars than with any stimulus of the sequence) and is in line with the absence of incongruence measured if multisensory processing is unattended (Busse et al., 2005). The evocative power of body odors, i.e., how they can inform about conspecifics and the high attraction towards faces appear at the core of our work. Both types of stimuli being highly relevant from the first stages of development, and as they relate to the presence of conspecifics (Reynolds and Roth, 2018; Schaal et al., 2020), the body odor selectively associating with face categories suggests that congruency is at least partly responsible for intersensory associations.

Indeed, in addition to genuine human faces, we further reveal that body odors also exert a facilitating effect on the categorization of facelike objects, an ensemble of common objects sharing the property of depicting an illusory face. We speculate that the social dimension borne by body odors, a species-related social chemosignal, strongly contributes to face pareidolia in these objects. This is corroborated by a recent study showing that face pareidolia particularly follows adaptation to social qualities (e.g., gaze direction), supporting the high social value projected to the face despite its inanimate source (Palmer and Clifford, 2020).

We show that simultaneous inputs from different sensory modalities are processed together already from early infancy, supporting the idea that knowledge is partly acquired from multisensory stimulations. The intersensory redundancy hypothesis (IRH) more precisely defines the best co-occurrence as emerging from *amodal* properties of objects, which infants would be able to detect at a very young age (Bahrick and Lickliter, 2000). As stated earlier in the introduction, the current definition of IRH seems to exclude olfactory inputs as they can hardly relate to amodal properties as those are currently defined (e.g., rhythm, rate duration, temporal synchrony). Hence, the semantic (i.e., congruency) as well as the physical characteristics of both, visual and olfactory, stimulations may very well take integral part in this phenomenon of IRH.

b. Leaving the social nest

In fact, the idea that body odor associates with facelike objects – to help categorizing them from the face pattern they depict – suggests that the intersensory congruency goes beyond genuine human face as a stimulus. The face pareidolia phenomenon stems in high-level representation of a facial configuration from a nonface stimulus (Omer et al., 2019). Hence, the interpretation of the body odor effect in terms of stimulus-driven attributes of genuine human faces (i.e., bottom-up) can be discarded thanks to this observation.

While faces and body odors were chosen due to their ecological relevance to conveniently allow comparison across ages using the same type of stimuli, we suspect similar effects to be observable outside the social sphere. Faces are arguably one of the most salient visual objects in humans, yet their importance lies in the quality we project more than the visual properties of this category: they are said to be special in *degree*, not in *kind* (Farah et al., 1998). A number of evidence found nonsocial intersensory associations between olfactory and visual stimulation at different levels highlighting differences related to projected importance linked with individual experiences. Odors are able to modulate our behaviors: for instance, mint tea is preferred by adult individuals exposed to it during childhood (Poncelet et al., 2010) and chamomile-scented objects are more manipulated by toddlers following reinforcing experience with chamomile at birth (Delaunay-El Allam et al., 2010). In addition, olfaction is more broadly able to modulate visual perception, including food perception (Mas et al., 2019; Seigneuric et al., 2010), binocular rivalry (Zhou et al., 2010), or color perception (Demattè et al., 2006). These effects were overall mostly described in adults and usually imply to measure the effect on a behavioral output, but it may function similarly in infancy, since nonsocial odors (e.g., strawberry) are able to orient towards faces bearing congruent qualities (e.g., happy expression, Godard et al., 2016). However these effects might be harder to measure on nonsocial visual responses in infancy, as infants are arguably more exposed to social than nonsocial visual cues.

2. A state of preparedness

The selectivity of body odors with faces may derive from the concurring exposure to these two stimuli, which together with the high ecological relevance of both inputs, lead to a strong and reinforced associative learning.

The olfactory system is not reputed for its conscious and explicit manifestation, although it is consensually admitted that it plays a fundamental role in alerting to environment hazards (Herrick, 1933). This alert function has been linked to visible fight/flight responses but is also suggested to contribute to a state of preparedness to respond to related stimuli. Evidence suggests that human chemosignals, for their ecological relevance, possess this kind of potency.

For instance, stress odors would prepare to respond to corresponding harm-related stimuli (de Groot et al., 2012; de Groot and Smeets, 2017; Mutic et al., 2016) and it may be extended to emotionally-neutral body odors, which also seem to promote socially-inclined responses (Camps et al., 2014; Cecchetto et al., 2019; Mutic et al., 2019). In fact, several known intersensory effects can be related to this phenomenon, mostly in the audio-visual integration. For instance, control of the context exerted by one of the senses can drive facilitation effect (Nickerson, 1973), suppression (Colavita, 1974) or changes in perceived quality (McGurk and MacDonald, 1976). This appears in line with compensatory effects from the haptic modality following a spontaneous and transient visual deprivation (Ernst and Banks, 2002). Going one step further, Lakatos et al. (2009) have shown that increased attention can come from the saliency of an input from one sensory modality, even when volitional attention is focused on another modality. This saliency results in a privileged processing of this particular sensory modality that shapes other sensory responses. Saliency thus dynamically determines the *leading sense*: a sensory dominance which is inherent to the situation and temporarily creates a neurophysiological context across modalities. In our work, the contextual presentation of body odor from the beginning of the visual stimulation along with their inherent ecological relevance may induce a specific saliency of olfactory cues leading to a privileged processing of social visual stimuli.

3. Acquired co-occurrence: cognitive and neural reinforcement

The ecological relevance of body odors and faces may contribute to an initial preferred attention towards both types of stimuli, so that exposure to them is optimal, and in the following stages of knowledge acquisition, associative learning may explain the retention and reinforcement of the importance of body odors and faces in our environment. They share a social dimension that the infant retrieves from accumulated experience with their caregivers with whom exposure generally equals to interaction. This learned congruency could become intrinsic to the co-occurrence of these stimuli and a diagnostic cue leading to their spontaneous association. In this specific case, maternal odor could be a particular proxy in promoting associative learning in the social realm. Indeed, maternal odor is a powerful cue allowing transnatal transference and benefiting from numerous positive reinforcement especially during the first year (in care, feeding behaviors, arousal; Schaal et al., 2020). From then, the developing individual gradually expands its social relations with variations in quality and number (Rennels and Davis, 2008), yet the co-occurrence with chemosignals is maintained; and children (e.g., Weisfeld et al., 2003) as well as adults (e.g., Lübke and Pause, 2015) are still sensitive to those cues (see de Groot et al., 2017; and Schaal et al., 2020 for recent reviews).

From a neurophysiological point of view, this is in line with different views of developmental neuroscience mechanisms where experience selectively shapes the genetically defined neural framework, partly constraining the connectivity between functional areas. The extensive co-occurrence of these two types of stimuli, channeled by distinct sensory modalities, could manifest in a reinforced connectivity between the areas dedicated to each processing (Bressler and Menon, 2010; Mahon and Caramazza, 2011). In his model of neuronal group selection, Edelman (1993) describes three influences shaping this pre-determined framework. Particularly, *reentrant signaling* is a dynamic process which reinforces connections between groups of neurons in a bidirectional and recursive fashion (i.e., only coexposure defines reinforcement, without notion of the quality/effectiveness of the signal). This neural reinforcement responds to spatiotemporal continuity so that after numerous encounters with one stimulus, particular patterns of groups of neurons are selected. Relating to our findings, the repeated prior exposures to concurrent body odors and faces could thus strengthen connectivity between neural pathways dedicated to each stimulus by reentrant signaling, so that one sensory input would be able to cross-modally activate the brain regions which process the other input.

4. Odors may help create categories

An alternative and non-exclusive interpretation could explain how body odor influences the visual categorization of faces. Having associated body odors and faces together yields a particularly positive outcome which is to extend the diagnostic cues in the identification of an object (i.e., one stimulus become part of the representation of the other). In categorization, adding a cue congruent to the target exemplars may promote disambiguation as the additional cue helps the recognition of the object at the exemplar level. On the one hand, it could heighten the discrimination between the target exemplar and the base objects because it is congruent only with the target: it has not been associated with the other stimuli and no (neural) reinforcement has been experienced. On the other hand, if each of the target exemplar is given a cue selective to the category and which is shared across all the exemplars of this category; it fosters a better generalization across these exemplars and favors the categorization response.

Using the FPVS-EEG approach might be especially sensitive in measuring this, considering the neural categorization response is yielded from a *contrast* between base and target stimuli. A better identification of the target leads to a higher categorization response, but the reverse is also true: a better identification of the base stimuli may also lead to a higher categorization response. These two processes appear mutually inclusive but are not equivalent. For instance, categorization of human faces among monkey faces does not yield the same result as monkey faces among human faces in infants (Peykarjou et al., 2017), an asymmetrical pattern which was similarly found for face-sex categorization in adults (Rekow et al., 2020a).

Moreover, preferential processing induced by the intersensory association could increase the selectivity of the neural categorization response. In other words, as the congruency is not the only shared cue (among the various target exemplars), but that incongruence is also shared among the base stimuli, it may thus serve both at (1) increasing similarity across the target exemplars (all congruent with the odor) and across the base stimuli (all incongruent with the odor) separately, and (2) increasing the difference between target and base stimuli (only the target exemplars are congruent). In this way, intersensory association reinforces the category inclusion as well as the category exclusion. This may be particularly relevant with olfactory stimulation presented as a context. Admittedly, this concurring effect is not specific to olfactory stimulation and could as well have been observed by using a contextual (congruent) auditory stimulation.

For now, we have proposed that body odors associate with faces because they are semantically-related and share congruency as they both evoke the presence of individuals (genuine, or illusory). This quality appears as the result of initial ecological relevance and accumulated experience that gradually shape neural responses across development. Yet it seems to remain dynamic and flexible to maintain an adaptive value. We will next consider the predictive value of intersensory co-occurrences in a larger extent.

B. Giving meaning to our senses

1. Looking back at past experiences…

a. Have a guess!

How can we relate our observations with theoretical considerations on perception and multisensory integration? "Perceptions are largely based on the past": this quote from Gregory (1997) serves as a reminder to our definition of perception. We proposed that perception was a dynamic filter bridging the gap between the outside (sensory inputs) and our cognition (representations) and allowing us to act/react/interact with our environment. To that end, it deeply relies on prior knowledge to attribute meaning to what we currently experience, i.e., prior experiences shape our present representation. Because sensory inputs are not sufficient by themselves for an accurate perception of our surroundings, perception corresponds to an interpretative mechanism (Ernst and Bülthoff, 2004; Gregory, 1997).

It has been formulated that this prior knowledge would manifest in the form of multiple hypotheses upon the world via top-down streams (Ullman, 1995) and facilitating object recognition (Bar, 2003). Bar's model states that top-down inferences elicited by poorly informative inputs orient towards possible candidates for visual object recognition. For instance, inputs from images in low spatial frequency project from the primary visual cortex to the orbitofrontal cortex (OFC; Barbas, 1995) where this insufficient information elicits probable and multiple hypotheses, or "initial guesses" stemmed from stored representation (Tanaka, 1996). Whatever the initial efficiency of these "guesses", information strikes back to visual cortices, particularly in the inferior temporal cortex where object recognition occurs (e.g., VOTC in the case of visual inputs, see Figure I-1B), and bottom up inputs are integrated with these top-down streams and simultaneously explore alternatives to yield the most probable response (Bar, 2003; Ullman, 1995). Along the same line, building upon illusory perception, Gregory (1997) suggested that perceptions are *hypotheses* that we make and are confirmed or infirmed by subsequent processing coming from the continuous flow of sensory information, hence not in a domain-specific manner.

b. A sensory overlap?

Interestingly, the OFC, where top-down inferences are proposed to arise (Bar, 2003), is one of the primary recipients of olfactory inputs (see section I. B.). This area is not considered part of the visual cortex, and it has notably been linked to the facilitation of danger processing (Carretié et al., 2005) which is again tempting to link to olfaction, especially the alert function (Herrick, 1933). Activations in the OFC were also related to the building of expectations (Elliott et al., 2000; Petrides et al., 2002), and since easily performed recognition recruit less the OFC than challenging initial inputs (Bar et al., 2006, 2001), it emphasizes the existence of a balance between interpretative and stimulus-driven responses. While the theoretical framework of this model received experimental evidence, it was only tested with unisensory – visual – inputs. Since top-down streams take root in stored representations (may it be another way of describing "prior knowledge"), could it involve multisensory priming?

Recent work corroborates the idea underlining this hypothesis, in favor of neural structures shared across the senses. Indeed, several studies have gathered evidence towards a multisensory scaffolding of the sensory cortices over the last couple decades, proposing that even typically unisensory cortices could process multisensory inputs and multisensory integration would occur from the earliest stages of neural activation (Schroeder and Foxe, 2005). In addition, distinct "unisensory" brain regions dedicated to the same semantic domain would be highly connected (Mahon and Caramazza, 2011), so that, for instance, implicit categorization spontaneously occurs at such abstract level that it can be retrieved immediately and independently of the nature of the input (picture or word describing the picture, Brady and Oliva, 2008). In line with this, it was recently evidenced that person-identity recognition reliably occurred crossmodally from face or name information, i.e., by presenting target and deviant identities either by their face, their name or an alternation of the two (Volfart et al., 2020). Moreover, using intracranial recording, authors also evidenced that while some populations of neurons were selectively responding to face or names, some were exclusively active during the crossmodal stimulation, bringing compelling argument for the involvement of multimodal regions in categorization, here with the representation of persons. Interestingly, a recent string of research suggested that the VOTC, a category-selective cortical area highly documented for its role in visual categorization (Grill-Spector and Weiner, 2014), also responded in the case of more abstract representations (e.g., Peelen and Downing, 2017). Going further, a recent study revealed that the development of categorical representation of the VOTC was not exclusively stemmed from visual experience (Mattioni et al., 2020). Indeed, by investigating category-selective responses from sounds in sighted and congenital blind individuals, but also from images in sighted people, authors revealed that the organization of the VOTC was very similar between auditory and visual information, with a functional topography that remained consistent even in blind individuals whose VOTC never fed from feed-forward visual inputs. These findings raise a load of interesting questions, for instance, it feels reasonable to speculate that other senses as well may play their part in this scaffolding, and that other sensory cortices might reflect equivalent crossmodal tuning. Finally, it is tempting to relate these pieces of evidence to our data, particularly the ones obtained in infants whose neural structures continue to mature. Considering that typically-visual regions are still poorly tuned by sole visual inputs during the first months of life, olfactory processing could constitute an (maybe one of many) upstream of the visual system.

Whether there actually is an overlap between olfactory processing and top-down inferences in the OFC, or not, the model of Bar (2003) could partly account for a heightened categorization response tuned by odors as relevant chemosignals such as (maternal) body odor easily constitutes a stored knowledge linked with person-related representation. Alternatively, but not exclusively, with a major contribution of the VOTC in category-selective response, olfactory-visual integration could also occur in these regions, especially that odor processing alone was related to activation of the visual cortex (Djordjevic et al., 2005; Gottfried et al., 2004; Royet et al., 2001, 1999; Zatorre et al., 2000), suggesting a fine meshing between these senses. While these relations are highly speculative as it stands, it seems henceforth highly relevant to consider multimodal channels in category-selective representations to better approximate the reality of how our brain categorizes unisensory inputs. Especially, these observations altogether suggest a form of neural plasticity in the way we are able to receive and process information from our surroundings.

2. … to predict our future sensory experience

Thanks to stored representations accumulated from past experiences, we may also be able to place bets on what will occur in the future. Creating representation to simplify our world is meant for us to rely on them and limit the cognitive cost (with the best tradeoff in speed and efficiency) so that a certain signal could predict another.

Categorization was described as one of these convenient tools, especially elicited to predict objects (Barsalou, 1990), i.e., suggested as a form of prior knowledge as it organizes relations between objects or concepts in a dynamic and thus manipulable fashion. Categorization is hence able to create expectancies which translates into predictability (e.g., predictable locations in scenes; Kaiser et al., 2020) by making neural "guesses" more probable in the same way as context, which is able to prime object identification (Kaiser et al., 2019, 2014; Kveraga et al., 2007; Oliva and Torralba, 2007; Quek and Peelen, 2020). Along this line, it has been suggested that face detection in infants was helped by contextual visual information as measured in eye-tracking using naturalistic scenes (e.g., a photograph depicting an individual in a room) where all the stereotypical information of the usual context is available and supposed to help detection of the face in this complex display (Kelly et al., 2019). This relates to our studies were (maternal) body odor also strongly help the categorization of faces and facelike objects in young infants, while face perception in naturalistic settings is still hard at this age (Frank et al., 2009; Kelly et al., 2019). The odor could thus predict the appearance of a face.

But are young infants already able to predict their environment? Although 4 months of age may appear young to have gained sufficient experience and built fine representation, especially with a slowly developing visual system, it is shown that infants are able to perform statistical inferences of their own actions and physical environment from early on, and to adjust these representations. This perspective, called *predictive processing*, relies on the very basic principle that any organism has to generate predictions on its own motor outcomes (Helmholtz, 1866). By analogy, it was further applied to higher cognitive functions and a recent line of studies provided evidence for infant neural ability to form prediction from prior knowledge (Emberson et al., 2015; Kayhan et al., 2019b, 2019c, 2019a; Kouider et al., 2015; Köster et al., 2020 for review). It appears somehow related to the action-perception loop proposed by Ernst & Bülthoff (2004), whereby mental representations are adjusted from experience and projected through Bayesian filter to predict our perceptions modulated by sensory inputs. Although these authors did not consider the developmental standpoint, the theoretical basis of this model may stem from similar considerations of the predictive processing principle and more generally Bayesian inferences applied to cognitive abilities, recently gaining interest in infant research (Gopnik and Bonawitz, 2015; Rao et al., 2007).

VIII. Perspectives

A. How does the odor effect evolve over the first year?

One of the main questions that may come to mind is: what does happen to the olfactory-visual integration between early infancy and adulthood? Based on the elements we have observed, and considering that 1) the visual system rapidly matures from 4 months onwards (Braddick and Atkinson, 2011); 2) face perception refines and develops dramatically over the first year (Pascalis et al., 2020); 3) changes in motor development allow the infant to become physically more independent (Leppänen and Nelson, 2012) and finally that 4) the physiological changes associated with recent birth and breastfeeding (e.g., Jacob et al., 2004) progressively fade; we predict that maternal odor will gradually loose its facilitating effect to categorize faces, which could be already visible over the first year. One way to examine this is to test infants over a large age range and observe the odor effect on face categorization as a function of age.

Preliminary data from infants ranging from 4- to 12.5-month-olds (*N* = 38; ongoing) are presented below (Figure VIII-1A). This study has been designed to be exactly identical to Study 1 (Leleu et al., 2020) in terms of olfactory stimuli collection and presentation, design of the study, duration of trials, experimental procedure and preprocessing of EEG data. Preliminary analyses were run on the ROIs a priori defined in Study 1. The face-selective response is expected over left and right occipital temporal ROI (lOT, rOT) comprising CP5/6, P7/8 and O1/2, respectively. The odor effect is particularly expected over the right occipital electrode O2, as previously observed; but is also expected to diminish as a function of age.

Evolution of the face categorization response. Considering the development of the visual system and the growing experience with faces and objects, we expect that the face-selective response will change 1) quantitatively, translating into a strong difference between the youngest and oldest infant tested in terms of amplitude and proportion of individual significance and 2) qualitatively, with an increasing number of harmonics (which gives an indication of the complexity of the neural response) to be considered in the response, following Lochy et al.'s (2019a) observation in preschoolers where the number of harmonics is higher than in infants but lower than in adults. For 1), we created three age groups from the preliminary sample of *N* = 38 infants, resulting in ten 4-to-6.5, eleven 7-to-9 and twelve 9.5-to-12.5-month-olds. The face-selective response (collapsed across odor contexts, same scale across age groups) shows a strong increase with age and the right dominance of the response is more visible in the oldest group (Figure VIII-1B).

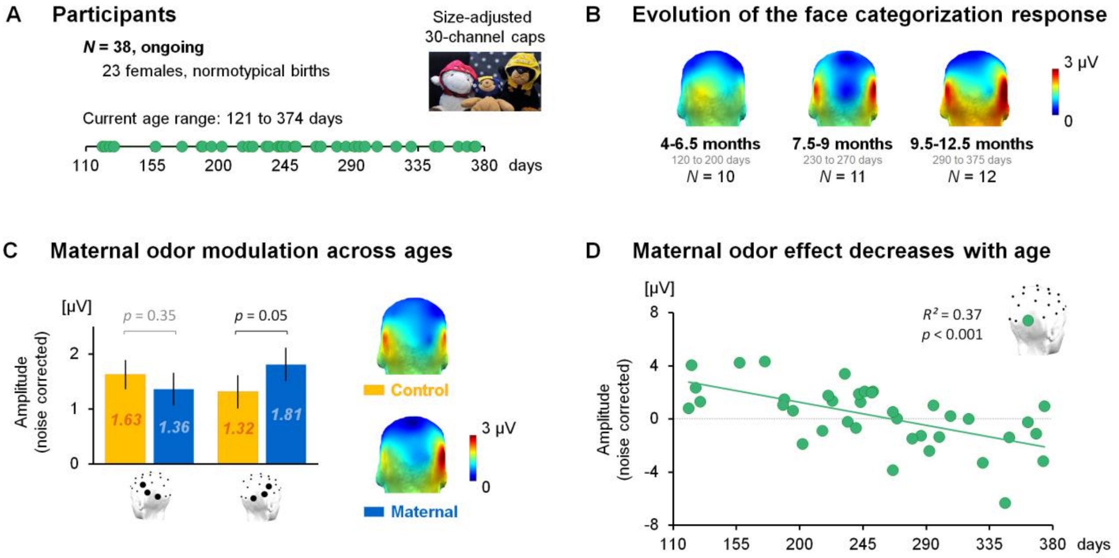


Figure VIII-1. Preliminary evidence for a diminished influence of maternal odor between 4 and 12.5 months old. A. Participant information and repartition of the infants by age. Recruitment aims to equalize the number of infants over the age range. EEG recording was made using the same EEG system and electrode organization than in Study 1 (Leleu et al., 2020), using adapted head-caps for each age. **B.** The face categorization response increases with age. Groups were created (equalized across number of infant and age range) for illustration purposes only. **C.** The maternal odor overall induces a stronger response over the right hemisphere for the face-selective response while a trend of reduced activation is observed over the left hemisphere. **D.** By plotting individual differences of the odor effect (maternal – control) as a function of age, a negative correlation is found over the right occipital electrode O2, defined a priori from Study 1 (Leleu et al., 2020). Error bars represent standard errors of the mean.

Apparent decrease of maternal odor effect as age increases. While infants and toddlers rapidly gain face perception abilities, an odor effect might still be overall observed over the right hemisphere, because the face response is not "adult-like" yet and the maturation of the visual system is still not achieved by the end of the first year. The response from each odor context is compared in each lateral ROI for the face-selective response across ages. It shows that the positive odor effect observed in Study 1 in 4-month-olds seem to remain present over rOT along with a slight non-significant reduction over lOT (Figure VIII-1C) which may create a right hemispheric dominance in the maternal odor context, as realiably observed in our different studies (see section VI. C.). More specifically, we particularly expect a progressive decline of the maternal odor effect over the most sensitive area found in 4-month-olds, the right occipital electrode O2. Plotting individual odor effects as a function of age, we reveal a strong decrease of the odor effect strength with age over this site (Pearson correlation, Figure VIII-1D). While the odor effect seems to be overall maintained, this decline could suggest a refinement of the face categorization response and a still very selective association between the mother's familiar odor and the perception of faces in 12-month-old infants, more confined to typical rOT face-selective areas (less middle occipital than for younger infants).

These preliminary data show promising results to describe the olfactory-visual association at stake during early development. Future studies will be needed to complete this investigation, and potentially highlight sensitive periods of development where olfactory cues are specifically inclined to promote visual categorization.

B. Has maternal body odor a genuine status for promoting generic face categorization?

Due to (obvious) age-related constraints and to ensure a good SNR while optimizing testing duration, the infant studies were conducted only with 2 conditions. In each study, the contrast has been focused on the olfactory conditions (maternal odor vs. baseline) alternating on the same visual stimulation (i.e., one condition per study: either face, car or facelike categorization). As a result, we did not introduce a non-human odorant as it was the case in Study 4 with adults (i.e., gasoline) as the control odor (from the t-shirt) represented the baseline response. This gives directions for future investigations.

Indeed, the mother's odor is a very rich olfactory cue with many facets. Literature evidenced comparable or dissociated effects between the infant own mother's odor and a stranger mother's odor (Durand et al., 2020; Jessen, 2020, respectively). While keeping in mind that these effects were observed on face individuation and facial expression recognition, respectively, and not face categorization, however, we do not know whether the identity, motherhood, humankind or sensory qualities are necessary, or if one of those might be sufficient to elicit "the" maternal odor effect. In other words, while the individual quality of the odor was tested in the aforementioned studies by comparing familiar vs. unfamiliar maternal odor, the same effect may as well have been yielded from for instance, the father's (familiar, non-female, non-mother), or another human's odor (non-familiar, non-mother). Future studies are thus needed to further delineate whether what we measured at a neural level is preserved across these different types of olfactory cues.

Although the intersensory associations evidenced along this work probably reflects a general effect of multisensory integration, an additional question could be addressed to further delineate the maternal odor effect. Is maternal odor effective only on faces or all social stimuli? We tested faces and facelike objects as "social" stimuli because they depicted faces, at the core of human interindividual interactions. Our interpretation is thus somehow limited to maternal odor promoting the processing of face patterns in 4-month-old infants. We have no direct evidence for comparable effects of maternal odor on other "social" categories. As future studies should definitively address this issue, it may be hypothesized that equivalent effects could be found for other social associations using nonface human stimuli: whole bodies or body parts for instance. Indeed, body parts are categorized specifically in adults (Jacques et al., 2016a) and hands particularly channel infants' attention more than faces after the second half of the first year (Fausey et al., 2016). In a complementary way, whole bodies represent a social cue recently gaining a lot of interest due to a privileged processing (Peelen and Downing, 2007) especially when presented in dyads, which represent interactive entities and are processed as a unitary visual object (Abassi and Papeo, 2020).

Finally, while olfaction possesses a special status in early infancy (early functionality, benefits from associative learning and body odor is particularly reinforced by feeding behavior in the first months), similar effects of context priming can be hypothesized for another type of stimuli, also already present as early as in utero: human voices. In addition, recent evidence challenge the presumed visual dominance of our perception (Barnhart et al., 2018; Hörberg et al., 2020; Hutmacher, 2019; see Appendix 1), which appears particularly relevant to consider during the first year of life.

C. Could body odors promote face perception in individuals suffering from neurodevelopmental disorders?

Olfaction possesses particularities in terms of diffusion and persistence (see **Box 1**), relationship to emotional processing and feeling (e.g., emotional contagion; Hatfield et al., 1993), and memory (Bensafi et al., 2002; Olofsson et al., 2020), which are corroborated by an emerging interest in unraveling the mysteries of this powerful channel. As a consequence, the sense of smell has recently been proposed to be the focus of future studies investigating socio-cognitive impairment in Autism Spectrum Disorder (ASD; Barros and Soares, 2020), and such issues could be easily extended to other neurodevelopmental disorders such as the 22q11.2 deletion syndrome (22q11.2DS) for instance.

Indeed, ASD and 22q11.2DS are both characterized by difficulties in social communication and interactions, and deteriorated socio-emotional behaviors (American Psychiatric Association, 2013; Jansen et al., 2007). Notably, deficits in face perception are consensually reported, whether they affect spontaneous face bias (Chawarska et al., 2013; Riby et al., 2012; Riby and Hancock, 2009), individuation and identity recognition (Tang et al., 2015 for review), or facial expression discrimination (e.g., Baron-Cohen et al., 1993; Leleu et al., 2019, 2016) to name a few. Regarding the sense of smell, without surprise, very little is known in these populations. Nevertheless, a few studies have ventured along this axis and revealed somehow impressive intersensory integrations. For instance, one study explored the effect of odor familiarization on food preferences in ASD children and revealed that children were more prone to pick the food odorized with the familiarized vs. a control neutral odor, highlighting a strong influence of odors in ASD individuals (Luisier et al., 2018). In another set of studies, social imitation was promoted by the presence of a familiar odor (the mother’s odor) in ASD children (Parma et al., 2014, 2013). Overall, these studies offer interesting observations and suggest that at least ASD individuals are sensitive to environmental odors that may be used to guide them towards specific items in order to compensate part of their deficits.

Although ASD children do not appear to suffer from an impaired generic face categorization (e.g., 8-12 years old, Vettori et al., 2019), it was not tested at younger ages. Our work can constitute a reference for what can be expected in normotypical development, particularly based on the fifth and last study briefly introduced above. Especially considering that a reduced face bias is observed as early as at 6 month-old in ASD infants (Chawarska et al., 2013), it could be that reinforcing the tuning of the neural processing of faces with odors may help to limit the later onset of symptoms. Besides, as body odors are strong informative cues (Lübke and Pause, 2015; Schaal et al., 2020) able to modulate face perception (de Groot et al., 2017) and of which ASD individuals appear sensitive to (Bogdashina, 2016), these reflections offer promising perspectives in neuropsychology with potential outcomes in remediation programs with a relatively poor cost because olfactory stimulation/modulation need not language and can be implemented in many populations (infants, individuals intellectually impaired or delayed, etc.).

IX. General conclusion

This thesis examined the role of body odor in the development of visual face categorization. To that extent, scalp electroencephalograms were recorded during a fast periodic visual stimulation (FPVS-EEG) while infants were exposed to the maternal vs. a control odor, and adults to body, gasoline or baseline odors. In periodic streams of natural images (6 Hz or 12 Hz, i.e., 6 or 12 stimuli per second, respectively), pictures of faces (Study 1 & 4), cars (Study 2 & 4) and nonface objects resembling faces (i.e., facelike stimuli; Study 3 & 4) were interspersed every 6th (Study 1 to 3) or 9th (Study 4) stimulus among other nonface objects, thus tagged at 1 Hz or 1.33 Hz respectively. In infants, the maternal odor effects were found for face and facelike objects but not for cars, while in adults, only body odor enhanced the visual categorization response, solely to the hard-to-get category, namely, facelike objects. We thus provide strong evidence for the tuning of face(like) categorization from congruent multisensory inputs, particularly in the developing brain and in adults for stimuli appearing ambiguous. It supports the view that from earliest ages, perception is based on the integration of information across the senses, tuning efficient category acquisition. Specifically, it shows that early-maturing systems such as olfaction can actively drive the acquisition of categories in later-developing systems such as vision, and still assist the mature visual system when the input is difficult to interpret.

This represents a fruitful and novel axis of research, leaving outstanding questions only waiting to be addressed. We have paved the way to further explore how multisensory inputs including the sense of smell drive category acquisition in the developing human brain. It carries considerable implications for our understanding of healthy as well as atypical perceptual development. The approach particularly appears as a precious tool in this endeavour and is able to provide insights on the semantic representation of objects as suggested in a recent study investigating semantic memory in normal aging (Milton et al., 2020). There is little doubt about the fruitful implementations which can be derived from the present work, declining studies along varied populations and intersensory associations.

Résumé de thèse

X. Résumé de thèse

Quand notre nez connait ce que l’on voit.

Développement multisensoriel de la catégorisation visuelle : démonstration au niveau cérébral par la catégorisation des visages induite par l’odeur

A. Introduction

Nous évoluons dans un monde riche d’informations sensorielles et il est essentiel que nous apprenions rapidement à comprendre ce qui le constitue et à distinguer ce qui est pertinent dans notre environnement. La perception est une fonction cognitive active qui nous permet d’intégrer les informations issues de nos différents sens en même temps (Gibson, 1966; Stein and Meredith, 1993) et ainsi identifier les objets pertinents pour une situation donnée. Grace à cela, nous nous plaçons dans le monde qui nous entoure, puisque notre perception nous permet d'agir, de réagir et d'interagir avec lui. Pour organiser ce monde et simplifier son appréhension, à l'échelle de l'objet particulièrement, la perception opère selon un principe de catégorisation (Barsalou, 1990; Rosch, 1978). Chaque objet perçu est automatiquement catégorisé (i.e., associé à une certaine catégorie représentée en mémoire), c’est-à-dire qu’il est différencié des autres objets qui l’entourent, et en même temps, associé à une représentation existante, permettant de produire rapidement une réponse envers cet objet même s’il est entièrement nouveau.

Plusieurs courants ont tenté de modéliser le fonctionnement de la perception. Ce travail s'inscrit dans une approche empirique de la perception, c'est-à-dire que nous considérons que nos interprétations sont guidées par des connaissances déjà acquises (Ernst and Bülthoff, 2004; Gregory, 1997). De plus, les objets n'apparaissent pas isolés dans notre environnement. De ce fait, l'information contextuelle constitue une aide supplémentaire et complémentaire pour guider notre perception (Lakatos et al., 2009; Oliva and Torralba, 2007). D'ailleurs, le lien entre l'objet et son environnement peut être partie intégrante de sa représentation, si bien que les informations contextuelles peuvent avoir une valeur prédictive : de l'organisation structurelle d'une scène visuelle découlent des attentes sur le positionnement absolu des objets dans l’espace et relatif entre les différents objets présents (Chun, 2000). Par exemple, une chaise est attendue « devant » la table et « sur » le sol, à l’inverse, un avion est généralement vu dans le ciel, c’est-à-dire dans la partie supérieure du champ visuel (Kaiser et al., 2019). Ces relations, décrites ici à l’aide d’exemples visuels, existent également pour les autres sens et pourraient déclencher des réponses privilégiées en présence d’informations associées, comme par exemple sentir l’odeur d’aliment peut influencer la manière dont on explore des scènes comprenant des aliments (Seigneuric et al., 2010). Nous proposons que les odeurs, qui sont rarement incluses dans les études sur la perception multisensorielle, constituent une source d'information contextuelle forte et importante dans certaines situations.

Développement perceptif.

Au début de la vie, tous les sens ne sont pas égaux face à un environnement d’une grande complexité. Dans le cas du nourrisson, le développement sensoriel de l'olfaction la place dans une position particulière et privilégiée par rapport à la vision (Schaal and Durand, 2012). La vision et l'olfaction possèdent chacune leurs spécificités anatomiques et fonctionnent différemment. Ces deux sens se mettent en place au cours de l'embryogénèse (1er trimestre de gestation), mais ne se développent pas à la même vitesse. En effet, alors que la maturation anatomique et fonctionnelle de l'olfaction est déjà observable au 3ème trimestre de gestation (Sarnat, 1978), permettant au fœtus une exposition soutenue aux molécules chimiques odorantes (Schaeffer, 1910), le système visuel doit au contraire limiter toute stimulation au risque d'une exposition délétère au bon développement de ce système immature (Graven and Browne, 2008). Ainsi, de grandes étapes du développement visuel sont acquises seulement quelques mois après la naissance (e.g., la vision en couleur apparaît à partir de 3 mois, Maurer and Lewis, 2001) alors que le nouveau-né a déjà été exposé depuis plusieurs mois à des stimulations olfactives qu’il est capable de reconnaitre après la naissance (e.g., Schaal et al., 2000).

La question de savoir quand le nourrisson devient capable d'intégrer les informations issues des différents sens a été l'objet de nombreux débats. En effet, une vue constructiviste (Piaget, 1952) propose que le fait de se représenter l'unité des objets perçus simultanément par différents sens nécessite une certaine maturation cognitive et résulte de l'apprentissage de l'objet par modalité isolée dans un premier temps. A l'inverse, une vue dite de différentiation (Gibson, 1969), postule que le nourrisson perçoit avant tout l'unité de l'objet grâce à la congruence des informations entre les sens et qu'il apprend progressivement à distinguer les différentes informations disponibles à chaque sens pour se représenter des relations sensorielles plus précises. Dans cette perspective, il est proposé que la redondance intersensorielle, c'est à dire, la présentation coordonnée spatialement et co-occurrente de la même information à travers plusieurs modalités sensorielles, guide l'attention du nourrisson et facilite l'apprentissage en optimisant la réponse à des informations spécifiques d'une modalité sensorielle donnée (Bahrick and Lickliter, 2012; Lewkowicz, 2010; Lickliter and Hellewell, 1992).

D’autres principes, notamment plusieurs principes généraux d'intégration multisensorielle, permettent de compléter ces approches déjà utiles pour comprendre le développement de la perception (Stein and Meredith, 1993). En particulier, le principe d'efficience inverse postule que l'intégration multisensorielle est à son maximum quand une modalité sensorielle n'est que peu efficace par elle-même.

Enclins à percevoir nos congénères

Il est indispensable à toute espèce du règne animal d'être capable d'identifier et d'être reconnue par les autres êtes vivants, alliés ou ennemis, pour garantir la survie (Snyder-Mackler et al., 2020). Dans le cas des espèces sociales, c'est une habilité d'autant plus fondamentale, garantissant le maintien de la cohésion sociale et du bien-être individuel (Holt-Lunstad et al., 2010). Chez l'humain, nous présentons ci-après deux modes de communication et de recueil d'information de nos congénères : la catégorisation visuelle des visages et l'utilisation de chimiosignaux par le biais de l’odeur corporelle.

La communication chimique humaine est révélée par l'exposition aux odeurs corporelles qui se trouve capable de modifier nos comportements, notre perception et d'autres activités cognitives. La catégorisation générique des visages correspond quant à elle à la réponse visuelle sélective à l’objet "visage", c'est à dire qu'elle n'est obtenue pour aucun autre objet visuel et qu'elle se généralise entre les différents exemplaires de visages en dépit de leur variabilité. Elle est un prérequis aux autres catégorisations qu’il est possible d’effectuer à partir d’un visage comme celles du genre, de l'ethnicité, de l’âge, etc.

La catégorisation des visages.

Les visages humains bénéficient d'un traitement privilégié par rapport à d'autres catégories visuelles car ils sont mieux perçus que les autres objets dans des ensembles d'images (Hershler and Hochstein, 2005) et déclenchent des saccades oculaires plus rapides (Fletcher-Watson et al., 2008). L'attraction des visages dans une scène visuelle, extrêmement rapide, semble automatique et irrépressible puisqu’elle est obtenue même lorsque la consigne est de détecter l’apparition d’un autre objet (Crouzet et al., 2010). Si l'activité cognitive est complexe, percevoir un visage peut se produire en présence de stimuli extrêmement basiques, comme des figures bicolores de Mooney (Mooney, 1957). Cette habilité témoigne d'une catégorisation opérant sur une grande variété de stimuli, même non faciaux, comme dans le cas de la paréidolie faciale, c'est à dire le fait de percevoir un visage dans un objet commun (voir les études 3 et 4 et la **Box 2** pour des exemples illustrés).

Dans une certaine mesure, cet avantage pour les visages est présent déjà dès la naissance, puisque les nourrissons s'orientent préférentiellement vers des stimuli ayant une configuration canonique d'un visage dès les premières heures de vie (Johnson et al., 1991). Cependant, lorsque les stimuli sont plus réalistes et les conditions de détection plus écologiques, la tâche paraît plus difficile (DeNicola et al., 2013; Frank et al., 2009) et ce n'est qu'à partir de 6 mois que le nourrisson détecte efficacement les visages en explorant des scènes naturelles (Kelly et al., 2019; Leppänen, 2016).

Au niveau cérébral.

Chez l'adulte, la réponse de catégorisation obtenue en électroencéphalographie (EEG, plus particulièrement avec une approche dite de présentation visuelle périodique rapide ou FPVS-EEG ; voir la méthodologie générale) se manifeste par une activation occipito-temporale bilatérale à dominance droite (Rossion et al., 2015) et est mesurée même en l'absence d'attention explicitement orientée vers les visages (Quek et al., 2018b). Elle a également été mesurée chez l'enfant d'âge préscolaire, où elle prend la forme d'une activation tout à fait bilatérale sur les régions occipito-temporales (Lochy et al., 2019a). A l'inverse, chez le nourrisson de 4 à 6 mois, la réponse de catégorisation visuelle des visages apparaît largement dominante dans l'hémisphère droit (de Heering and Rossion, 2015). Ces réponses mesurées à la surface du crâne sont liées à des activations de la partie ventrale du cortex occipito-temporal (VOTC) (Grill-Spector and Weiner, 2014), pour lequel de nombreuses études convergent sur une latéralisation hémisphérique chez l'adulte (dominance à droite) à travers différentes techniques de mesures (Sergent et al., 1992; pour une revue, Grill-Spector et al., 2017). Toutefois, l'origine de cette latéralisation, liée ou non au développement plus tardif d'autres fonctions cognitives comme l'acquisition de la lecture, est aujourd'hui encore largement débattue (Behrmann and Plaut, 2020 pour une discussion récente).

Les odeurs corporelles.

Contrairement à l'étude de la perception visuelle de nos congénères, l'intérêt scientifique pour la communication sociale chimiosensorielle est relativement récent. Le corps humain sécrète de nombreux signaux chimiques différents, le plus souvent odorants, qui renseignent le receveur sur l'état physiologique de l'émetteur. Nous nous intéresserons exclusivement aux odeurs corporelles provenant de la sueur axillaire, inodore lorsqu'elle n'a pas encore été dégradée par les bactéries résidentes du microbiome de la peau (James et al., 2013). La qualité perçue de la sueur (ci-après "odeur corporelle") est modulée par les variations physiologiques du corps (e.g., variations hormonales) ou des facteurs externes (e.g., alimentaires) pour chaque individu au cours du temps, mais chaque individu possède une forme d'empreinte olfactive unique (Havlícek et al., 2017).

Du fait de la précocité fonctionnelle de notre système olfactif, le nouveau-né prématuré montre déjà des réactions aux odorants à partir de 30 semaines de gestation (Sarnat, 1978). Dans les premiers mois de la vie, l'odeur corporelle, en particulier celle de la mère qui inclut de nombreux indices olfactifs surajoutés (colostrum/lait, odeur du sein), tient une place importance et est particulièrement saillante pour le nourrisson (Doucet et al., 2007; Porter et al., 1991; Schaal, 2010). Le nourrisson apparaît pré-équipé pour détecter et réagir à ces stimulations olfactives dès le début de la vie, notamment les indices chimiques de ses parents qui apparaissent comme vecteur des relations interindividuelles précoces (Schaal et al., 2020). Une fois adultes, nous sommes toujours sensibles aux odeurs de nos proches (Lundström et al., 2009), mais aussi à notre propre odeur (Platek et al., 2001) et à celle d'étrangers (de Groot et al., 2017). Il a récemment été montré que nous sommes particulièrement enclin à s'auto-sentir, en particulier après une interaction avec un autre individu (e.g., propension à se sentir la main après une poignée de mains avec un inconnu, Frumin et al., 2015). Par ailleurs, les odeurs corporelles entreraient en jeu dans la reproduction en orientant vers des partenaires potentiels et modulant le système endocrinien des femmes exposées (Lübke and Pause, 2015). Des informations comme la personnalité (Sorokowska et al., 2012), le stress (Dalton et al., 2013), l'état de santé (Sarolidou et al., 2020), sont véhiculées par les sécrétions axillaires et perçues par les individus, influençant parfois très fortement les interactions sociales qui en découlent (de Groot et al., 2017; Schaal et al., 2020 pour revues). S'il est vrai que la plupart de ces effets sont ténus, leur observation systématique suggère une réelle implication dans le tissage et le maintien de nos liens sociaux au cours de la vie.

Au niveau cérébral.

En ce qui concerne les structures cérébrales sous-jacentes au traitement des odeurs de nos congénères, plusieurs études s'accordent sur des activations impliquant les gyri occipital et angulaire et le cortex cingulaire antérieur et postérieur (Lundström et al., 2009, 2008; Mujica-Parodi et al., 2009; Prehn-Kristensen et al., 2009; Zhou and Chen, 2008; pour une revue, voir Parma et al., 2017). En particulier, il est suggéré que l'activation dans la région occipitale, qui abrite le cortex visuel primaire, servirait d'amorce et préparerait le système visuel à répondre à la vue d'une personne (Haxby et al., 2002; Lübke and Pause, 2015; Lundström and Olsson, 2010). Les autres régions mentionnées ont été également observées en réponse au traitement de stimuli suggérant la présence de congénères : perception du corps (Seghier, 2013), stimuli émotionnels (Cato et al., 2004; Maddock, 1999).

Les odeurs corporelles peuvent-elles aider à catégoriser les visages ?

A ce jour, le nombre d'études ayant exploré la perception des visages en contexte d'odeur corporelle est restreint. Il a été illustré que des odeurs corporelles contextuelles perçues de manière passive et implicite contribuent à notre expérience visuelle puisqu'elles influencent nos réponses (comportementale et neurales) de reconnaissance des visages (Cecchetto et al., 2020). D'autres études se sont plus spécifiquement intéressées à la perception des expressions faciales, en utilisant en particulier des odeurs de stress, c'est-à-dire des odeurs corporelles qui avaient été collectées alors que les donneurs vivaient un évènement particulièrement stressant (e.g., premier saut en parachute ou examen de fin d'étude). Ces odeurs de stress, présentées explicitement ou implicitement, s'avèrent capables d'influencer la perception des expressions faciales, soit en facilitant la reconnaissance de certaines émotions négatives (Mujica-Parodi et al., 2009; Rubin et al., 2012; Wudarczyk et al., 2016; Zhou and Chen, 2009), soit en entravant celle d'émotions positives (Pause et al., 2004; Zernecke et al., 2011). Par ailleurs, ces effets ont particulièrement été observés dans les cas où l'information visuelle était ambigüe, par exemple lorsque l'expression faciale est peu intense (Rubin et al., 2012; Zernecke et al., 2011; Zhou and Chen, 2009).

Chez le nourrisson, à ce jour, seules trois études ont exploré l'influence d'odeurs corporelles sur la perception des visages en utilisant des odeurs maternelles. Il a ainsi été montré qu'à 4 mois, la préférence pour un visage (présenté en paire avec une voiture) était fortement accentuée si le nourrisson était simultanément exposé à l'odeur de sa mère (Durand et al., 2013). Par ailleurs, au même âge, le temps de regard porté au visage d'une étrangère (présenté en paire avec le visage de la mère) est réduit lorsque l'on présente au nourrisson l'odeur de sa mère ou l'odeur d'une autre mère (Durand et al., 2020). Plus tard, chez le nourrisson de 7 mois, l'odeur de la mère réduit la réponse cérébrale aux visages de peur sans moduler la réponse pour les visages joyeux, alors que l'odeur d'une autre mère est sans effet (Jessen, 2020).

Dans l'ensemble, ces études suggèrent que l'odeur corporelle (maternelle) joue un rôle dans le comportement social du nourrisson en orientant son regard vers les informations congruentes avec l'odeur, et qu'elle structure la cognition visuelle mesurée sur des tâches de discrimination et au niveau cérébral. Il est également clair que la présence de l'odeur corporelle influence la perception des visages chez l'adulte. Il est à noter qu'aucune des études proposées ci-dessus ne s'est intéressée à la catégorisation des visages à proprement parler, ni à comment l'odeur corporelle, congruente avec la présence de visages dans l'environnement visuel, pouvait moduler ces réponses, ce à quoi nous proposons de nous intéresser.

Nous avons vu que notre perception, multisensorielle, s'appuie principalement sur la catégorisation puisqu'elle nous permet de répondre de manière identique à des stimuli similaires, bien que variables, afin de faciliter notre compréhension de l'environnement. En étudiant le développement de nos systèmes sensoriels, nous avons par ailleurs vu que l'olfaction est fonctionnelle plus précocement que la vision, ce qui lui donne une place de choix pour assister le développement de la perception visuelle. De plus, nous avons montré que l'odeur corporelle tout comme le visage, est un signal important pour percevoir nos congénères dès le début de la vie. L'association intersensorielle de l'odeur corporelle et des visages n'a que peu été étudiée jusqu'alors, mais les études permettent déjà de montrer que l'odeur corporelle est capable d'influencer la perception d'indices faciaux (de Groot et al., 2017), et même d'orienter le regard du nourrisson vers le visage par la congruence de l'association intersensorielle (Durand et al., 2013). Cependant, il reste à déterminer si l'odeur aide à catégoriser les visages et dans quelles circonstances.

Hypothèses et prédictions.

Etant donné que les odeurs apportent de nombreuses informations que nous sommes capables de détecter, nous faisons l'hypothèse que les odeurs contribuent activement à traiter les informations visuelles congruentes. Cette hypothèse sera testée au cours de 4 études visant à illustrer cette association olfacto-visuelle par l'intégration des odeurs corporelles et de la catégorisation des visages.

L'importance écologique des visages et des odeurs corporelles, qui se traduit en une allocation attentionnelle accrue au niveau comportemental, est reflétée par l'activation d'aires cérébrales dédiées. De ce fait, puisque ces indices co-occurrent également dans les interactions quotidiennes, ils bénéficient d'un apprentissage associatif qui renforce leur congruence biologique. En conséquence, nous prédisons que (1) l'influence de l'odeur corporelle est sélective à la perception des congénères. En présentant l'odeur sous forme de contexte, elle constituerait une amorce à d'autres indices sensoriels liés à la présence d'une personne (Durand et al., 2013). De même, aucun effet de l'odeur corporelle n'est attendu pour des objets qui ne représentent pas des visages, mais aussi, une odeur non humaine n'influencera pas la catégorisation des visages.

De plus, il a été montré que les odeurs congruentes modifient la perception des visages particulièrement lorsque l'information est ambigüe, en accord avec un mécanisme multisensoriel compensateur si l'un des sens ne permet pas une saisie d'information suffisante (principe d'efficience inverse cité plus haut). Ainsi, nous prédisons également que (2) l'odeur facilite la perception quand l'information visuelle seule ne permet pas une catégorisation optimale. Cette prédiction sera testée à l'aide de deux cas : lorsque le système visuel est encore immature (chez le nourrisson), et lorsque le système visuel est mature (chez l'adulte) mais que les informations sont difficiles à interpréter et résultent en une catégorisation ambigüe.

Les quatre expériences seront regroupées ainsi (Figure X-1, conditions expérimentales) :

Chapitre 1. Au cours du développement précoce, alors que la vision n'est pas encore mature et que l'odeur corporelle est un indice particulièrement saillant qui module les comportements du nourrisson, l'odeur maternelle pourrait favoriser sélectivement la catégorisation des visages. Cela sera testé dans une première série d'études. En vue de déterminer la sélectivité de l'odeur maternelle, trois groupes de nourrissons de 4 mois seront testés, chacun avec une catégorie visuelle différente (étude 1 à 3).

Chapitre 2. Avec la maturation du système visuel et l'expérience visuelle associée, la catégorisation visuelle est plus efficace sans l'ajout d'autres informations sensorielles. Il est donc attendu que l'odeur perdra son effet facilitateur, sauf dans le cas où l'information visuelle est ambigüe. Cette hypothèse sera testée au cours d'une 4ème étude : une expérience conduite chez l'adulte permettra de vérifier que l'effet de l'odeur corporelle est obtenu seulement lorsque l'information est congruente et seulement en cas d'ambiguïté du stimulus.

Méthodologie générale.

L'ensemble des études présentées utilise une approche d'étiquetage fréquentiel en EEG qui quantifie directement des marqueurs robustes et fiables d'une perception rapide dans le cerveau humain. Cette approche est particulièrement adaptée pour l'étude de la catégorisation au niveau cérébral, ayant été récemment adaptée en stimulation visuelle périodique rapide (FPVS-EEG). Elle repose sur la synchronisation du système cérébral à la périodicité de la stimulation sensorielle. En étiquetant **deux réponses cérébrales dissociées à deux fréquences distinctes** au sein d'une même séquence de stimulation, il est possible de mesurer une réponse sélective à une catégorie cible (Figure X-1, paradigme). En effet, d'une part, les stimuli sont présentés rapidement à une fréquence de base **F** (6 ou 12 Hz) à laquelle est mesurée une réponse reflétant la synchronisation du cerveau à tous les indices visuels qui oscillent à cette fréquence, c'est-à-dire une **(1) réponse visuelle générale** au flux rapide d'images. En insérant une catégorie cible tous les **n** stimuli (tous les 6 ou 9), une **(2) réponse sélective de catégorisation** est

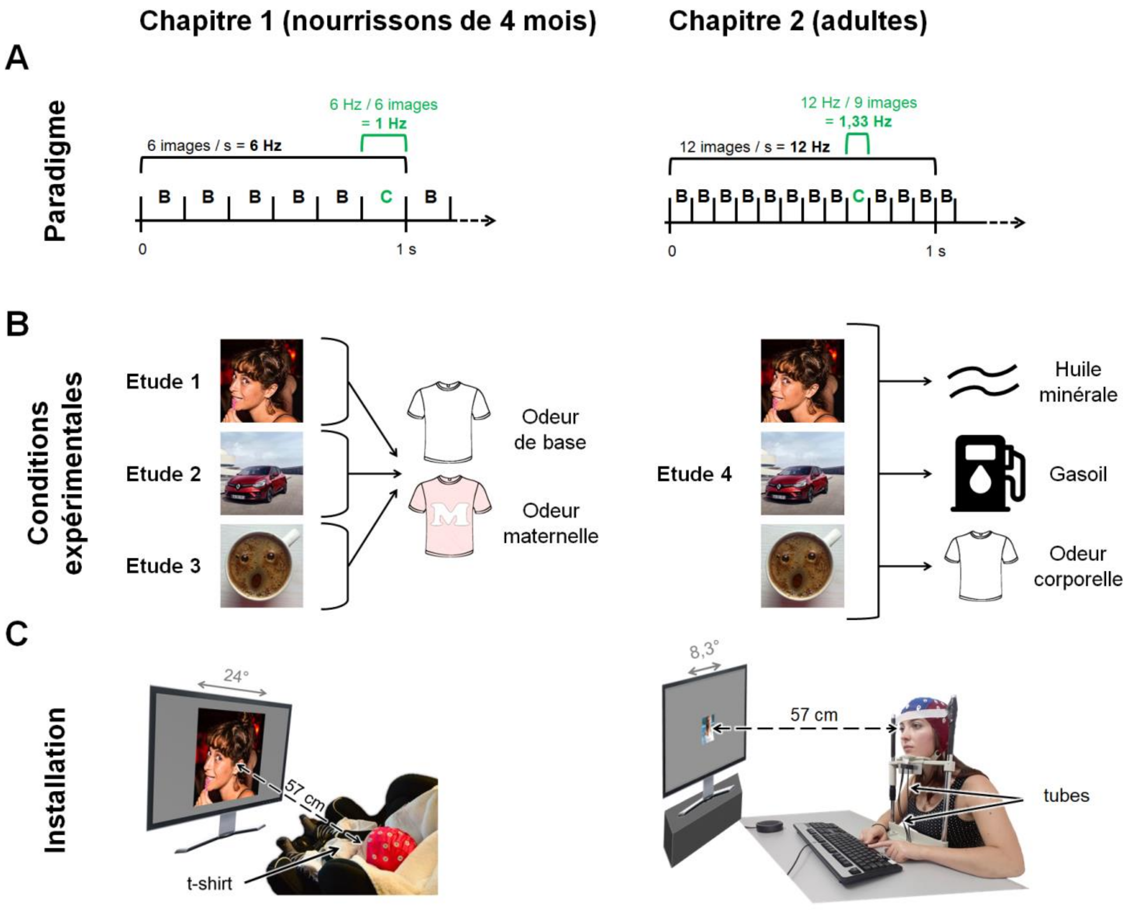


Figure X-1. Synthèse de la méthodologie des quatre études présentées. Paradigme (A), conditions expérimentales (B) et installation avec mode de diffusion des odeurs (C) pour les études chez le nourrisson (gauche, études 1 à 3) et l'adulte (droite, étude 4). Chez le nourrisson, la catégorisation des visages (étude 1), des voitures (étude 2) et des paréidolies (étude 3) ont été testés en contexte olfactif de base vs. maternel présenté à l'aide de t-shirts pour chacune des études dans des séquences visuelles présentant les images à 6 Hz, et la catégorie cible à 1 Hz. Chez l'adulte, ces trois mêmes catégories ont été testées à l'aide de séquences à 12 Hz avec la catégorie à 1,33 Hz chez le même groupe de participants en alternant trois contextes olfactifs (huile minérale, gasoil, odeur corporelle) présentés implicitement à l'aide de tubes dissimulés dans la mentonnière.

observable dans le spectre EEG à la fréquence **F/n** (1 Hz ou 1,33 Hz, respectivement) et reflète une catégorisation riche, impliquant la discrimination des stimuli cibles et des stimuli présentés à la fréquence de base et la généralisation de cette discrimination aux nombreux stimuli utilisés pour la catégorie cible.

En utilisant cette approche en FPVS-EEG, les odeurs étaient présentées sous la forme de contextes olfactifs, diffusées en continu au cours de la stimulation visuelle (i.e., une odeur par séquence de stimulation), maintenant ainsi une forme d'exposition écologique induite par la stabilité de la stimulation olfactive (Figure X-1, installation).

B. Chapitre 1 : Délimiter l'influence des odeurs maternelles sur la catégorisation visuelle chez le nourrisson

Pour mettre en évidence un effet de congruence des odeurs sur la catégorisation visuelle, une manière consiste à tester une catégorie visuelle importante, pour laquelle un effet est particulièrement attendu. Si en effet, une modulation par l'odeur est observée, la sélectivité de l'association devrait être confirmée ultérieurement par le test d'une nouvelle association olfacto-visuelle, non congruente cette fois, pour confirmer un effet nul de non-congruence. De plus, pour approfondir davantage à quel point et dans quelles circonstances les associations intersensorielles congruentes aident la cognition visuelle du nourrisson, une troisième catégorie visuelle, idéalement d'une importance équivalente à la première mais surajoutée d'une difficulté rendant sa perception moins évidente, pourrait être testée.

Dans ce premier chapitre, nous nous intéresserons à l'effet de l'odeur maternelle sur la catégorisation des visages (étude 1), d'un autre objet non facial (des voitures, étude 2) et de visages illusoires (paréidolies faciales, étude 3) chez le nourrisson de 4 mois. Il est montré qu'à cet âge, la perception des visages s'améliore grandement (Pascalis et al., 2011), tout comme l'attention visuelle volontaire (Bronson, 1994). Notre travail s'inspire particulièrement de deux études : la mesure de catégorisation des visages au niveau cérébral (à travers l'approche FPVS-EEG) chez des nourrissons de 4 à 6 mois (de Heering and Rossion, 2015), et le renforcement de la préférence pour les visages (par mesure du comportement visuel) dans un contexte d'odeur maternelle à 4 mois (Durand et al., 2013). **Nous avons émis l'hypothèse qu'au niveau cérébral, l'odeur maternelle influencera la réponse cérébrale de catégorisation des visages (étude 1) mais pas des voitures (étude 2).** Cette comparaison est une étape importante pour définir la sélectivité de l'association olfacto-visuelle : elle montrerait qu'elle ne dépend pas d'un effet modulatoire général sur la physiologie du nourrisson (e.g., éveil) ou basé sur la stabilité induite par une odeur contextuelle, quelle qu'elle soit, qui pourrait améliorer la réponse envers n'importe quel stimulus visuel si tant est qu'il soit périodique (i.e., "stable").

Le mécanisme d'intégration olfacto-visuel sera enfin mis à l'épreuve en utilisant une catégorie visuelle plus difficile à isoler, les paréidolies faciales (étude 3). La paréidolie faciale s'observe à partir d'objets communs variés qui évoquent des visages mais qui n'en sont pas. Ces visages illusoires sont ainsi plus difficiles à catégoriser du fait de la variabilité des objets évoquant des visages. Leur catégorisation implique de (1) faire la différence entre le pattern du visage et la configuration canonique de l'objet-support d'une part (autrement dit de discriminer ces objets-visages des autres objets communs présentés dans la séquence), et (2) de généraliser cette discrimination entre les objets-visages malgré leur grande variabilité. Dans l'environnement, les visages sont appris grâce aux interactions sociales, où le corps, la tête et les épaules sont visibles et constituent un contexte habituel pour la présence du visage (dont une partie est préservée dans les images naturelles utilisées (tête, cou et épaules)) ; à l'inverse, les objets sources de paréidolies faciales n'ont pas d'équivalent contextuel permettant de créer un effet d'attente à la présence de visage. Par conséquent, **si l'odeur aide effectivement la catégorisation visuelle, elle pourrait être facilitatrice dans le cas de la catégorisation de paréidolies faciales (étude 3).**

1. Etude 1 : L'odeur maternelle façonne la catégorisation rapide des visages au niveau cérébral chez le nourrisson

Leleu, A.*, Rekow, D.*, Poncet, F.*, Schaal, B., Durand, K., Rossion, B., & J.-Y. Baudouin. (2020) Maternal odor shapes rapid face categorization in the infant brain. *Developmental Science*, 23 (2), e12877. doi:10.1111/desc.12877 *contributions équivalentes

Afin de réussir à interagir avec un environnement visuel riche et ambigu, notre cerveau apprend rapidement à différencier les stimuli visuels et à produire la même réponse à un sous-ensemble de ces stimuli malgré leurs différences physiques. Bien que cette fonction de catégorisation visuelle ait traditionnellement été étudiée d'un point de vue unisensoriel, son développement précoce est par essence contraint par des entrées multisensorielles. En particulier, l'olfaction, un système sensoriel à la maturation précoce, parait idéalement placé pour assister le système visuel immature du nourrisson en lui apportant stabilité et familiarité dans un environnement visuel rapidement changeant. Dans cette première étude, nous testons l'hypothèse que la catégorisation visuelle rapide des visages, des signaux visuels saillants pour le cerveau du nourrisson, est façonnée par l'odeur maternelle, une autre information humaine pertinente et amenée par le système olfactif.

Une série d'images d'objets visuels variés (vivants, manufacturés, etc.) était présentée à la fréquence de 6 Hz (i.e., 6 images par seconde) avec des visages humaines tous les 6 images (à 1 Hz). Dix-huit nourrissons de 4 mois étaient alternativement exposés à l'odeur de leur mère (par le biais d'un t-shirt porté 3 nuits), ou une odeur contrôle (un t-shirt équivalent mais non porté) tandis que nous enregistrions leur activité cérébrale en EEG (Figure IV-1). Ainsi, nous avons mesuré une signature neurale de la catégorisation des visages à 1 Hz dans le spectre fréquentiel de l'EEG (Figure IV-2) sous la forme d'une activation bilatérale des régions occipito-temporales. La réponse cérébrale obtenue dans l'hémisphère droit est augmentée significativement dans le contexte olfactif maternel (Figure IV-2 et Figure IV-3). Cet effet est observable chez une très grande majorité de nourrissons. A l'inverse, une absence de différence entre les conditions olfactives a été observée pour la réponse cérébrale suscitée à la fois par les images de visages et des autres objets (i.e., réponse visuelle générale à 6 Hz, Figure IV-4). Cette absence d'effet exclut que le contexte olfactif maternel entraine une simple augmentation d'éveil ou d'attention visuelle et suggère que l'odeur maternelle est sélectivement associée aux visages puisqu'elle ne module pas l'activité générale du cortex visuel.

Ces observations démontrent que chez le nourrisson de 4 mois, une activité neurale sélective aux visages est modulée par la présence d'une odeur corporelle (maternelle), qui assure un rôle de tuteur pour le système visuel en guidant l'acquisition d'une catégorie dans le cerveau humain en développement. Ces résultats ont des répercussions sur notre compréhension du développement de la perception humaine. Cependant, bien que l'effet d'une augmentation indifférenciée de l'attention soit écarté par un effet de l'odeur uniquement mesurée sur la réponse sélective aux visages, et non sur la réponse générale, il reste à confirmer que l'odeur, parce qu'elle est plus stable, ne facilite pas la catégorisation de n'importe quelle information visuelle périodique dans notre séquence de stimulation.

2. Etude 2 : Catégorisation au niveau cérébral d'objets et de visages chez le nourrisson et sa sensibilité à l'odeur maternelle : évidence supplémentaire du rôle de la congruence intersensorielle dans le développement perceptif

Rekow, D., Leleu, A., Poncet, F., Damon, F., Rossion, B, Durand, K., Schaal, B., & Baudouin, J.-Y. Categorization of objects and faces in the infant brain and its sensitivity to maternal odor: further evidence for the role of intersensory congruency in perceptual development. *Cognitive Development, 55C, 10093* doi: 10.1016/j.cogdev.2020.100930

Dans la première étude, nous avons montré que chez le nourrisson de 4 mois, la réponse neurale de catégorisation visuelle des visages est améliorée par la présence d'odeur maternelle concomitante, sans que la réponse générale ne soit modulée par l'odeur (Leleu et al., 2020). Afin d'explorer davantage cette association multisensorielle, nous avons testé, dans cette deuxième étude, la catégorisation de stimuli ne représentant pas des visages (des voitures) tout en maintenant l'exposition à l'odeur maternelle vs. une odeur contrôle auprès de nourrissons de 4 mois.

Nous avons mesuré l'activité cérébrale de 18 nourrissons de 4 mois en réponse à une stimulation visuelle périodique rapide intercalant des voitures (à 1 Hz) parmi d'autres objets (i.e., les mêmes que dans la première étude) dans des séquences d'images naturelles défilant à 6 Hz (Figure IV-5). La réponse sélective aux voitures a été observée à la fréquence prédéfinie de 1 Hz au niveau de la région occipitale droite, montrant qu'à cet âge, le cerveau du nourrisson est déjà capable de catégoriser des objets très variés et peu pertinents écologiquement (Figure IV-6). Cette réponse de catégorisation a été retrouvée équivalente dans les deux contextes olfactifs (avec et sans odeur maternelle, à nouveau présentés par le biais de t-shirts). L'odeur maternelle n'a donc pas modulé la réponse cérébrale de catégorisation des voitures. De la même manière, la réponse visuelle générale, commune au traitement de tous les stimuli et enregistrée à 6 Hz se trouve également insensible à l'effet de l'odeur maternelle (Figure IV-7). Pour aller plus loin, ces données ont été comparées à celles obtenues dans l'étude précédente sur le premier groupe de nourrissons de 4 mois. Cette analyse complémentaire révèle que l'effet de l'odeur dans l'hémisphère droit n'est présent que chez les nourrissons exposés à la catégorie des visages (Figure IV-8).

Ces résultats montrent tout d'abord qu'il est possible de mesurer une réponse de catégorisation visuelle en une fixation pour une autre catégorie que les visages, dès 4 mois, en utilisant des images naturelles extrêmement variées : la réponse est stable et présente chez un grand nombre de nourrissons. Ils confirment par ailleurs que le développement cognitif intègre, déjà dans ses premiers stades, des informations olfactives et visuelles congruentes.

3. Etude 3 : Comme de vrais visages : le nourrisson catégorise les visages illusoires grâce à l'odeur

Rekow, D., Baudouin, J.-Y., Poncet, F., Damon, F., Durand, K., Schaal, B., Rossion, B. & Leleu, A. Smells like real faces: Odor-driven categorization of illusory faces in the infant brain *(in revision)*

Comment le nourrisson organise-t-il la foule d'informations sensorielles qui provient de son environnement pour en créer des catégories distinctes ? Dans cette troisième étude, nous avons testé l'hypothèse qu'un autre sens que la vision joue un rôle prépondérant dans l'*initiation* de la catégorisation visuelle.

Pour ce faire, nous avons testé 20 nourrissons de 4 mois exposés à une odeur de base ou l'odeur de leur mère (par le biais de t-shirts suivant la même procédure que précédemment), tout en enregistrant leur activité EEG. Des images naturelles et variées d'objets étaient présentées à une fréquence de base de 6 Hz entrecoupées toutes les 6 images (i.e., à 1 Hz) par des objets à configuration de visage (induisant une paréidolie faciale) à partir des mêmes catégories d'objets présentés en base. En d'autres termes, les nourrissons voyaient des séries d'images présentant uniquement des objets de plusieurs catégories, et au sein de cette série, des objets évoquant des visages étaient présentés périodiquement une fois par seconde (Figure IV-9).

Dans le contexte olfactif de base, une faible réponse cérébrale de catégorisation des paréidolies est obtenue à 1 Hz dans le spectre fréquentiel de l'EEG au niveau de régions occipito-temporales droite et gauche. Lors de l'ajout de l'odeur maternelle, la réponse sélective à ces objets est amplifiée et devient latéralisée à droite (Figure IV-10 et Figure IV-11). Ceci montre que des indices non visuels qui ont été systématiquement associé à des visages humains dans l'expérience du nourrisson sont capables de moduler l'interprétation des objets ressemblant à des visages dans l'hémisphère droit, qui est dominant dans le cas de la catégorisation de vrais visages (de Heering and Rossion, 2015; Rossion et al., 2015). De plus, au niveau individuel, cette influence intersensorielle apparaît particulièrement forte lorsque le nourrisson ne présente pas de réponse significative de catégorisation des paréidolies dans le contexte olfactif de base (Figure IV-12). En d'autres termes, plus la réponse aux paréidolies est faible en contexte olfactif de base, plus l'effet de l'odeur maternelle est fort. Conformément aux précédentes observations, la réponse visuelle générale est à nouveau insensible à la variation du contexte olfactif (Figure IV-13).

Ces observations fournissent la preuve que l'apparition précoce d'une activité sélective aux visages (illusoires) peut être nourrie d'entrées multisensorielles pour le cerveau en développement. Elles suggèrent que le développement perceptif intègre des informations reçues à travers plusieurs sens pour une acquisition efficace de la catégorie. Des systèmes sensoriels au développement précoce, comme l'olfaction, peuvent ainsi déterminer l'acquisition de catégories dans des systèmes au développement plus tardif, comme la vision.

4. Passage à l'âge adulte

Ces trois premières études ont tout d'abord confirmé la capacité impressionnante du nourrisson de 4 mois pour traiter l'information rapidement (les séquences d'images à 6 Hz impliquent 167 ms de temps de fixation pour chaque stimulus) et de la catégoriser à partir de stimuli variables en termes de conditions d'exposition, angles de vue, etc. Plus important encore, nous avons pu délimiter l'influence de l'odeur maternelle sur la catégorisation visuelle. Celle-ci prend la forme d'une association intersensorielle congruente, particulièrement efficace quand l'information visuelle est difficile à interpréter. En effet, l'odeur maternelle, qui est un indice olfactif sûr et presque omniprésent dans la bulle sensorielle du jeune nourrisson au début de sa vie (Schaal and Durand, 2012), joue un rôle dans l'établissement et le maintien du lien dans les premiers mois (Schaal et al., 2020) et sur le comportement visuel du nouveau-né (Doucet et al., 2007) et du nourrisson (Durand et al., 2020, 2013).

Ces observations suggèrent un mécanisme d'intégration multisensorielle plus large, où des entrées sensorielles co-occurrentes contribuent ensemble à une représentation commune unifiée (Ernst and Bülthoff, 2004), et ne sont donc pas limitées à l'association entre des catégories sociales (faciales) et des odeurs corporelles (maternelles), utilisées ici pour leur pertinence et leur importance dans les premiers stades de développement. De plus, en montrant que l'effet de l'odeur est le plus fort lorsque la réponse initiale est la plus faible au niveau individuel, nos résultats orientent vers le mécanisme d'efficience inverse (Stein and Meredith, 1993) appliqué aux aptitudes perceptuelles, et qui est en jeu dès les premiers stades du développement cognitif (Bahrick and Lickliter, 2012; Holmes, 2007).

Cependant, étant donné que les connaissances et la capacité à percevoir les visages évoluent rapidement dans les premiers mois de vie, et que les adultes sont ensuite réputés être des « experts en visage », mais que, par ailleurs, la littérature rapporte plusieurs cas pour lesquels l'effet de l'odeur sur la perception visuelle de l'adulte est observable, **qu'en est-il de l'influence des odeurs corporelles sur la catégorisation des visages avec le développement ?**

Dans le cadre du développement cognitif à court terme, nous prédisons que l'effet de l'odeur maternelle diminuera progressivement avec 1) la maturation du système visuel (Braddick and Atkinson, 2011) et du développement des capacités liées à la perception des visages dans le domaine visuel (Pascalis et al., 2011) ; 2) le développement de la motricité qui s'accompagne d'une évolution dans le rapport à autrui (plus distancié et moins focalisé sur le visage, e.g., Fausey et al., 2016; Leppänen and Nelson, 2012) et 3) l'atténuation des modifications physiologiques caractérisant la qualité « maternelle » de l'odeur corporelle de la mère (Jacob et al., 2004). Ces éléments seront discutés davantage dans la section « perspectives » de cette thèse, illustrée par des données préliminaires de nourrissons plus âgés (de 4 à 12 mois).

Chez l'adulte, nous suggérons que les odeurs ont un effet sur la réponse visuelle à condition qu'elle ne soit pas optimale, comme par exemple lorsque la catégorie cible est ambiguë. Une proposition pour vérifier cette prédiction est présentée dans l'étude 4 qui correspond au chapitre suivant.

C. Chapitre 2 : Les odeurs continuent d'affiner la catégorisation visuelle pour le système visuel adulte

Chez l'adulte, nos connaissances scientifiques sur la catégorisation visuelle sont plus approfondies que chez le nourrisson, en particulier en ce qui concerne les mesures en FPVS-EEG. En plus des visages, les marqueurs neuraux de la catégorisation de maisons (Jacques et al., 2016a; Hagen et al., 2020), de membres du corps (Jacques et al., 2016a) et des objets induisant une paréidolie faciale (Appendix 6) ont été isolés et quantifiés.

La dernière étude présentée ci-après combine ensemble les trois études réalisées ci-dessus chez le nourrisson, avec de légères adaptations. A la place de l'odeur corporelle de la mère, la sueur axillaire d'individus non familiers a été collectée à l'aide de compresses stériles, et diffusée alternativement avec un autre odorant (du gasoil, harmonisé avec les odeurs corporelles en termes de valence hédonique et intensité) ou de l'huile minérale inodore (correspondant à la condition olfactive de base). Ces contextes olfactifs ont été associés aux trois mêmes catégories visuelles que précédemment (visages, voitures et objets ressemblant aux visages, utilisant les mêmes stimuli visuels que dans les études chez le nourrisson). **Dans quelle mesure l'odeur**

peut-elle aider à catégoriser ces objets visuels, étant donné que le système visuel adulte est extrêmement efficace ?

Malgré de bonnes performances visuelles générales, il est intéressant de noter que les adultes présentent des différences interindividuelles dans la paréidolie faciale. Cela est dû à l'ambiguïté intrinsèque de la perception des visages illusoires à partir d'objets communs qui constitue un défi pour le système visuel puisque la source de l'illusion est un objet *existant* isolément et la paréidolie faciale correspond à un biais dominant envers les visages interférant avec la perception de l'objet support. Dans cette perspective, la catégorisation de ces objets ressemblant aux visages peut être décrite comme ambigüe et peut constituer une catégorie intéressante en vue d'étudier l'effet de l'odeur chez l'adulte : la paréidolie n'est pas systématique (Zhou and Meng, 2020) même si le système visuel mature est particulière efficace.

1. Etude 4 : Sentir ce que l'on voit à peine : l'odeur assiste la catégorisation visuelle

Rekow, D., Baudouin, J.-Y., Durand, K., & Leleu, A. Smell what you hardly see: Odors assist categorization in the human visual cortex *(in preparation)*

Dans cette quatrième et dernière étude, nous avons testé si, chez l'adulte, les odeurs influençaient la catégorisation visuelle, cette capacité du cerveau à répondre rapidement et automatiquement aux informations visuelles de manière sélective à une catégorie (différentes réponses inter-catégorielles et mêmes réponses intracatégorielles) malgré des entrées sensorielles hautement variables. Il est attendu que les odeurs facilitent la réponse neurale de catégorisation pour les objets visuels congruents, et en particulier quand la catégorie visuelle est ambigüe.

Nous avons enregistré l'EEG de 26 participants tandis qu'ils réalisaient une tâche orthogonale (détection d'une croix apparaissant aléatoirement au centre de l'écran) au cours de séquences de stimulation visuelle à 12 Hz (12 images par secondes). Dans ces séquences, toutes les 9 images, des exemplaires variables de la catégorie cible (visage humain, voiture ou objet ressemblant à un visage, dans des séquences dédiées) étaient intercalés pour étiqueter une réponse sélective à la catégorie à la fréquence de 12/9 = 1,33 Hz dans le spectre fréquentiel de l'EEG. De plus, les participants étaient alternativement exposés de manière implicite à des contextes olfactifs (odeur corporelle, de gasoil ou de base à partir d'huile minérale inodore) pour toute la durée d'une séquence (Figure V-1).

Pour chaque catégorie, une réponse nette et sélective a été identifiée au niveau du cortex occipito-temporal, sous forme d'une réponse bilatérale, avec une dominance dans l'hémisphère droit. La réponse avec la plus grande amplitude a été observée pour les visages humains, et celle avec la plus faible amplitude, pour les objets ressemblant à des visages (Figure V-2). En ce qui concerne l'effet des odeurs, nous avons révélé l'effet de l'odeur corporelle sur la réponse de catégorisation des paréidolies, du fait de leur ambiguïté (i.e., perçu soit en tant qu'objet commun soit en tant que visage) au niveau de l'hémisphère droit (Figure V-3) et en particulier pour les participants ayant explicitement remarqué leur présence dans la séquence de stimulation (Figure V-4). A l'inverse, les autres odeurs n'ont pas modulé de réponses de catégorisation, et aucune odeur n'a influencé la réponse visuelle générale mesurée à 12 Hz (Figure V-5). Ces résultats témoignent d'une influence spécifique de l'odeur corporelle sur la catégorisation de stimuli congruents et dans le cas d'une perception de stimuli ambigus pour le système visuel adulte.

Ces résultats démontrent que, même chez l'adulte, le cerveau utilise activement des indices provenant des différents sens pour catégoriser immédiatement les informations visuelles, et que l'olfaction, généralement considérée comme à peine fonctionnelle chez l'humain, se trouve bien placée pour lever l'ambiguïté des informations visuelles. De plus, l'effet de l'odeur a ici été mesuré lors d'une catégorisation implicite à partir d'informations visuelles extrêmement variées et rapides, démontrant le caractère automatique et précis de cette association olfacto-visuelle.

D. Discussion

Pour rappel, nous avons souligné dans l'introduction que des interactions intersensorielles étaient observées chez l'humain. Alors que la perception des congénères est particulièrement saillante au niveau visuel par le biais des visages, comme en témoignent des réseaux neuronaux dédiés et notre propension à les détecter dès notre plus jeune âge, nous avons montré que notre sensibilité aux odeurs humaines est également importante dans nos interactions avec nos pairs, familiers ou non. Cette revue de littérature a néanmoins laissé quelques questions en suspens, notamment, en ce qui concerne les capacités d'intégrations multisensorielles incluant l'olfaction chez le nourrisson. Afin de vérifier si les odeurs contribuent à la construction des connaissances visuelles congruentes, nous avons proposé quatre expériences visant notamment à mesurer si 1) l'odeur corporelle facilite la perception des visages humains ou illusoires de manière sélective et si 2) aucun effet de l'odeur corporelle n'est obtenu pour la réponse de catégorisation des voitures et l'odeur non corporelle (gasoil) ne module pas la réponse de catégorisation des visages humains ou illusoires. De plus, en lien avec le principe d'efficience inverse, il est particulièrement attendu que 3) l'effet de l'odeur soit le plus fort quand la réponse visuelle n'est pas à son maximum, c'est à dire dans le cas d'une catégorisation difficile à cause de l'immaturité du système visuel ou de l'ambiguïté des stimuli.

Synthèse des résultats principaux

En utilisant une approche FPVS-EEG, nous avons testé la catégorisation de visages, de voitures et d'objet ressemblant à un visage insérés périodiquement au sein de séquences d'images variées, en utilisant le même matériel visuel chez le nourrisson et l'adulte. Des odeurs contextuelles étaient présentées en même temps que la stimulation visuelle, permettant d'exposer les nourrissons à une odeur de base ou l'odeur de mère par le biais d'un t-shirt porté la nuit (études 1 à 3, chapitre 1), et de diffuser implicitement des odorants (odeur corporelle, gasoil ou odeur de base) à des participants adultes à l'aide d'un système de diffusion d'air (étude 4, chapitre 2).

Dans le chapitre 1, nous avons illustré la sélectivité de l'odeur maternelle pour les visages chez le nourrisson de 4 mois, sous la forme d'une forte amplification de la réponse cérébrale au niveau de l'hémisphère droit. A l'inverse, alors qu'une réponse significative de catégorisation des voitures a pu être isolée, l'odeur maternelle n'a pas eu d'effet sur cette réponse. Par contre, nous avons révélé un effet facilitateur de l'odeur en réponse aux paréidolies faciales à nouveau dans l'hémisphère droit. Cet effet est caractérisé par une activation cérébrale strictement latéralisée à

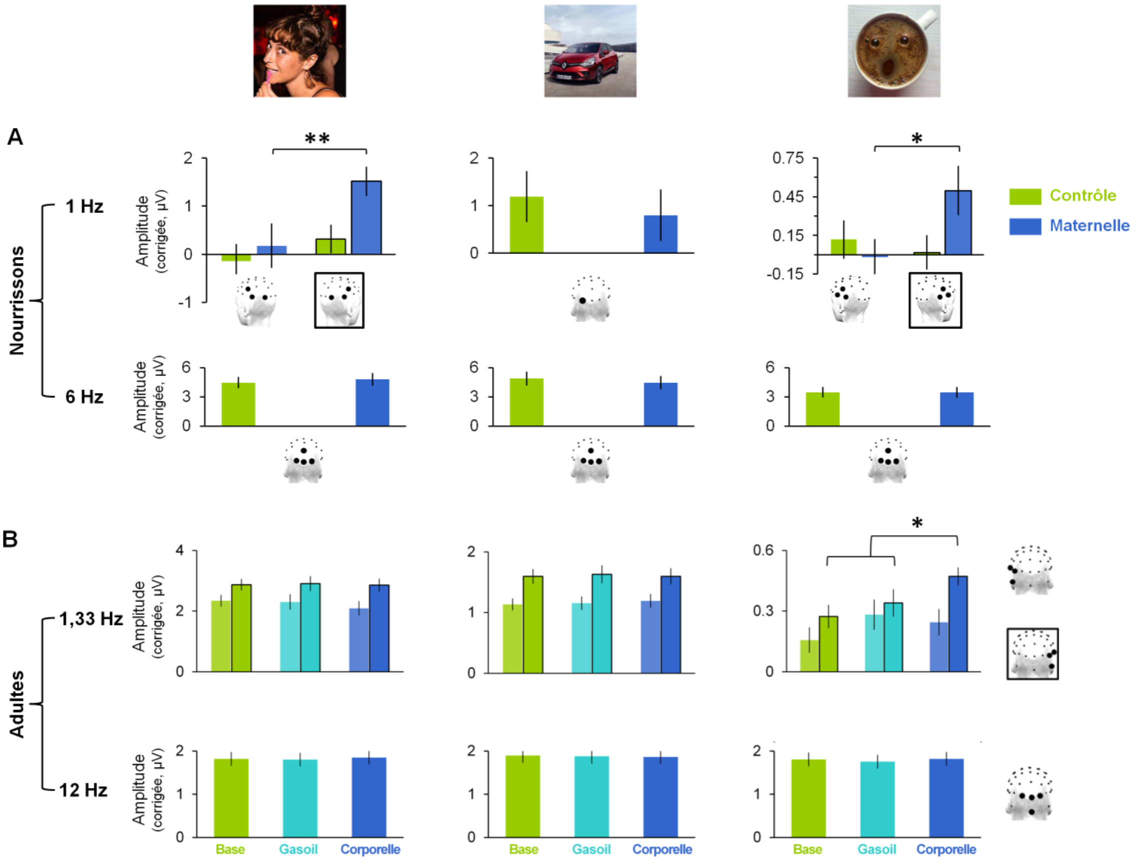


Figure X-2. Synthèse des résultats concernant l'effet de l'odeur observé à travers les études. A. Chez le nourrisson, l'effet de l'odeur maternelle est retrouvé uniquement pour la réponse sélective de catégorisation (i.e., 1 Hz) des vrais visages et des visages illusoires, manifesté par une augmentation de la réponse visuelle dans l'hémisphère droit. La réponse visuelle générale (6 Hz) n'est pas modulée par l'odeur et est équivalente entre les catégories. **B**. Chez l'adulte, la réponse sélective de catégorisation (i.e., 1,33 Hz) n'est modulée que dans le cas des paréidolies, en augmentant la réponse dans l'hémisphère droit. En ce qui concerne la réponse visuelle générale (i.e., 12 Hz), à nouveau, aucun effet de l'odeur, ni de la catégorie, ne sont observés.

droite après ajout de l'odeur maternelle et révèle qu'au niveau individuel, l'odeur permet l'émergence de la réponse de catégorisation aux visages illusoires (Figure X-2 A-1 Hz).

Avec la poursuite de ces observations chez l'adulte, nous avons montré, dans le chapitre 2, que l'effet de l'odeur (corporelle) était toujours présent dans certaines circonstances. En effet, le seul effet de l'odeur mesuré concernait une odeur associée à une catégorie visuelle congruente et dans le cas précis où le stimulus est difficile à percevoir : l'odeur corporelle améliore la réponse de catégorisation des paréidolies faciales (Figure X-2 B-1,33 Hz). Par ailleurs, cet effet est le plus fort chez les participants ayant rapporté les paréidolies dans la séquence, ce qui suggère que l'odeur pourrait avoir aidé à les rendre conscients de la présence des visages illusoires.

Il est également à noter, qu'à travers ces différentes études, aucun effet du statut alimentaire (biberon vs. allaitement chez le nourrisson), ni du sexe des participants (adulte ou nourrisson) n'a été relevé. La réponse visuelle générale n'a également pas montré de sensibilité à la variation des contextes olfactifs, ni de différence d'amplitude entre les catégories (Figure X-2 A-6 Hz et B-12 Hz).

L'efficacité de l'odeur dépend de la difficulté à percevoir le stimulus visuel

A partir du principe d'efficience inverse décrit comme l'une des règles d'intégration multisensorielle (Stein and Meredith, 1993) et qui stipule que la force de l'intégration multisensorielle dépend de la performance initiale mesurée dans une modalité isolée, nous avions fait l'hypothèse que l'effet de l'odeur serait particulièrement fort dans le cas où le traitement visuel est difficile, c'est-à-dire quand l'information visuelle seule est difficile à interpréter. De ce fait, cela était attendu comme un phénomène général chez le nourrisson où le système visuel est particulièrement immature sur la première moitié de la première année de vie.

De ce fait, nous avons montré dans l'étude 3 que l'odeur maternelle était capable d'initier la réponse de catégorisation des visages illusoires au niveau individuel, puisque l'effet de l'odeur était le plus fort chez les participants qui ne présentaient pas de réponse significative dans le contexte olfactif de base. Cela a également été démontré par le biais d'une corrélation négative révélant une relation linéaire inversée entre la force de la réponse de base et la force de l'effet de l'odeur, comme cela était prédit par l'efficience inverse (Figure VI-1A). Rétrospectivement, nous avons conduit la même analyse sur l'effet de l'odeur mesuré dans la première étude et la corrélation est également significative (R^2 = 0.74, p < .001, Figure VI-1B). Cela montre que même dans le cas de vrais visages, l'intégration multisensorielle dépend de la performance unisensorielle. L'observation de ce phénomène chez le nourrisson suggère que les connaissances visuelles au début de la vie s'acquièrent de manière multisensorielle.

Pour aller plus loin, nous avons également testé cette corrélation dans l'étude 4, pour la situation où un effet de l'odeur a été observé, c'est-à-dire en comparant l'amplitude de la réponse de catégorisation aux visages illusoires dans le contexte olfactif de base vs. dans le contexte des odeurs corporelles. A nouveau, la corrélation est négative et significative (R^2 = 0.27, p = .006, Figure VI-1C) montrant que cet effet n'est pas restreint à une fenêtre de développement puisqu'on peut l'observer chez des adultes typiques où le système visuel est mature et très performant. Dans l'ensemble, ces données corroborent des observations menées chez des modèles animaux et chez l'humain (Helfer, 1998; Holmes, 2009, 2007; Meredith and Stein, 1983; Stein et al., 1988; Stevenson et al., 2012; Stevenson and James, 2009) principalement concernant des interactions audio-visuelles pour leur synchronie temporelle précise. Nous montrons de ce fait que l'efficience inverse peut également s'appliquer dans le cas de stimulation contextuelle olfactive.

L'influence des odeurs sur la catégorisation visuelle

Congruence et sélectivité

A travers nos études, nous avons observé l'effet de l'odeur corporelle uniquement sur la réponse de catégorisation et uniquement dans le cas de catégories visuelles congruentes (visages humains ou illusoires). Cette observation soutient l'idée que de telles associations intersensorielles ne sont pas fortuites et que les odeurs corporelles ne favorisent pas la détection de n'importe quelle stimulation périodique du fait de son aspect régulier et stable.

Nos résultats apparaissent en accord avec le principe de congruence intersensorielle, c'est à dire l'idée que les informations issues des différents sens sont combinées ensemble si elles se complètent (Bahrick and Lickliter, 2012; Ernst and Bülthoff, 2004). En effet, aucun effet d'incongruence n'a été trouvé dans nos études. Les visages et les odeurs corporelles sont deux types de stimuli possédant une grande importance dès les premiers stades du développement et sont liés à la présence de congénères (Reynolds and Roth, 2018; Schaal et al., 2020) : l'association sélective entre les odeurs corporelles et la catégorisation des visages suggère en effet que la congruence est au moins en partie responsable des associations intersensorielles. Par ailleurs, en plus des visages humains, l'odeur corporelle (maternelle) a un effet facilitateur sur la catégorisation des visages illusoires, représentées par un ensemble d'objets communs qui partagent la propriété d'évoquer un visage. La dimension sociale portée par l'odeur corporelle, en tant que chimiosignal social et spécifique à l'espèce, contribue potentiellement à l'occurence des paréidolies. En effet, une étude récente a précisément mis en avant la haute valeur sociale que le percevant projette sur ces visages en dépit de leur support inanimé (Palmer and Clifford, 2020).

Nous avions choisi les visages et les odeurs corporelles pour leur importance écologique présente dès le début de la vie et maintenue chez l'adulte, permettant de comparer ces deux tranches d'âge le plus directement possible. Mais observer l'effet d'une odeur "sociale" sur un stimulus intrinsèquement "non social", simplement parce qu'il évoque un visage, suggère que la congruence intersensorielle dépasse une association induite strictement par le caractère intrinsèquement social du stimulus et de ce fait limité aux visages humains. Ceci est également suggéré par de nombreuses études mettant en évidence des associations olfacto-visuelles à partir d'éléments non sociaux, par exemple la perception d'aliments (Mas et al., 2019) ou de la couleur (Demattè et al., 2006).

Détection de la saillance des stimuli

La sélectivité de l'odeur corporelle pour les visages pourrait provenir de l'exposition simultanée à ces deux stimuli. L'olfaction n'est pas réputée pour son aspect explicite et manifeste, bien qu'il soit majoritairement admis que les odeurs peuvent jouer un rôle d'alerte important (Herrick, 1933). Suivant cette propriété, il a été suggéré que les odeurs pouvaient induire un état de préparation en vue de réagir à des stimuli associés : les odeurs de stress prépareraient à répondre à des stimuli évoquant le danger (de Groot et al., 2012; de Groot and Smeets, 2017; Mutic et al., 2016) et des odeurs corporelles sans valence émotionnelle marquée favoriseraient des réponses prosociales (Camps et al., 2014; Cecchetto et al., 2019; Mutic et al., 2019).

Il a été montré que la saillance d'un stimulus sensoriel était responsable de l'attention envers ce stimulus, même lorsque l'attention volontaire est portée sur une autre modalité sensorielle (Lakatos et al., 2009). Les auteurs proposent de considérer l'existence d'un sens "guidant" temporairement le traitement des informations provenant d'autres modalités sensorielles. Dans le cas de nos études, l'odeur corporelle pourrait constituer ce guide pour aider à interpréter les informations visuelles co-occurrentes congruentes.

Un apprentissage associatif renforçateur

L'importance écologique des odeurs corporelles et des visages, une propriété intrinsèque à ces stimuli, pourrait contribuer à initier une attention préférentielle créant une exposition optimale à ces stimuli. Par la suite, l'apprentissage associatif permettrait de retenir et renforcer l'importance des odeurs corporelles et des visages dans l'environnement. L'odeur maternelle pourrait en effet être un proxy favorisant l'apprentissage associatif dans le domaine social (Schaal et al., 2020), initialement restreint à la mère, puis graduellement étendu aux autres individus à mesure que le jeune enfant grandit (Rennels and Davis, 2008).

Ce renforcement concorde avec certaines conceptions du développement neuronal où l'expérience modèle une architecture neuronale déterminée génétiquement en contraignant partiellement la connectivité entre des régions fonctionnelles (Bressler and Menon, 2010; Mahon and Caramazza, 2011). Par exemple, il est proposé que la connectivité neuronale est renforcée par un signal réentrant déterminé par la co-exposition aux différents stimuli. Ce signal réentrant serait induit par la continuité spatio-temporelle de la co-occurrence des inputs, et deviendrait responsable de l'activation de groupes de neurones dédiés en réponse à la détection d'un des stimuli (Edelman, 1993). Concernant nos résultats, il serait possible que l'exposition soutenue aux visages en même temps qu'aux odeurs corporelles renforce la connectivité entre les voies neurales dédiées à chaque stimulus, si bien que grâce au signal réentrant, un seul des inputs soit capable d'activer également les aires traitant l'autre input.

Par ailleurs, par apprentissage associatif, les odeurs corporelles et les visages deviennent liés et ce lien pourrait devenir un des indices d'identification pour l'objet (i.e., un stimulus devient partie intégrante de la représentation de l'autre). En ce qui concerne la catégorisation, ajouter un indice congruent avec la cible peut rendre la perception plus efficace puisqu'il aide la reconnaissance de la catégorie par deux aspects : d'une part, cela améliore la discrimination entre chaque exemplaire cible et les distracteurs à cause d'une congruence exclusive avec la cible, qui d'autre part, favorise la généralisation à travers les différents exemplaires.

Donner sens à nos sens

Notre perception est un mécanisme interprétatif pour attribuer du sens à ce que nous vivons au présent, en se basant sur nos expériences antérieures (Ernst and Bülthoff, 2004; Gregory, 1997). Il a été proposé que ces inférences que nous portons sur le monde, illustré par exemple dans le cas des illusions perceptives hautement interprétatives (Gregory, 1997), correspondent à des processus cognitifs descendants (top-down). Le modèle de Bar (2003) notamment, propose une vue dynamique où nos inférences sont déclenchées par le traitement d'informations sensorielles incomplètes qui orientent vers des hypothèses interprétatives issues de nos représentations en mémoire et sont confirmées ou infirmées par les autres informations sensorielles. Des informations sensorielles ascendantes venant du cortex visuel seraient simultanément intégrées à des processus descendants du cortex orbito-frontal (correspondant aux inférences) afin de permettre l'exploration d'alternatives parallèles en vue de la réponse la plus probable, i.e., l'identification de l'objet dans le cortex inféro-temporal.

Une dissociation neuronale ?

Il est intéressant de noter que le siège neural des inférences tel que proposé par le modèle de Bar (Bar, 2003; Bar et al., 2006) se trouve être l'un des relais primaires du système olfactif : le cortex orbitofrontal. Ce modèle n'a été testé qu'avec des stimuli visuels, mais puisque les processus descendants seraient liés aux représentations en mémoire, cela pourrait-il être également observé en cas de traitement multisensoriel ? Des travaux récents amènent des preuves expérimentales de structures neurales partagées par différentes modalités sensorielles. En effet, des conceptions récentes proposent que des cortex traditionnellement considérés unisensoriels pourraient répondre à des entrées multisensorielles (Mahon and Caramazza, 2011;

Schroeder and Foxe, 2005). De même, la catégorisation pourrait spontanément correspondre à un certain niveau d'abstraction de sorte qu'une catégorie peut être extraite immédiatement et indépendamment de la nature de l'input (image ou mot décrivant l'image, Brady and Oliva, 2008). Au niveau de la représentation d'un individu, il a récemment été montré que la reconnaissance d'une identité au niveau cérébral était équivalente selon si elle était basée sur le visage, le nom, ou les deux (Volfart et al., 2020). Dans cette dernière étude, les auteurs ont également révélé que des populations de neurones étaient actives exclusivement lors d'une stimulation multisensorielle, alors que d'autres répondaient sélectivement pour le visage, ou pour le nom. Dans le cas du développement de la catégorisation dans le VOTC (voir Grill-Spector and Weiner, 2014 pour revue), il a récemment été mis en évidence que l'acquisition des connaissances catégorielles dans cette aire visuelle pouvait se faire en l'absence totale d'input visuel au cours de la vie (en testant des catégories de sons chez des aveugles congénitaux et des voyants, Mattioni et al., 2020). De cette manière, il apparait possible de considérer que les odeurs pourraient activer des réponses de catégorisation dans le VOTC, notamment car cela a été observé au niveau du cortex occipital (Djordjevic et al., 2005; Gottfried et al., 2004; Royet et al., 2001, 1999; Zatorre et al., 2000), suggérant un maillage particulier entre les odeurs et la vision.

Simplifier pour prédire

Les représentations que nous avons en mémoire peuvent prédire nos expériences futures. Elles servent à simplifier notre appréhension du monde puisqu'en se basant dessus, nous limitons le coût cognitif requis pour traiter toutes les nouvelles informations que nous rencontrons à chaque instant. La catégorisation représente une forme de ces représentations, structurant des relations entre les objets (Barsalou, 1990), ce qui engendre des attentes et se traduit en prédiction (d'un objet dans une scène par exemple; Kaiser et al., 2019). Est-ce que les jeunes nourrissons sont déjà capables de telles prédictions ? Bien que 4 mois puisse paraître jeune, il a été montré que les nourrissons sont capables de réaliser des inférences statistiques ajustées sur leurs actions et leurs conséquences, et leur environnement physique, au même titre que n'importe quel être vivant (Helmholtz, 1866). Appliqué à des fonctions cognitives de haut niveau, un ensemble d'études récentes a démontré les capacités du nourrisson à former des prédictions à partir de ses connaissances acquises, au niveau cérébral (Emberson et al., 2015; Kayhan et al., 2019b, 2019c, 2019a; Kouider et al., 2015; Köster et al., 2020 pour revue). Ces conceptions sont en lien avec une représentation prédictive de notre perception et de l'apport des inférences bayésiennes dans les performances cognitives, qui bénéficient d'un intérêt récent dans l'étude du développement cognitif (Gopnik and Bonawitz, 2015; Rao et al., 2007).

Perspectives

L'effet de l'odeur évolue-t-il au cours de la première année ?

Il est possible de se demander comment l'intégration olfacto-visuelle évolue entre la petite enfance et l'âge adulte. A partir de nos observations, et en prenant en compte que 1) le système visuel évolue rapidement à partir de 4 mois (Braddick and Atkinson, 2011), 2) la perception des visages s'affine et se développe drastiquement au cours de la première année (Pascalis et al., 2011), 3) l'arrivée de la motricité s'accompagne d'une première forme d'indépendance physique pour le nourrisson modifiant ses relations avec ses proches (Leppänen and Nelson, 2012) et enfin que 4) les modifications physiologiques maternelles associées à une naissance récente s'estompent graduellement (Jacob et al., 2004); nous prédisons que l'odeur maternelle va progressivement perdre son effet facilitateur observé pour la catégorisation des visages. Afin d'étudier cela, nous avons testé des nourrissons âgés de 4 à 12,5 mois et observé l'évolution de l'effet de l'odeur sur la catégorisation des visages.

Des données préliminaires collectées sur 38 nourrissons sont présentées ci-après (Figure VIII-1A). L'étude utilise le même paradigme que celui utilisé dans l'étude 1 (Leleu et al., 2020) en termes de stimulation olfactive et de stimuli visuels utilisés, de mode de présentation, de durée des essais, de procédure expérimentale et d'analyse des données EEG. Les analyses ont été réalisées sur les ROIs définis dans la 1ere étude (rOT et lOT), et nous attendons une diminution de l'effet de l'odeur sur la région occipito-temporale droite (particulièrement au niveau de l'électrode occipitale droite O2) en fonction de l'âge. Dans un premier temps, nous pouvons déjà observer une évolution de la réponse de catégorisation des visages à partir de 3 groupes de nourrissons (jeunes, médians, âgés), montrant que la réponse devient plus forte en amplitude et semble se latéraliser à droite chez les plus âgés (9,5-12,5 mois, Figure VIII-1B). De plus, alors que l'effet de l'odeur paraît présent au niveau du groupe sur l'hémisphère droit (Figure VIII-1C), une diminution de l'effet de l'odeur en fonction de l'âge est également observée sur l'électrode O2 (Figure VIII-1D). Ces données préliminaires sont encourageantes et pourront apporter des résultats importants dans la compréhension de l'association olfacto-visuelle en jeu au cours du développement visuel. Par ailleurs, les résultats de l'étude finalisée pourront potentiellement aider à identifier des fenêtres critiques de développement où les odeurs peuvent particulièrement aider l'acquisition des catégories visuelles.

Les odeurs maternelles bénéficient-elles d'un statut particulier pour favoriser la catégorisation des visages ?

Pour des raisons liées à l'âge, les trois études conduites chez le nourrisson se sont limitées à tester seulement deux conditions, permettant ainsi un contraste olfactif intra-sujet mais limité dans la présentation des catégories visuelles, ainsi présentées isolément par groupe de nourrisson. De ce fait, contrairement à l'étude 4 chez l'adulte, nous n'avons pas pu tester d'odorant non humain, ce qui ouvre la voie à de futures études.

En effet, l'odeur maternelle correspond à un mélange d'informations chimiques riches (odeur corporelle axillaire, du sein, sécrétions des glandes mammaires, du lait, etc., Schaal, 2010). Si la littérature a révélé des effets comparables ou dissociés entre l'odeur maternelle familière vs. non familière (Durand et al., 2020; Jessen, 2020, respectivement), cela ne permet pas de conclure sur un éventuel indice chimique qui pourrait être nécessaire et suffisant pour déclencher « l'effet » de l'odeur maternelle. Il reste effectivement à comprendre si l'identité, la maternité ou l'humanité serait isolément un indice suffisant pour le nourrisson.

Par ailleurs, la délimitation de l'effet de l'odeur maternelle peut également être évaluée d'une autre manière, par exemple en testant si l'effet de l'odeur est observé sur des stimuli sociaux humains autres que des visages. Il est possible que des stimuli visuels comme le corps entier ou des membres du corps bénéficient également d'une intégration particulière avec l'odeur maternelle, étant donné que l'attirance pour certains membres du corps, comme les mains, émerge au cours de la première année de vie (Fausey et al., 2016). De plus, la perception de corps entiers, principalement par le biais de dyades (i.e., silhouettes se faisant face pour représenter une interaction entre deux individus), a été l'objet de récentes études (Peelen and Downing, 2007), montrant un traitement privilégié et unitaire de ce stimulus, qui aurait une forte connotation sociale, en tout cas chez l'adulte (Abassi and Papeo, 2020).

Enfin, il est à noter que l'effet des odeurs, particulièrement fort dans le début de la vie, est supposé être lié à la précocité développementale de l'olfaction comparé à la vision. De ce fait, il est fort possible que des effets facilitateurs équivalents puissent être trouvés avec un autre type de stimuli présents également plus précocement que la vision et eux aussi associés à des personnes, à savoir des voix humaines.

Les odeurs peuvent-elles favoriser la perception des visages chez des individus atteints de troubles neurodéveloppementaux ?

Il a récemment été proposé que l'olfaction pourrait être un allié dans l'étude des déficits socio-cognitifs associés au syndrome du trouble autistique (ASD, Barros and Soares, 2020), et cela pourrait également être valable pour d'autres troubles neurodéveloppementaux comme le syndrome de délétion génétique 22q11.2 (22q11.2DS). En effet, ces troubles sont caractérisés par des difficultés dans la communication et les interactions sociales, des comportements socio-émotionnels délétères (Jansen et al., 2007). Notamment, des déficits dans la perception des visages sont fréquemment rapportés, affectant par exemple la préférence spontanée pour les visages (Chawarska et al., 2013; Riby et al., 2012; Riby and Hancock, 2009), la reconnaissance individuelle (Tang et al., 2015) ou la discrimination des expressions faciales (e.g., Leleu et al., 2019). Quelques études se sont directement intéressées aux effets de l'odeur dans ces populations et ont montré notamment qu'une odeur rendue familière pouvait influencer le choix d'un aliment chez des enfants ASD (Luisier et al., 2018) et qu'en particulier l'odeur maternelle favorisait l'imitation sociale, également chez des enfants ASD (Parma et al., 2014, 2013). Dans l'ensemble, ces études proposent que les individus ASD seraient sensibles aux odeurs de leur environnement et que celles-ci pourraient être utilisées pour les guider vers des items spécifiques afin de compenser certains de leurs déficits.

Conclusion générale

Cette thèse a examiné le rôle de l'odeur corporelle dans le développement de la catégorisation des visages. Pour ce faire, l'EEG de surface a été enregistré pendant une stimulation périodique rapide (FPVS-EEG) où des nourrissons de 4 mois étaient exposés à l'odeur de leur mère ou une odeur contrôle, ou des adultes à des odeurs corporelles, du gasoil ou de l'huile minérale inodore. Dans ces séquences d'images périodiques présentées à 6 ou 12 Hz, des images de visages (études 1 et 4), de voitures (études 2 et 4) ou d'objets ressemblant à des visages (études 3 et 4) étaient intercalées à intervalle régulier toutes les 6 (études 1 à 3) ou 9 images (étude 4), c'est-à-dire étiquetées à 1 ou 1,33 Hz respectivement. Chez le nourrisson, l'effet de l'odeur maternelle est retrouvé pour la catégorisation des visages humains et illusoires mais pas pour la catégorisation des voitures. Chez l'adulte, seule l'odeur corporelle a modulé la réponse visuelle, augmentant seulement la réponse pour la catégorie difficile à percevoir, à savoir celle des visages illusoires. Ces travaux démontrent que les odeurs corporelles guident le développement de la perception des visages (humains ou illusoires) au début de la vie et que leur effet se retrouve à l'âge adulte quand l'interprétation du visage est difficile pour le système visuel seul. Ils soutiennent l'idée que dès les premiers stades du développement, notre perception intègre des informations sensorielles congruentes issues de nos différents sens pour façonner l'acquisition des catégories. En particulier, nous avons montré que des sens au développement précoce, comme l'olfaction, peuvent activement déterminer l'acquisition des catégories dans un sens au développement plus tardif comme la vision. L'ensemble de ce travail représente un axe de recherche riche, novateur et prometteur. Les recherches présentées dans cette thèse ne sont qu'une porte d'entrée à l'étude du développement de la catégorisation en adoptant une approche multisensorielle et qui intègre le sens de l'odorat.

References

Abassi, E., Papeo, L., 2020. The Representation of Two-Body Shapes in the Human Visual Cortex. J. Neurosci. 40, 852–863. https://doi.org/10.1523/JNEUROSCI.1378-19.2019

Ache, B.W., Young, J.M., 2005. Olfaction: Diverse Species, Conserved Principles. Neuron 48, 417–430. https://doi.org/10.1016/j.neuron.2005.10.022

Ackerl, K., Atzmueller, M., Grammer, K., 2002. The scent of fear. Neuroendocrinology Letters 23, 79–84.

Adibpour, P., Dubois, J., Dehaene-Lambertz, G., 2018. Right but not left hemispheric discrimination of faces in infancy. Nature Human Behaviour 2, 67–79. https://doi.org/10.1038/s41562-017-0249-4

Adolph, D., Meister, L., Pause, B.M., 2013. Context counts! social anxiety modulates the processing of fearful faces in the context of chemosensory anxiety signals. Frontiers in human neuroscience 7, 283. https://doi.org/10.3389/fnhum.2013.00283

Adolph, D., Schlösser, S., Hawighorst, M., Pause, B.M., 2010. Chemosensory signals of competition increase the skin conductance response in humans. Physiology & Behavior 101, 666–671. https://doi.org/10.1016/j.physbeh.2010.08.004

Adrian, E.D., Matthews, B.H., 1934. The interpretation of potential waves in the cortex. The Journal of Physiology 81, 440–471.

Akcan, E., Polat, S., 2016. Comparative effect of the smells of amniotic fluid, breast milk, and lavender on newborns' pain during heel lance. Breastfeeding Medicine 11, 309–314. https://doi.org/10.1089/bfm.2015.0174

Alho, L., Soares, S.C., Ferreira, J., Rocha, M., Silva, C.F., Olsson, M.J., 2015. Nosewitness Identification: Effects of Negative Emotion. PLOS ONE 10, e0116706. https://doi.org/10.1371/journal.pone.0116706

Allison, T., McCarthy, G., Nobre, A., Puce, A., Belger, A., 1994. Human Extrastriate Visual Cortex and the Perception of Faces, Words, Numbers, and Colors. Cereb Cortex 4, 544–554. https://doi.org/10.1093/cercor/4.5.544

American Psychiatric Association, 2013. Diagnostic and Statistical Manual of Mental Disorders, Fifth Edition. ed. American Psychiatric Association. https://doi.org/10.1176/appi.books.9780890425596

Amsellem, S., Höchenberger, R., Ohla, K., 2018. Visual–Olfactory Interactions: Bimodal Facilitation and Impact on the Subjective Experience. Chem Senses 43, 329–339. https://doi.org/10.1093/chemse/bjy018

Aoyama, S., Toshima, T., Saito, Y., Konishi, N., Motoshige, Ishikawa, N., Nakamura, K., Kobayashi, M., 2010. Maternal breast milk odour induces frontal lobe activation in neonates: a NIRS study. Early Hum Dev 86, 541–545. https://doi.org/10.1016/j.earlhumdev.2010.07.003

Arcaro, M.J., Schade, P.F., Vincent, J.L., Ponce, C.R., Livingstone, M.S., 2017. Seeing faces is necessary for face-domain formation. Nat Neurosci 20, 1404–1412. https://doi.org/10.1038/nn.4635

Arterberry, M.E., Kellman, P.J., Arterberry, M.E., 2016. Development of perception in infancy: the cradle of knowledge revisited. Oxford University Press, New York.

Auffarth, B., 2013. Understanding smell—The olfactory stimulus problem. Neuroscience & Biobehavioral Reviews 37, 1667–1679. https://doi.org/10.1016/j.neubiorev.2013.06.009

Baccarani, A., Grondin, S., Laflamme, V. *et al.* 2020. Relaxing and stimulating effects of odors on time perception and their modulation by expectancy. *Atten Percept Psychophys*. https://doi.org/10.3758/s13414-020-02182-0

Bader, A.P., Phillips, R.D., 2002. Fathers' recognition of their newborns by visual-facial and olfactory cues. Psychology of Men & Masculinity 3, 79–84. https://doi.org/10.1037/1524-9220.3.2.79

Badiee, Z., Asghari, M., Mohammadizadeh, M., 2013. The Calming Effect of Maternal Breast Milk Odor on Premature Infants. Pediatrics & Neonatology 54, 322–325. https://doi.org/10.1016/j.pedneo.2013.04.004

Bahrick, L.E., Lickliter, R., 2012. The role of intersensory redundancy in early perceptual, cognitive, and social development, in: Bremner, A., Lewkowicz, D.J., Spence, C. (Eds.), Multisensory Development. Oxford University Press, Oxford, England, pp. 183–205. https://doi.org/10.1093/acprof:oso/9780199586059.003.0008

Bahrick, L.E., Lickliter, R., 2000. Intersensory redundancy guides attentional selectivity and perceptual learning in infancy. Developmental psychology 36, 190. https://doi.org/10.1037/0012-1649.36.2.190

Bahrick, L.E., Lickliter, R., Flom, R., 2004. Intersensory Redundancy Guides the Development of Selective Attention, Perception, and Cognition in Infancy. Current Directions in Psychological Science 13, 99–102. https://doi.org/10.1111/j.0963-7214.2004.00283.x

Bar, M., 2003. A Cortical Mechanism for Triggering Top-Down Facilitation in Visual Object Recognition. Journal of Cognitive Neuroscience 15, 600–609. https://doi.org/10.1162/089892903321662976

Bar, M., Kassam, K.S., Ghuman, A.S., Boshyan, J., Schmid, A.M., Dale, A.M., Hämäläinen, M.S., Marinkovic, K., Schacter, D.L., Rosen, B.R., Halgren, E., 2006. Top-down facilitation of visual recognition. PNAS 103, 449–454. https://doi.org/10.1073/pnas.0507062103

Bar, M., Tootell, R.B.H., Schacter, D.L., Greve, D.N., Fischl, B., Mendola, J.D., Rosen, B.R., Dale, A.M., 2001. Cortical Mechanisms Specific to Explicit Visual Object Recognition. Neuron 29, 529–535. https://doi.org/10.1016/S0896-6273(01)00224-0

Barbas, H., 1995. Anatomic basis of cognitive-emotional interactions in the primate prefrontal cortex. Neuroscience & Biobehavioral Reviews 19, 499–510. https://doi.org/10.1016/0149-7634(94)00053-4

Barnhart, W.R., Rivera, S., Robinson, C.W., 2018. Different patterns of modality dominance across development. Acta Psychologica 182, 154–165. https://doi.org/10.1016/j.actpsy.2017.11.017

Baron-Cohen, S., Spitz, A., Cross, P., 1993. Do children with autism recognise surprise? A research note. Cognition and Emotion 7, 507–516. https://doi.org/10.1080/02699939308409202

Barros, F., Soares, S.C., 2020. Giving meaning to the social world in Autism Spectrum Disorders: Olfaction as a missing piece of the puzzle? Neuroscience & Biobehavioral Reviews. https://doi.org/10.1016/j.neubiorev.2020.06.008

Barry-Anwar, R., Hadley, H., Conte, S., Keil, A., Scott, L.S., 2018. The developmental time course and topographic distribution of individual-level monkey face discrimination in the infant brain. Neuropsychologia 108, 25–31. https://doi.org/10.1016/j.neuropsychologia.2017.11.019

Barsalou, L.W., 1990. Access and inference in categorization. Bull. Psychon. Soc. 28, 268–271. https://doi.org/10.3758/BF03334020

Bartocci, M., Winberg, J., Ruggiero, C., Bergqvist, L.L., Serra, G., Lagercrantz, H., 2000. Activation of Olfactory Cortex in Newborn Infants After Odor Stimulation: A Functional Near-Infrared Spectroscopy Study. Pediatr Res 48, 18–23. https://doi.org/10.1203/00006450-200007000-00006

Bartrip, J., Morton, J., de Schonen, S., 2001. Responses to mother's face in 3-week to 5-month-old infants. British Journal of Developmental Psychology 19, 219–232. https://doi.org/10.1348/026151001166047

Barwich, A.-S., 2019. A Critique of Olfactory Objects. Front. Psychol. 10. https://doi.org/10.3389/fpsyg.2019.01337

Behrmann, M., Plaut, D.C., 2020. Hemispheric Organization for Visual Object Recognition: A Theoretical Account and Empirical Evidence. Perception 030100661989904. https://doi.org/10.1177/0301006619899049

Beidler, L.M., 1961. The chemical senses. Annual review of psychology 12, 363–388. https://doi.org/10.1146/annurev.ps.12.020161.002051

Bell, M.A., Wolfe, C.D., 2008. The use of the electroencephalogram in research on cognitive development, in: Developmental Psychophysiology: Theory, Systems, and Methods. Cambridge University Press, New York, NY, US, pp. 150–170.

Bensafi, M., Rouby, C., Farget, V., Bertrand, B., Vigouroux, M., Holley, A., 2002. Autonomic Nervous System Responses to Odours: the Role of Pleasantness and Arousal. Chem Senses 27, 703–709. https://doi.org/10.1093/chemse/27.8.703

Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological Studies of Face Perception in Humans. Journal of Cognitive Neuroscience 8, 551–565. https://doi.org/10.1162/jocn.1996.8.6.551

Bodamer, J., 1947. Die prosop-agnosie. Archiv für Psychiatrie und Nervenkrankheiten 179, 6–53.

Bogdashina, O., 2016. Sensory perceptual issues in autism and asperger syndrome: different sensory experiences-different perceptual worlds. Jessica Kingsley Publishers.

Botvinick, M., Nystrom, L.E., Fissell, K., Carter, C.S., Cohen, J.D., 1999. Conflict monitoring versus selection-for-action in anterior cingulate cortex. Nature 402, 179–181. https://doi.org/10.1038/46035

Bracci, S., Op de Beeck, H.P., 2016. Dissociations and Associations between Shape and Category Representations in the Two Visual Pathways | Journal of Neuroscience. The Journal of Neuroscience 36, 432–444. https://doi.org/10.1523/JNEUROSCI.2314-15.2016

Braddick, O., Atkinson, J., 2011. Development of human visual function. Vision Research, Vision Research 50th Anniversary Issue: Part 2 51, 1588–1609. https://doi.org/10.1016/j.visres.2011.02.018

Brady, T.F., Oliva, A., 2008. Statistical Learning Using Real-World Scenes: Extracting Categorical Regularities Without Conscious Intent. Psychol Sci 19, 678–685. https://doi.org/10.1111/j.1467-9280.2008.02142.x

Brand, G., Millot, J.-L., Henquell, D., 2001. Complexity of olfactory lateralization processes revealed by functional imaging: a review. Neuroscience & Biobehavioral Reviews 25, 159–166. https://doi.org/10.1016/S0149-7634(01)00005-7

Bremner, A.J., Lewkowicz, D.J., Spence, C., 2012. The multisensory approach to development, in: Multisensory Development. Oxford University Press, Oxford, pp. 1–26.

Bressler, S.L., Menon, V., 2010. Large-scale brain networks in cognition: emerging methods and principles. Trends in Cognitive Sciences 14, 277–290. https://doi.org/10.1016/j.tics.2010.04.004

Bristow, D., Dehaene-Lambertz, G., Mattout, J., Soares, C., Gliga, T., Baillet, S., Mangin, J.-F., 2008. Hearing Faces: How the Infant Brain Matches the Face It Sees with the Speech It Hears. Journal of Cognitive Neuroscience 21, 905–921. https://doi.org/10.1162/jocn.2009.21076

Bronson, G.W., 1994. Infants' Transitions toward Adult-like Scanning. Child Development 65, 1243–1261. https://doi.org/10.1111/j.1467-8624.1994.tb00815.x

Bruce, V., Young, A., 1986. Understanding face recognition. British Journal of Psychology 77, 305–327. https://doi.org/10.1111/j.2044-8295.1986.tb02199.x

Bugatus, L., Weiner, K.S., Grill-Spector, K., 2017. Task alters category representations in prefrontal but not high-level visual cortex. NeuroImage 155, 437–449. https://doi.org/10.1016/j.neuroimage.2017.03.062

Busse, L., Roberts, K.C., Crist, R.E., Weissman, D.H., Woldorff, M.G., 2005. The spread of attention across modalities and space in a multisensory object. PNAS 102, 18751–18756. https://doi.org/10.1073/pnas.0507704102

Buswell, G.T., 1935. How people look at pictures: a study of the psychology and perception in art. Univ. Chicago Press, Oxford, England.

Butenandt, V.A., 1959. Uber den sexsual-lockstoff des seidenspinners Bombyx mori. Reindarstellung und konstitution. Z. Naturforschg, b 14, 283.

Caharel, S., Leleu, A., Bernard, C., Viggiano, M.-P., Lalonde, R., Rebaï, M., 2013. Early holistic face-like processing of Arcimboldo paintings in the right occipito-temporal cortex: Evidence from the N170 ERP component. International Journal of Psychophysiology 90, 157–164. https://doi.org/10.1016/j.ijpsycho.2013.06.024

Cain, W.S., 1979. To know with the nose: keys to odor identification. Science 203, 467–470. https://doi.org/10.1126/science.760202

Campbell, R., Landis, T., Regard, M., 1986. Face recognition and lipreading: a neurological dissociation. Brain 109, 509–521. https://doi.org/10.1093/brain/109.3.509

Camps, J., Stouten, J., Tuteleers, C., van Son, K., 2014. Smells like cooperation? Unpleasant body odor and people’s perceptions and helping behaviors. Journal of Applied Social Psychology 44, 87–93. https://doi.org/10.1111/jasp.12203

Cantafio, L.J., 2004. Human olfactory communication of alarm and safety.

Cantlon, J.F., Pinel, P., Dehaene, S., Pelphrey, K.A., 2011. Cortical Representations of Symbols, Objects, and Faces Are Pruned Back during Early Childhood. Cereb Cortex 21, 191–199. https://doi.org/10.1093/cercor/bhq078

Carretié, L., Hinojosa, J.A., Mercado, F., Tapia, M., 2005. Cortical response to subjectively unconscious danger. NeuroImage 24, 615–623. https://doi.org/10.1016/j.neuroimage.2004.09.009

Case, T.I., Repacholi, B.M., Stevenson, R.J., 2006. My baby doesn’t smell as bad as yours: The plasticity of disgust. Evolution and Human Behavior 27, 357–365. https://doi.org/10.1016/j.evolhumbehav.2006.03.003

Cato, M.A., Crosson, B., Gökçay, D., Soltysik, D., Wierenga, C., Gopinath, K., Himes, N., Belanger, H., Bauer, R.M., Fischler, I.S., Gonzalez-Rothi, L., Briggs, R.W., 2004. Processing Words with Emotional Connotation: An fMRI Study of Time Course and Laterality in Rostral Frontal and Retrosplenial Cortices. Journal of Cognitive Neuroscience 16, 167–177. https://doi.org/10.1162/089892904322984481

Cecchetto, C., Fischmeister, F.P.S., Gorkiewicz, S., Schuehly, W., Bagga, D., Parma, V., Schöpf, V., 2020. Human body odor increases familiarity for faces during encoding-retrieval task. Human Brain Mapping. https://doi.org/10.1002/hbm.24920

Cecchetto, C., Lancini, E., Bueti, D., Rumiati, R.I., Parma, V., 2019. Body odors (even when masked) make you more emotional: behavioral and neural insights. Scientific Reports 9. https://doi.org/10.1038/s41598-019-41937-0

Cernoch, J.M., Porter, R.H., 1985. Recognition of Maternal Axillary Odors by Infants. Child Development 56, 1593–1598. https://doi.org/10.2307/1130478

Chawarska, K., Macari, S., Shic, F., 2013. Decreased Spontaneous Attention to Social Scenes in 6-Month-Old Infants Later Diagnosed with Autism Spectrum Disorders. Biological Psychiatry 74, 195–203. https://doi.org/10.1016/j.biopsych.2012.11.022

Chen, D., Katdare, A., Lucas, N., 2006. Chemosignals of fear enhance cognitive performance in humans. Chemical senses 31, 415–423. https://doi.org/10.1093/chemse/bjj046

Chun, M.M., 2000. Contextual cueing of visual attention. Trends in Cognitive Sciences 4, 170–178. https://doi.org/10.1016/S1364-6613(00)01476-5

Colavita, F.B., 1974. Human sensory dominance. Perception & Psychophysics 16, 409–412. https://doi.org/10.3758/BF03203962

Cone, T.E., 1968. Diagnosis and treatment: Some diseases, syndromes, and conditions associated with an unusual odor. Pediatrics 41, 993–995.

Conte, S., Richards, J.E., Guy, M.W., Xie, W., Roberts, J.E., 2020. Face-sensitive brain responses in the first year of life. NeuroImage 116602. https://doi.org/10.1016/j.neuroimage.2020.116602

Contreras, C.M., Gutiérrez-García, A.G., Mendoza-López, R., Rodríguez-Landa, J.F., Bernal-Morales, B., Díaz-Marte, C., 2013. Amniotic fluid elicits appetitive responses in human newborns: Fatty acids and appetitive responses. Dev. Psychobiol. 55, 221–231. https://doi.org/10.1002/dev.21012

Cook, S., Fallon, N., Wright, H., Thomas, A., Giesbrecht, T., Field, M., Stancak, A., 2015. Pleasant and Unpleasant Odors Influence Hedonic Evaluations of Human Faces: An Event-Related Potential Study. Front. Hum. Neurosci. 9. https://doi.org/10.3389/fnhum.2015.00661

Cook, S., Kokmotou, K., Soto, V., Fallon, N., Tyson-Carr, J., Thomas, A., Giesbrecht, T., Field, M., Stancak, A., 2017. Pleasant and unpleasant odour-face combinations influence face and odour perception: An event-related potential study. Behavioural Brain Research 333, 304–313. https://doi.org/10.1016/j.bbr.2017.07.010

Cook, S., Kokmotou, K., Soto, V., Wright, H., Fallon, N., Thomas, A., Giesbrecht, T., Field, M., Stancak, A., 2018. Simultaneous odour-face presentation strengthens hedonic evaluations and event-related potential responses influenced by unpleasant odour. Neuroscience Letters 672, 22–27. https://doi.org/10.1016/j.neulet.2018.02.032

Crouzet, S.M., Kirchner, H., Thorpe, S.J., 2010. Fast saccades toward faces: Face detection in just 100 ms. Journal of Vision 10, 1–17. https://doi.org/10.1167/10.4.16

Croy, I., Frackowiak, T., Hummel, T., Sorokowska, A., 2017. Babies Smell Wonderful to Their Parents, Teenagers Do Not: an Exploratory Questionnaire Study on Children's Age and Personal Odor Ratings in a Polish Sample. Chem. Percept. 10, 81–87. https://doi.org/10.1007/s12078-017-9230-x

Dalrymple, K.A., Khan, A.F., Duchaine, B., Elison, J.T., 2020. Visual input to the left versus right eye yields differences in face preferences in 3-month-old infants. Developmental Science e13029. https://doi.org/10.1111/desc.13029

Dalton, P., Mauté, C., Jaén, C., Wilson, T., 2013. Chemosignals of stress influence social judgments. PLoS ONE 8, e77144. https://doi.org/10.1371/journal.pone.0077144

Damasio, A.R., Damasio, H., Van Hoesen, G.W., 1982. Prosopagnosia: anatomic basis and behavioral mechanisms. Neurology 32, 331–331. https://doi.org/10.1212/WNL.32.4.331

de Groot, J.H.B., Semin, G.R., Smeets, M.A.M., 2017. On the communicative function of body odors: a theoretical integration and review. Perspectives on Psychological Science 12, 306–324. https://doi.org/10.1177/1745691616676599

de Groot, J.H.B., Smeets, M.A.M., 2017. Human Fear Chemosignaling: Evidence from a Meta-Analysis. Chem Senses 42, 663–673. https://doi.org/10.1093/chemse/bjx049

de Groot, J.H.B., Smeets, M.A.M., Kaldewaij, A., Duijndam, M.J.A., Semin, G.R., 2012. Chemosignals Communicate Human Emotions. Psychol Sci 23, 1417–1424. https://doi.org/10.1177/0956797612445317

de Groot, J.H.B., Smeets, M.A.M., Rowson, M.J., Bulsing, P.J., Blonk, C.G., Wilkinson, J.E., Semin, G.R., 2015a. A sniff of happiness. Psychological science 26, 684–700. https://doi.org/10.1177/0956797614566318

de Groot, J.H.B., Smeets, M.A.M., Semin, G.R., 2015b. Rapid Stress System Drives Chemical Transfer of Fear from Sender to Receiver. PLOS ONE 10, e0118211. https://doi.org/10.1371/journal.pone.0118211

de Haan, M., Johnson, M.H., Halit, H., 2003. Development of face-sensitive event-related potentials during infancy: A review. International Journal of Psychophysiology 51, 45–58. https://doi.org/10.1016/S0167-8760(03)00152-1

de Haan, M., Nelson, C.A., 1999. Brain activity differentiates face and object processing in 6-month-old infants. Developmental Psychology 35, 1113–1121. https://doi.org/10.1037/0012-1649.35.4.1113

de Haan, M., Pascalis, O., Johnson, M.H., 2002. Specialization of neural mechanisms underlying face recognition in human infants. Journal of Cognitive Neuroscience 14, 199–209. https://doi.org/10.1162/089892902317236849

de Heering, A., Rossion, B., 2015. Rapid categorization of natural face images in the infant right hemisphere. eLife 4, 14. https://doi.org/10.7554/eLife.06564

de Schonen, S., Mathivet, E., 1990. Hemispheric Asymmetry in a Face Discrimination Task in Infants. Child Development 61, 1192–1205. https://doi.org/10.1111/j.1467-8624.1990.tb02853.x

de Schonen, S., Mathivet, E., 1989. First come, first served: A scenario about the development of hemispheric specialization in face recognition during infancy. Cahiers de Psychologie Cognitive/Current Psychology of Cognition 9, 3–44.

De Valois, R.L., De Valois, K.K., 1993. A multi-stage color model. Vision Research 33, 1053–1065. https://doi.org/10.1016/0042-6989(93)90240-W

DeCasper, A.J., Spence, M.J., 1986. Prenatal maternal speech influences newborns' perception of speech sounds. Infant Behavior and Development 9, 133–150. https://doi.org/10.1016/0163-6383(86)90025-1

Deen, B., Richardson, H., Dilks, D.D., Takahashi, A., Keil, B., Wald, L.L., Kanwisher, N., Saxe, R., 2017. Organization of high-level visual cortex in human infants. Nature Communications 8. https://doi.org/10.1038/ncomms13995

Dehaene, S., Cohen, L., Morais, J., Kolinsky, R., 2015. Illiterate to literate: behavioural and cerebral changes induced by reading acquisition. Nature Reviews Neuroscience 16, 234–244. https://doi.org/10.1038/nrn3924

Delaunay-El Allam, M., Marlier, L., Schaal, B., 2006. Learning at the breast: Preference formation for an artificial scent and its attraction against the odor of maternal milk. Infant Behavior and Development 29, 308–321. https://doi.org/10.1016/j.infbeh.2005.12.008

Delaunay-El Allam, M., Soussignan, R., Patris, B., Marlier, L., Schaal, B., 2010. Long-lasting memory for an odor acquired at the mother's breast. Developmental Science 13, 849–863. https://doi.org/10.1111/j.1467-7687.2009.00941.x

Demattè, M.L., Österbauer, R., Spence, C., 2007. Olfactory cues modulate facial attractiveness. Chemical Senses 32, 603–610. https://doi.org/10.1093/chemse/bjm030

Demattè, M.L., Sanabria, D., Spence, C., 2009. Olfactory discrimination: when vision matters? Chemical Senses 34, 103–109. https://doi.org/10.1093/chemse/bjn055

Demattè, M.L., Sanabria, D., Spence, C., 2006. Cross-Modal Associations Between Odors and Colors. Chemical Senses 31, 531–538. https://doi.org/10.1093/chemse/bjj057

DeNicola, C.A., Holt, N.A., Lambert, A.J., Cashon, C.H., 2013. Attention-orienting and attention-holding effects of faces on 4- to 8-month-old infants: International Journal of Behavioral Development. https://doi.org/10.1177/0165025412474751

Di Giorgio, E., Turati, C., Altoè, G., Simion, F., 2012. Face detection in complex visual displays: An eye-tracking study with 3- and 6-month-old infants and adults. Journal of Experimental Child Psychology 113, 66–77. https://doi.org/10.1016/j.jecp.2012.04.012

Djordjevic, J., Zatorre, R.J., Petrides, M., Boyle, J.A., Jones-Gotman, M., 2005. Functional neuroimaging of odor imagery. NeuroImage 24, 791–801. https://doi.org/10.1016/j.neuroimage.2004.09.035

Doty, R.L., Cometto-Muñiz, E.J., 2003. Trigeminal Chemosensation, in: Doty, R. (Ed.), Handbook of Olfaction and Gustation. CRC Press. https://doi.org/10.1201/9780203911457.ch47

Doucet, S., Soussignan, R., Sagot, P., Schaal, B., 2012. An overlooked aspect of the human breast: Areolar glands in relation with breastfeeding pattern, neonatal weight gain, and the dynamics of lactation. Early Human Development 88, 119–128. https://doi.org/10.1016/j.earlhumdev.2011.07.020

Doucet, S., Soussignan, R., Sagot, P., Schaal, B., 2007. The '"Smellscape"' of Mother's Breast : Effects of Odor Masking and Selective Unmasking on Neonatal Arousal, Oral, and Visual Responses. Wiley 49, 129–138. https://doi.org/10.1002/dev

Drewes, J., Trommershaeuser, J., Gegenfurtner, K.R., 2009. The effect of context on rapid animal detection. Journal of Vision 9, 1177–1177. https://doi.org/10.1167/9.8.1177

Driver, J., Noesselt, T., 2008. Multisensory Interplay Reveals Crossmodal Influences on 'Sensory-Specific' Brain Regions, Neural Responses, and Judgments. Neuron 57, 11–23. https://doi.org/10.1016/j.neuron.2007.12.013

Duc, G., Largo, R.H., 1986. Anterior fontanel: size and closure in term and preterm infants. Pediatrics 78, 904–908.

Dundas, E.M., Plaut, D.C., Behrmann, M., 2014. An ERP investigation of the co-development of hemispheric lateralization of face and word recognition. Neuropsychologia 61, 315–323. https://doi.org/10.1016/j.neuropsychologia.2014.05.006

Dundas, E.M., Plaut, D.C., Behrmann, M., 2013. The joint development of hemispheric lateralization for words and faces. Journal of Experimental Psychology: General 142, 348. https://doi.org/10.1037/a0029503

Durand, K., Baudouin, J.-Y., Lewkowicz, D.J., Goubet, N., Schaal, B., 2013. Eye-catching odors: olfaction elicits sustained gazing to faces and eyes in 4-month-old infants. PLoS ONE 8, 1–8. https://doi.org/10.1371/journal.pone.0070677

Durand, K., Schaal, B., Goubet, N., Lewkowicz, D.J., Baudouin, J.-Y., 2020. Does any mother's body odor stimulate interest in mother's face in 4-month-old infants? Infancy 25. https://doi.org/10.1111/infa.12322

Edelman, G.M., 1993. Neural darwinism: selection and reentrant signaling in higher brain function. Neuron 10, 115–125. https://doi.org/10.1016/0896-6273(93)90304-A

Edmond, K.M., Kirkwood, B.R., Amenga-Etego, S., Owusu-Agyei, S., Hurt, L.S., 2007. Effect of early infant feeding practices on infection-specific neonatal mortality: an investigation of the causal links with observational data from rural Ghana. The American journal of clinical nutrition 86, 1126–1131. https://doi.org/10.1093/ajcn/86.4.1126

Edmond, K.M., Zandoh, C., Quigley, M.A., Amenga-Etego, S., Owusu-Agyei, S., Kirkwood, B.R., 2006. Delayed breastfeeding initiation increases risk of neonatal mortality. Pediatrics 117, e380–e386. https://doi.org/10.1542/peds.2005-1496

Eimas, P.D., Quinn, P.C., 1994. Studies on the formation of perceptually based basic-level categories in young infants. Child development 65, 903–917. https://doi.org/10.1111/j.1467-8624.1994.tb00792.x

Eimer, M., 2011. The Face-Sensitive N170 Component of the Event-Related Brain Potential, in: Calder, A.J., Rhodes, G., Johnson, M.H., Haxby, J.V. (Eds.), The Oxford Handbook of Face Perception. Oxford University Press. https://doi.org/10.1093/oxfordhb/9780199559053.013.0017

Ekman, P., 1993. Facial expression and emotion. American psychologist 48, 384. https://doi.org/10.1037//0003-066x.48.4.384

Elliott, R., Dolan, R.J., Frith, C.D., 2000. Dissociable Functions in the Medial and Lateral Orbitofrontal Cortex: Evidence from Human Neuroimaging Studies. Cereb Cortex 10, 308–317. https://doi.org/10.1093/cercor/10.3.308

Elsabbagh, M., Gliga, T., Pickles, A., Hudry, K., Charman, T., Johnson, M.H., 2013. The development of face orienting mechanisms in infants at-risk for autism. Behavioural Brain Research, SI:Neurobiology of Autism 251, 147–154. https://doi.org/10.1016/j.bbr.2012.07.030

Elsner, B., Jeschonek, S., Pauen, S., 2013. Event-related potentials for 7-month-olds' processing of animals and furniture items. Developmental Cognitive Neuroscience 3, 53–60. https://doi.org/10.1016/j.dcn.2012.09.002

Emberson, L.L., Richards, J.E., Aslin, R.N., 2015. Top-down modulation in the infant brain: Learning-induced expectations rapidly affect the sensory cortex at 6 months. PNAS 112, 9585–9590. https://doi.org/10.1073/pnas.1510343112

Ernst, M.O., Banks, M.S., 2002. Humans integrate visual and haptic information in a statistically optimal fashion. Nature 415, 429–433. https://doi.org/10.1038/415429a

Ernst, M.O., Bülthoff, H.H., 2004. Merging the senses into a robust percept. Trends in Cognitive Sciences 8, 162–169. https://doi.org/10.1016/j.tics.2004.02.002

Faas, A.E., Spontón, E.D., Moya, P.R., Molina, J.C., 2000. Differential responsiveness to alcohol odor in human neonates: Efects of maternal consumption during gestation. Alcohol 22, 7–17. https://doi.org/10.1016/S0741-8329(00)00103-8

Farah, M.J., Wilson, K.D., Drain, M., Tanaka, J.N., 1998. What is "special" about face perception? Psychological Review 105, 482–498. https://doi.org/10.1037/0033-295X.105.3.482

Farzin, F., Hou, C., Norcia, A.M., 2012. Piecing it together: Infants' neural responses to face and object structure. Journal of Vision 12, 6–6. https://doi.org/10.1167/12.13.6

Fausey, C.M., Jayaraman, S., Smith, L.B., 2016. From faces to hands: Changing visual input in the first two years. Cognition 152, 101–107. https://doi.org/10.1016/j.cognition.2016.03.005

Ferdenzi, C., Schaal, B., Roberts, S.C., 2010. Family Scents: Developmental Changes in the Perception of Kin Body Odor? J Chem Ecol 36, 847–854. https://doi.org/10.1007/s10886-010-9827-x

Fialová, J., Roberts, S.C., Havlícek, J., 2016. Consumption of garlic positively affects hedonic perception of axillary body odour. Appetite 97, 8–15. https://doi.org/10.1016/j.appet.2015.11.001

Fialová, J., Třebický, V., Kuba, R., Stella, D., Binter, J., Havlícek, J., 2020. Losing stinks! The effect of competition outcome on body odour quality. Philosophical Transactions of the Royal Society B: Biological Sciences 375, 20190267. https://doi.org/10.1098/rstb.2019.0267

Field, T., Healy, B., Goldstein, S., Perry, S., Bendell, D., Schanberg, S., Zimmerman, E.A., Kuhn, C., 1988. Infants of Depressed Mothers Show "Depressed" Behavior Even with Nondepressed Adults. Child Development 59, 1569–1579. https://doi.org/10.2307/1130671

Fletcher-Watson, S., Findlay, J.M., Leekam, S.R., Benson, V., 2008. Rapid Detection of Person Information in a Naturalistic Scene. Perception 37, 571–583. https://doi.org/10.1068/p5705

Forscher, E.C., Li, W., 2012. Hemispheric Asymmetry and Visuo-Olfactory Integration in Perceiving Subthreshold (Micro) Fearful Expressions. J. Neurosci. 32, 2159–2165. https://doi.org/10.1523/JNEUROSCI.5094-11.2012

Frank, M.C., Vul, E., Johnson, S.P., 2009. Development of infants' attention to faces during the first year. Cognition 110, 160–170. https://doi.org/10.1016/j.cognition.2008.11.010

Fransson, P., Metsäranta, M., Blennow, M., Åden, U., Lagercrantz, H., Vanhatalo, S., 2013. Early development of spatial patterns of power-law frequency scaling in fMRI resting-state and EEG data in the newborn brain. Cereb Cortex 23, 638–646. https://doi.org/10.1093/cercor/bhs047

Fredrikson, M., Wik, G., Fischer, H., Andersson, J., 1995. Affective and attentive neural networks in humans: A PET study of Pavlovian conditioning. Neuroreport: An International Journal for the Rapid Communication of Research in Neuroscience 7, 97–101. https://doi.org/10.1097/00001756-199512000-00023

Frie, J., Bartocci, M., Kuhn, P., 2019. Neonatal cortical perceptions of maternal breast odours: A fNIRS study. Acta Paediatrica 1–8. https://doi.org/10.1111/apa.15114

Frumin, I., Perl, O., Endevelt-Shapira, Y., Eisen, A., Eshel, N., Heller, I., Shemesh, M., Ravia, A., Sela, L., Arzi, A., Sobel, N., 2015. A social chemosignaling function for human handshaking. eLife 4, e05154. https://doi.org/10.7554/eLife.05154

Fujioka, T., Mourad, N., He, C., Trainor, L.J., 2011. Clinical neurophysiology comparison of artifact correction methods for infant EEG applied to extraction of event-related potential signals. Clinical Neurophysiology 122, 43–51. https://doi.org/10.1016/j.clinph.2010.04.036

Gaby, J.M., Dalton, P., 2019. Discrimination Between Individual Body Odors Is Unaffected by Perfume: Perception. https://doi.org/10.1177/0301006619872055

Gaby, J.M., Zayas, V., 2017. Smelling is Telling: Human Olfactory Cues Influence Social Judgments in Semi-Realistic Interactions. Chem Senses 42, 405–418. https://doi.org/10.1093/chemse/bjx012

Gao, X., Gentile, F., Rossion, B., 2018. Fast periodic stimulation (FPS): a highly effective approach in fMRI brain mapping. Brain Structure and Function 223, 2433–2454. https://doi.org/10.1007/s00429-018-1630-4

Gao, X., Vuong, Q.C., Rossion, B., 2019. The cortical face network of the prosopagnosic patient PS with fast periodic stimulation in fMRI. Cortex 119, 528–542. https://doi.org/10.1016/j.cortex.2018.11.008

Gasper, K., Clore, G.L., 2002. Attending to the Big Picture: Mood and Global Versus Local Processing of Visual Information. Psychol Sci 13, 34–40. https://doi.org/10.1111/1467-9280.00406

Gathers, A.D., Bhatt, R., Corbly, C.R., Farley, A.B., Joseph, J.E., 2004. Developmental shifts in cortical loci for face and object recognition: NeuroReport 15, 1549–1553. https://doi.org/10.1097/01.wnr.0000133299.84901.86

Gauthier, I., Skudlarski, P., Gore, J.C., Anderson, A.W., 2000. Expertise for cars and birds recruits brain areas involved in face recognition. Nature neuroscience 3, 191–197. https://doi.org/10.1038/72140

George, N., Jemel, B., Fiori, N., Chaby, L., Renault, B., 2005. Electrophysiological correlates of facial decision: Insights from upright and upside-down Mooney-face perception. Cognitive Brain Research 24, 663–673. https://doi.org/10.1016/j.cogbrainres.2005.03.017

Ghazanfar, A., Schroeder, C., 2006. Is neocortex essentially multisensory? Trends in Cognitive Sciences 10, 278–285. https://doi.org/10.1016/j.tics.2006.04.008

Giard, M.-H., Besle, J., 2010. Methodological considerations: electrophysiology of multisensory interactions in humans, in: Multisensory Object Perception in the Primate Brain. Springer, pp. 55–70.

Gibbs, B.G., Forste, R., Lybbert, E., 2018. Breastfeeding, Parenting, and Infant Attachment Behaviors. Matern Child Health J 22, 579–588. https://doi.org/10.1007/s10995-018-2427-z

Gibson, E.J., 2000. Perceptual Learning in Development: Some Basic Concepts. Ecological Psychology 12, 295–302. https://doi.org/10.1207/S15326969ECO1204_04

Gibson, E.J., 1969. Principles of perceptual learning and development, Principles of perceptual learning and development. Appleton-Century-Crofts, East Norwalk, CT, US.

Gibson, J.J., 1966. The senses considered as perceptual systems, The senses considered as perceptual systems. Houghton Mifflin, Oxford, England.

Gilchrist, I.D., Proske, H., 2006. Anti-saccades away from faces: evidence for an influence of high-level visual processes on saccade programming. Exp Brain Res 173, 708–712. https://doi.org/10.1007/s00221-006-0455-1

Gildersleeve, K.A., Haselton, M.G., Larson, C.M., Pillsworth, E.G., 2012. Body odor attractiveness as a cue of impending ovulation in women: evidence from a study using hormone-confirmed ovulation. Hormones and behavior 61, 157–166. https://doi.org/10.1016/j.yhbeh.2011.11.005

Gliga, T., Dehaene-Lambertz, G., 2007. Development of a view-invariant representation of the human head. Cognition 102, 261–288. https://doi.org/10.1016/j.cognition.2006.01.004

Gliga, T., Dehaene-Lambertz, G., 2005. Structural encoding of body and face in human infants and adults. Journal of Cognitive Neuroscience 17, 1328–1340. https://doi.org/10.1162/0898929055002481

Gliga, T., Elsabbagh, M., Andravizou, A., Johnson, M.H., 2009. Faces Attract Infants' Attention in Complex Displays. Infancy 14, 550–562. https://doi.org/10.1080/15250000903144199

Gluckman, M., Johnson, S.P., 2013. Attentional capture by social stimuli in young infants. Front. Psychol. 4. https://doi.org/10.3389/fpsyg.2013.00527

Godard, O., Baudouin, J.-Y., Schaal, B., Durand, K., 2016. Affective matching of odors and facial expressions in infants: shifting patterns between 3 and 7 months. Developmental Science 19, 155–163. https://doi.org/10.1111/desc.12292

Gomes, N., Silva, F., Semin, G.R., 2020. The lasting smell of emotions: The effects of reutilizing fear sweat samples. Behavior Research Methods. https://doi.org/10.3758/s13428-020-01412-5

Gopnik, A., Bonawitz, E., 2015. Bayesian models of child development. WIREs Cognitive Science 6, 75–86. https://doi.org/10.1002/wcs.1330

Goren, C.C., Sarty, M., Wu, P.Y.K., 1975. Visual Following and Pattern Discrimination of Face-like Stimuli by Newborn Infants. Pediatrics 56, 544–549.

Gottfried, J.A., Dolan, R.J., 2003. The Nose Smells What the Eye Sees: Crossmodal Visual Facilitation of Human Olfactory Perception. Neuron 39, 375–386. https://doi.org/10.1016/S0896-6273(03)00392-1

Gottfried, J.A., Smith, A.P.R., Rugg, M.D., Dolan, R.J., 2004. Remembrance of Odors Past: Human Olfactory Cortex in Cross-Modal Recognition Memory. Neuron 42, 687–695. https://doi.org/10.1016/S0896-6273(04)00270-3

Gottlieb, G., 1971. Ontogenesis of sensory function in birds and mammals, in: Tobach, E., Aronson, L., Shaw, E. (Eds.), The Biopsychology of Development. Academic Press, New York, pp. 67–128.

Granqvist, P., Vestbrant, K., Döllinger, L., Liuzza, M.T., Olsson, M.J., Blomkvist, A., Lundström, J.N., 2019. The scent of security: Odor of romantic partner alters subjective discomfort and autonomic stress responses in an adult attachment-dependent manner. Physiology & Behavior 198, 144–150. https://doi.org/10.1016/j.physbeh.2018.08.024

Graven, S.N., 2004. Early neurosensory visual development of the fetus and newborn. Clinics in Perinatology 31, 199–216. https://doi.org/10.1016/j.clp.2004.04.010

Graven, S.N., Browne, J.V., 2008. Visual Development in the Human Fetus, Infant, and Young Child. Newborn and Infant Nursing Reviews, Brain Development of the Neonate 8, 194–201. https://doi.org/10.1053/j.nainr.2008.10.011

Gregory, R.L., 1997. Knowledge in perception and illusion. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 352, 1121–1127. https://doi.org/10.1098/rstb.1997.0095

Grill-Spector, K., Knouf, N., Kanwisher, N., 2004. The fusiform face area subserves face perception, not generic within-category identification. Nat Neurosci 7, 555–562. https://doi.org/10.1038/nn1224

Grill-Spector, K., Weiner, K.S., 2014. The functional architecture of the ventral temporal cortex and its role in categorization. Nature Publishing Group. https://doi.org/10.1038/nrn3747

Grill-Spector, K., Weiner, K.S., Gomez, J., Stigliani, A., Natu, V.S., 2018. The functional neuroanatomy of face perception: from brain measurements to deep neural networks. Interface Focus 8, 20180013. https://doi.org/10.1098/rsfs.2018.0013

Grill-Spector, K., Weiner, K.S., Kay, K., Gomez, J., 2017. The Functional Neuroanatomy of Human Face Perception. Annual Review of Vision Science 3, 167–196. https://doi.org/10.1146/annurev-vision-102016-061214

Gronau, Q.F., Ly, A., Wagenmakers, E.-J., 2020. Informed Bayesian t-Tests. The American Statistician 74, 137–143. https://doi.org/10.1080/00031305.2018.1562983

Grossmann, T., 2013. The role of medial prefrontal cortex in early social cognition. Front. Hum. Neurosci. 7. https://doi.org/10.3389/fnhum.2013.00340

Grossmann, T., Gliga, T., Johnson, M.H., Mareschal, D., 2009. The neural basis of perceptual category learning in human infants. Journal of Cognitive Neuroscience 21, 2276–2286. https://doi.org/10.1162/jocn.2009.21188

Gschwind, M., Pourtois, G., Schwartz, S., Van De Ville, D., Vuilleumier, P., 2012. White-Matter Connectivity between Face-Responsive Regions in the Human Brain. Cereb Cortex 22, 1564–1576. https://doi.org/10.1093/cercor/bhr226

Guellaï, B., Coulon, M., Streri, A., 2011. The role of motion and speech in face recognition at birth. Visual Cognition 19, 1212–1233. https://doi.org/10.1080/13506285.2011.620578

Guy, M.W., Richards, J.E., Tonnsen, B.L., Roberts, J.E., 2018. Neural correlates of face processing in etiologically-distinct 12-month-old infants at high-risk of autism spectrum disorder. Developmental Cognitive Neuroscience, Autism Spectrum Condition – understanding sensory and social features 29, 61–71. https://doi.org/10.1016/j.dcn.2017.03.002

Guy, M.W., Zieber, N., Richards, J.E., 2016. The Cortical Development of Specialized Face Processing in Infancy. Child Development 87, 1581–1600. https://doi.org/10.1111/cdev.12543

Haegler, K., Zernecke, R., Kleemann, A.M., Albrecht, J., Pollatos, O., Brückmann, H., Wiesmann, M., 2010. No fear no risk! Human risk behavior is affected by chemosensory anxiety signals. Neuropsychologia 48, 3901–3908. https://doi.org/10.1016/j.neuropsychologia.2010.09.019

Hagen, S., Jacques, C., Maillard, L., Colnat-Coulbois, S., Rossion, B., Jonas, J., 2020. Spatially Dissociated Intracerebral Maps for Face- and House-Selective Activity in the Human Ventral Occipito-Temporal Cortex. Cereb Cortex. https://doi.org/10.1093/cercor/bhaa022

Halit, H., de Haan, M., Johnson, M.H., 2003. Cortical specialisation for face processing: Face-sensitive event-related potential components in 3- and 12-month-old infants. NeuroImage. https://doi.org/10.1016/S1053-8119(03)00076-4

Haller, R., Rummel, C., Henneberg, S., Pollmer, U., Köster, E.P., 1999. The influence of early experience with vanillin on food preference later in life. Chemical senses 24, 465.

Hare, R.M., Schlatter, S., Rhodes, G., Simmons, L.W., 2017. Putative sex-specific human pheromones do not affect gender perception, attractiveness ratings or unfaithfulness judgements of opposite sex faces. Royal Society Open Science 4, 160831. https://doi.org/10.1098/rsos.160831

Harker, M., 2013. Psychological Sweating: A Systematic Review Focused on Aetiology and Cutaneous Response. SPP 26, 92–100. https://doi.org/10.1159/000346930

Harnad, S., 2003. Categorical Perception, in: Encyclopedia of Cognitive Science. Presented at the Encyclopedia of Cognitive Science (01/12/03), Nature Publishing Group: Macmillan.

Hatfield, E., Cacioppo, J.T., Rapson, R.L., 1993. Emotional contagion. Current directions in psychological science 2, 96–100.

Havlícek, J., Fialová, J., Roberts, S.C., 2017. Individual Variation in Body Odor, in: Buettner, A. (Ed.), Springer Handbook of Odor, Springer Handbooks. Springer International Publishing, Cham, pp. 125–126. https://doi.org/10.1007/978-3-319-26932-0_50

Havlícek, J., Lenochova, P., 2006. The effect of meat consumption on body odor attractiveness. Chemical senses 31, 747–752. https://doi.org/10.1093/chemse/bjl017

Havlícek, J., Roberts, S.C., 2009. MHC-correlated mate choice in humans: A review. Psychoneuroendocrinology 34, 497–512. https://doi.org/10.1016/j.psyneuen.2008.10.007

Havlícek, J., Saxton, T.K., Roberts, S.C., Jozifkova, E., Lhota, S., Valentova, J., Flegr, J., 2008. He sees, she smells? Male and female reports of sensory reliance in mate choice and non-mate choice contexts. Personality and Individual Differences 45, 565–570. https://doi.org/10.1016/j.paid.2008.06.019

Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., Pietrini, P., 2001. Distributed and Overlapping Representations of Faces and Objects in Ventral Temporal Cortex. Science 293, 2425–2430. https://doi.org/10.1126/science.1063736

Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2002. Human neural systems for face recognition and social communication. Biological Psychiatry, Social Anxiety: From Laboratory Studies to Clinical Practice 51, 59–67. https://doi.org/10.1016/S0006-3223(01)01330-0

Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. Review: The distributed human neural system for face perception. Trends in Cognitive Sciences 4, 223–232. https://doi.org/10.1016/S1364-6613(00)01482-0

Hedrick, P.W., Black, F.L., 1997. HLA and mate selection: no evidence in South Amerindians. The American Journal of Human Genetics 61, 505–511. https://doi.org/10.1086/515519

Helfer, K.S., 1998. Auditory and auditory-visual recognition of clear and conversational speech by older adults. Journal of the American Academy of Audiology 9, 234–242.

Helmholtz, H. von, 1866. Concerning the perceptions in general. Treatise on physiological optics. New York: Dover.

Heron-Delaney, M., Damon, F., Quinn, P.C., Méary, D., Xiao, N.G., Lee, K., Pascalis, O., 2017. An adult face bias in infants that is modulated by face race. International journal of behavioral development 41, 581–587. https://doi.org/10.1177/0165025416651735

Herrick, C.J., 1933. Morphogenesis of the brain. Journal of Morphology 54, 233–258. https://doi.org/10.1002/jmor.1050540202

Hershler, O., Hochstein, S., 2005. At first sight: A high-level pop out effect for faces. Vision Research 45, 1707–1724. https://doi.org/10.1016/j.visres.2004.12.021

Herz, R.S., Cahill, E.D., 1997. Differential use of sensory information in sexual behavior as a function of gender. Hum Nat 8, 275–286. https://doi.org/10.1007/BF02912495

Herz, R.S., Inzlicht, M., 2002. Sex differences in response to physical and social factors involved in human mate selection: The importance of smell for women. Evolution and Human Behavior 23, 359–364. https://doi.org/10.1016/S1090-5138(02)00095-8

Herz, R.S., von Clef, J., 2001. The Influence of Verbal Labeling on the Perception of Odors: Evidence for Olfactory Illusions? Perception 30, 381–391. https://doi.org/10.1068/p3179

Hillger, L.A., Koenig, O., 1991. Separable Mechanisms in Face Processing: Evidence from Hemispheric Specialization. Journal of Cognitive Neuroscience 3, 42–58. https://doi.org/10.1162/jocn.1991.3.1.42

Hoehl, S., 2016. The development of category specificity in infancy — What can we learn from electrophysiology? Neuropsychologia 83. https://doi.org/10.1016/j.neuropsychologia.2015.08.021

Hoehl, S., Peykarjou, S., 2012. The early development of face processing — What makes faces special? Neuroscience Bulletin 28, 765–788. https://doi.org/10.1007/s12264-012-1280-0

Hofer, M.K., Chen, F.S., 2020. The Scent of a Good Night's Sleep: Olfactory Cues of a Romantic Partner Improve Sleep Efficiency: Psychological Science. https://doi.org/10.1177/0956797620905615

Holmes, N.P., 2009. The Principle of Inverse Effectiveness in Multisensory Integration: Some Statistical Considerations. Brain Topogr 21, 168–176. https://doi.org/10.1007/s10548-009-0097-2

Holmes, N.P., 2007. The law of inverse effectiveness in neurons and behaviour: Multisensory integration versus normal variability. Neuropsychologia 45, 3340–3345. https://doi.org/10.1016/j.neuropsychologia.2007.05.025

Holt-Lunstad, J., Smith, T.B., Layton, J.B., 2010. Social Relationships and Mortality Risk: A Meta-analytic Review. PLOS Medicine 7, e1000316. https://doi.org/10.1371/journal.pmed.1000316

Honda, Y., Nakato, E., Otsuka, Y., Kanazawa, S., Kojima, S., Yamaguchi, M.K., Kakigi, R., 2010. How do infants perceive scrambled face?: A near-infrared spectroscopic study. Brain research 1308, 137–146. https://doi.org/10.1016/j.brainres.2009.10.046

Hörberg, T., Larsson, M., Ekström, I., Sandöy, C., Lundén, P., Olofsson, J.K., 2020. Olfactory Influences on Visual Categorization: Behavioral and ERP Evidence. Cereb Cortex. https://doi.org/10.1093/cercor/bhaa050

Hummel, T., Nordin, S., 2005. Olfactory disorders and their consequences for quality of life. Acta Oto-Laryngologica 125, 116–121. https://doi.org/10.1080/00016480410022787

Hutmacher, F., 2019. Why Is There So Much More Research on Vision Than on Any Other Sensory Modality? Front. Psychol. 10. https://doi.org/10.3389/fpsyg.2019.02246

Ichikawa, H., Kanazawa, S., Yamaguchi, M.K., 2011. Finding a face in a face-like object. Perception 40, 500–502. https://doi.org/10.1068/p6926

Itier, R.J., Taylor, M.J., 2004. N170 or N1? Spatiotemporal Differences between Object and Face Processing Using ERPs. Cereb Cortex 14, 132–142. https://doi.org/10.1093/cercor/bhg111

Jackman, P.J.H., Noble, W.C., 1983. Normal axillary skin in various populations. Clinical and Experimental Dermatology 8, 259–268. https://doi.org/10.1111/j.1365-2230.1983.tb01778.x

Jackson, A.F., Bolger, D.J., 2014. The neurophysiological bases of EEG and EEG measurement: A review for the rest of us: Neurophysiological bases of EEG. Psychophysiology 51, 1061–1071. https://doi.org/10.1111/psyp.12283

Jacob, S., McClintock, M.K., Zelano, B., Ober, C., 2002. Paternally inherited HLA alleles are associated with women's choice of male odor. Nature genetics 30, 175–179. https://doi.org/10.1038/ng830

Jacob, S., Spencer, N.A., Bullivant, S.B., Sellergren, S.A., Mennella, J.A., McClintock, M.K., 2004. Effects of breastfeeding chemosignals on the human menstrual cycle. Hum Reprod 19, 422–429. https://doi.org/10.1093/humrep/deh057

Jacques, C., Retter, T.L., Rossion, B., 2016a. A single glance at natural face images generate larger and qualitatively different category-selective spatio-temporal signatures than other ecologically-relevant categories in the human brain. NeuroImage 137, 21–33. https://doi.org/10.1016/j.neuroimage.2016.04.045

Jacques, C., Witthoft, N., Weiner, K.S., Foster, B.L., Rangarajan, V., Hermes, D., Miller, K.J., Parvizi, J., Grill-Spector, K., 2016b. Corresponding ECoG and fMRI category-selective signals in human ventral temporal cortex. Neuropsychologia, Special Issue: Functional Selectivity in Perceptual and Cognitive Systems - A Tribute to Shlomo Bentin (1946-2012) 83, 14–28. https://doi.org/10.1016/j.neuropsychologia.2015.07.024

Jadauji, J.B., Djordjevic, J., Lundstrom, J.N., Pack, C.C., 2012. Modulation of Olfactory Perception by Visual Cortex Stimulation. Journal of Neuroscience 32, 3095–3100. https://doi.org/10.1523/JNEUROSCI.6022-11.2012

Jakobsen, K.V., Umstead, L., Simpson, E.A., 2016. Efficient human face detection in infancy: Infant Face Detection. Developmental Psychobiology 58, 129–136. https://doi.org/10.1002/dev.21338

James, A.G., Austin, C.J., Cox, D.S., Taylor, D., Calvert, R., 2013. Microbiological and biochemical origins of human axillary odour. FEMS Microbiology Ecology 83, 527–540. https://doi.org/10.1111/1574-6941.12054

Jansen, P.W., Duijff, S.N., Beemer, F.A., Vorstman, J.A.S., Klaassen, P.W.J., Morcus, M.E.J., Heineman-de Boer, J.A., 2007. Behavioral problems in relation to intelligence in children with 22q11. 2 deletion syndrome: a matched control study. American Journal of Medical Genetics Part A 143, 574–580. https://doi.org/10.1002/ajmg.a.31623

Jayaraman, S., Fausey, C.M., Smith, L.B., 2015. The faces in infant-perspective scenes change over the first year of life. PloS one 10, e0123780. https://doi.org/10.1371/journal.pone.0123780

Jebreili, M., Neshat, H., Seyyedrasouli, A., Ghojazade, M., Hosseini, M.B., Hamishehkar, H., 2015. Comparison of Breastmilk Odor and Vanilla Odor on Mitigating Premature Infants'

Response to Pain During and After Venipuncture. Breastfeeding Medicine 10, 362–365. https://doi.org/10.1089/bfm.2015.0060

Jessen, S., 2020. Maternal odor reduces the neural response to fearful faces in human infants. Developmental Cognitive Neuroscience 45, 100858. https://doi.org/10.1016/j.dcn.2020.100858

Johnson, M.H., 2011. Interactive Specialization: A domain-general framework for human functional brain development? Developmental Cognitive Neuroscience 1, 7–21. https://doi.org/10.1016/j.dcn.2010.07.003

Johnson, M.H., Dziurawiec, S., Ellis, H., Morton, J., 1991. Newborns' preferential tracking of face-like stimuli and its subsequent decline. Cognition 40, 1–19. https://doi.org/10.1016/0010-0277(91)90045-6

Jonas, J., Jacques, C., Liu-Shuang, J., Brissart, H., Colnat-Coulbois, S., Maillard, L., Rossion, B., 2016. A face-selective ventral occipito-temporal map of the human brain with intracerebral potentials. Proceedings of the National Academy of Sciences 113, E4088–E4097. https://doi.org/10.1073/pnas.1522033113

Kaiser, D., Häberle, G., Cichy, R.M., 2020. Real-world structure facilitates the rapid emergence of scene category information in visual brain signals. Journal of Neurophysiology 124, 145–151. https://doi.org/10.1152/jn.00164.2020

Kaiser, D., Quek, G.L., Cichy, R.M., Peelen, M.V., 2019. Object Vision in a Structured World. Trends in Cognitive Sciences 23, 672–685. https://doi.org/10.1016/j.tics.2019.04.013

Kaiser, D., Stein, T., Peelen, M.V., 2014. Object grouping based on real-world regularities facilitates perception by reducing competitive interactions in visual cortex. Proceedings of the National Academy of Sciences 111, 11217–11222. https://doi.org/10.1073/pnas.1400559111

Kaitz, M., Good, A., Rokem, A.M., Eidelman, A.I., 1987. Mothers' recognition of their newborns by olfactory cues. Developmental Psychobiology 20, 587–591. https://doi.org/10.1002/dev.420200604

Kamiloğlu, R.G., Smeets, M.A.M., de Groot, J.H.B., Semin, G.R., 2018. Fear Odor Facilitates the Detection of Fear Expressions Over Other Negative Expressions. Chem Senses 43, 419–426. https://doi.org/10.1093/chemse/bjy029

Kamps, F.S., Hendrix, C.L., Brennan, P.A., Dilks, D.D., 2020. Connectivity at the origins of domain specificity in the cortical face and place networks. PNAS 117, 6163–6169. https://doi.org/10.1073/pnas.1911359117

Kanwisher, N., McDermott, J., Chun, M.M., 1997. The Fusiform Face Area: A Module in Human Extrastriate Cortex Specialized for Face Perception. The Journal of Neuroscience 17, 4302–4311. https://doi.org/10.1523/JNEUROSCI.17-11-04302.1997

Karlson, P., Lüscher, M., 1959. 'Pheromones': a New Term for a Class of Biologically Active Substances. Nature 183, 55–56. https://doi.org/10.1038/183055a0

Kayhan, E., Heil, L., Kwisthout, J., Rooij, I. van, Hunnius, S., Bekkering, H., 2019a. Young children integrate current observations, priors and agent information to predict others' actions. PLOS ONE 14, e0200976. https://doi.org/10.1371/journal.pone.0200976

Kayhan, E., Hunnius, S., O'Reilly, J.X., Bekkering, H., 2019b. Infants differentially update their internal models of a dynamic environment. Cognition 186, 139–146. https://doi.org/10.1016/j.cognition.2019.02.004

Kayhan, E., Meyer, M., O'Reilly, J.X., Hunnius, S., Bekkering, H., 2019c. Nine-month-old infants update their predictive models of a changing environment. Developmental Cognitive Neuroscience 38, 100680. https://doi.org/10.1016/j.dcn.2019.100680

Kelly, D.J., Duarte, S., Meary, D., Bindemann, M., Pascalis, O., 2019. Infants rapidly detect human faces in complex naturalistic visual scenes. Developmental Science e12829. https://doi.org/10.1111/desc.12829

Kelly, D.J., Quinn, P.C., Slater, A.M., Lee, K., Gibson, A., Smith, M., Ge, L., Pascalis, O., 2005. Three-month-olds, but not newborns, prefer own-race faces. Developmental Science 8, 31–36. https://doi.org/10.1111/j.1467-7687.2005.0434a.x.

Kermen, F., Chakirian, A., Sezille, C., Joussain, P., Le Goff, G., Ziessel, A., Chastrette, M., Mandairon, N., Didier, A., Rouby, C., Bensafi, M., 2011. Molecular complexity determines the number of olfactory notes and the pleasantness of smells. Sci Rep 1, 1–6. https://doi.org/10.1038/srep00206

Kirchner, H., Thorpe, S.J., 2006. Ultra-rapid object detection with saccadic eye movements: Visual processing speed revisited. Vision Research 46, 1762–1776. https://doi.org/10.1016/j.visres.2005.10.002

Kirk-Smith, M.D., Booth, D.A., 1980. Effects of androstenone on choice of location in other’s presence. Olfaction and Taste VII. IRL Press, London 397–400.

Knasko, S.C., 1995. Pleasant Odors and Congruency: Effects on Approach Behavior. Chem Senses 20, 479–487. https://doi.org/10.1093/chemse/20.5.479

Knasko, S.C., 1992. Ambient odor’s effect on creativity, mood, and perceived health. Chem Senses 17, 27–35. https://doi.org/10.1093/chemse/17.1.27

Kobayashi, M., Otsuka, Y., Nakato, E., Kanazawa, S., Yamaguchi, M.K., Kakigi, R., 2012. Do infants recognize the Arcimboldo images as faces? Behavioral and near-infrared spectroscopic study. Journal of Experimental Child Psychology 111, 22–36. https://doi.org/10.1016/j.jecp.2011.07.008

Koelega, H.S., Köster, E.P., 1974. Some experiments on sex differences in odor perception. Annals of the New York Academy of Sciences 237, 234–246. https://doi.org/10.1111/j.1749-6632.1974.tb49859.x

Köster, M., Kayhan, E., Langeloh, M., Hoehl, S., 2020. Making Sense of the World: Infant Learning From a Predictive Processing Perspective: Perspectives on Psychological Science. https://doi.org/10.1177/1745691619895071

Kouider, S., Long, B., Le Stanc, L., Charron, S., Fievet, A.-C., Barbosa, L.S., Gelskov, S.V., 2015. Neural dynamics of prediction and surprise in infants. Nature Communications 6, 8537. https://doi.org/10.1038/ncomms9537

Kouider, S., Stahlhut, C., Gelskov, S.V., Barbosa, L.S., Dutat, M., de Gardelle, V., Christophe, A., Dehaene, S., Dehaene-Lambertz, G., 2013. A neural marker of perceptual consciousness in infants. Science 340, 376–380. https://doi.org/10.1126/science.1232509

Kovács, G., Gulyás, B., Savic, I., Perrett, D.I., Cornwell, R.E., Little, A.C., Jones, B.C., Burt, D.M., Gál, V., Vidnyánszky, Z., 2004. Smelling human sex hormone-like compounds affects face gender judgment of men. NeuroReport 15, 1275–1277. https://doi.org/10.1097/01.wnr.0000130234.51411.0e

Krol, K.M., Monakhov, M., Lai, P.S., Ebstein, R.P., Grossmann, T., 2015a. Genetic variation in CD38 and breastfeeding experience interact to impact infants’ attention to social eye cues. PNAS 112, E5434–E5442. https://doi.org/10.1073/pnas.1506352112

Krol, K.M., Rajhans, P., Missana, M., Grossmann, T., 2015b. Duration of exclusive breastfeeding is associated with differences in infants’ brain responses to emotional body expressions. Front. Behav. Neurosci. 8. https://doi.org/10.3389/fnbeh.2014.00459

Küçük Alemdar, D., Kardaş Özdemir, F., 2017. Effects of Having Preterm Infants Smell Amniotic Fluid, Mother’s Milk, and Mother’s Odor During Heel Stick Procedure on Pain, Physiological Parameters, and Crying Duration. Breastfeeding Medicine 12, 297–304. https://doi.org/10.1089/bfm.2017.0006

Kuefner, D., De Heering, A., Jacques, C., Palmero-Soler, E., Rossion, B., 2010. Early visually evoked electrophysiological responses over the human brain (P1, N170) show stable patterns of face-sensitivity from 4 years to adulthood. Front. Hum. Neurosci. 3. https://doi.org/10.3389/neuro.09.067.2009

Kuhn, F., Natsch, A., 2009. Body odour of monozygotic human twins: a common pattern of odorant carboxylic acids released by a bacterial aminoacylase from axilla secretions contributing to an inherited body odour type. Journal of the Royal Society Interface 6, 377–392. https://doi.org/10.1098/rsif.2008.0223

Kveraga, K., Ghuman, A.S., Bar, M., 2007. Top-down predictions in the cognitive brain. Brain and Cognition 65, 145–168. https://doi.org/10.1016/j.bandc.2007.06.007

Kwon, M.-K., Setoodehnia, M., Baek, J., Luck, S.J., Oakes, L.M., 2016. The development of visual search in infancy: Attention to faces versus salience. Dev Psychol 52, 537–555. https://doi.org/10.1037/dev0000080

Lakatos, P., O'Connell, M.N., Barczak, A., Mills, A., Javitt, D.C., Schroeder, C.E., 2009. The Leading Sense: Supramodal Control of Neurophysiological Context by Attention. Neuron 64, 419–430. https://doi.org/10.1016/j.neuron.2009.10.014

Lambon Ralph, M.A., 2014. Neurocognitive insights on conceptual knowledge and its breakdown. Philosophical Transactions of the Royal Society B: Biological Sciences 369, 20120392. https://doi.org/10.1098/rstb.2012.0392

Lambon Ralph, M.A., Jefferies, E., Patterson, K., Rogers, T.T., 2017. The neural and computational bases of semantic cognition. Nat Rev Neurosci 18, 42–55. https://doi.org/10.1038/nrn.2016.150

Larsson, M., Tirado, C., Wiens, S., 2017. A Meta-Analysis of Odor Thresholds and Odor Identification in Autism Spectrum Disorders. Frontiers in Psychology 8. https://doi.org/10.3389/fpsyg.2017.00679

Laska, M., Shepherd, G.M., 2007. Olfactory discrimination ability of CD-1 mice for a large array of enantiomers. Neuroscience 144, 295–301. https://doi.org/10.1016/j.neuroscience.2006.08.063

Lecanuet, J.-P., Schaal, B., 1996. Fetal sensory competencies. European Journal of Obstetrics & Gynecology and Reproductive Biology 68, 1–23. https://doi.org/10.1016/0301-2115(96)02509-2

Leleu, A., Demily, C., Franck, N., Durand, K., Schaal, B., Baudouin, J.-Y., 2015a. The Odor Context Facilitates the Perception of Low-Intensity Facial Expressions of Emotion. PloS ONE 10, 1–19. https://doi.org/10.1371/journal.pone.0138656

Leleu, A., Favre, E., Yailian, A., Fumat, H., Klamm, J., Amado, I., Baudouin, J.-Y., Franck, N., Demily, C., 2019. An implicit and reliable neural measure quantifying impaired visual coding of facial expression: evidence from the 22q11.2 deletion syndrome. Transl Psychiatry 9, 1–11. https://doi.org/10.1038/s41398-019-0411-z

Leleu, A., Godard, O., Dollion, N., Durand, K., Schaal, B., Baudouin, J.-Y., 2015b. Contextual odors modulate the visual processing of emotional facial expressions : An ERP study. Neuropsychologia 77, 366–379. https://doi.org/10.1016/j.neuropsychologia.2015.09.014

Leleu, A., Rekow, D., Poncet, F., Schaal, B., Durand, K., Rossion, B., Baudouin, J.-Y., 2020. Maternal odor shapes rapid face categorization in the infant brain. Developmental Science 23, e12877. https://doi.org/10.1111/desc.12877

Leleu, A., Saucourt, G., Rigard, C., Chesnoy, G., Baudouin, J.-Y., Rossi, M., Edery, P., Franck, N., Demily, C., 2016. Facial emotion perception by intensity in children and adolescents with 22q11.2 deletion syndrome. European Child & Adolescent Psychiatry 25, 297–310. https://doi.org/10.1007/s00787-015-0741-1

Lenochova, P., Havlícek, J., 2011. Fragrant expectations - Changes of female body odour quality during pregnancy and after delivery. Presented at the Proc. VIth Eur. Human Behav. Evolution Assoc. Conf., Giessen.

Lenochova, P., Roberts, S.C., Havlícek, J., 2008. Methods of Human Body Odor Sampling: The Effect of Freezing. Chemical Senses 34, 127–138. https://doi.org/10.1093/chemse/bjn067

Leo, I., Simion, F., 2009. Newborns' Mooney-Face Perception. Infancy 14, 641–653. https://doi.org/10.1080/15250000903264047

Leppänen, J.M., 2016. Using Eye Tracking to Understand Infants' Attentional Bias for Faces. Child Development Perspectives 10, 161–165. https://doi.org/10.1111/cdep.12180

Leppänen, J.M., Hietanen, J.K., 2003. Affect and Face Perception: Odors Modulate the Recognition Advantage of Happy Faces. Emotion 3, 315–326. https://doi.org/10.1037/1528-3542.3.4.315

Leppänen, J.M., Nelson, C.A., 2012. Early Development of Fear Processing. Current Directions in Psychological Science 21, 200–204. https://doi.org/10.1177/0963721411435841

Lewkowicz, D.J., 2010. The ontogeny of human multisensory object perception: a constructivist account, in: Kaiser, J., Naumer, M.J. (Eds.), Multisensory Object Perception in the Primate Brain. Springer, New York, NY, US, pp. 303–327.

Lewkowicz, D.J., 2000. The development of intersensory temporal perception: an epigenetic systems/limitations view. Psychological bulletin 126, 281–308. https://doi.org/10.1037/0033-2909.126.2.281

Lewkowicz, D.J., 1992. Infants' response to temporally based intersensory equivalence: The effect of synchronous sounds on visual preferences for moving stimuli. Infant Behavior and Development 15, 297–324. https://doi.org/10.1016/0163-6383(92)80002-C

Lewkowicz, D.J., Ghazanfar, A.A., 2009. The emergence of multisensory systems through perceptual narrowing. Trends in Cognitive Sciences 13, 470–478. https://doi.org/10.1016/j.tics.2009.08.004

Lewkowicz, D.J., Lickliter, R., 1994. The Development of Intersensory Perception : Comparative Perspectives. Psychology Press. https://doi.org/10.4324/9780203773079

Li, W., Moallem, I., Paller, K.A., Gottfried, J.A., 2007. Subliminal Smells can Guide Social Preferences. Psychol Sci 18, 1044–1049. https://doi.org/10.1111/j.1467-9280.2007.02023.x

Libertus, K., Needham, A., 2011. Reaching experience increases face preference in 3-month-old infants. Developmental science 14, 1355–1364. https://doi.org/10.1111/j.1467-7687.2011.01084.x

Lickliter, R., Bahrick, L.E., 2004. Perceptual Development and the Origins of Multisensory Responsiveness., in: Calvert, G., Spence, C., Stein, B.E. (Eds.), The Handbook of Multisensory Processes. MIT Press, Cambridge, Massachusetts, pp. 643–654.

Lickliter, R., Bahrick, L.E., 2000. The development of infant intersensory perception: Advantages of a comparative convergent-operations approach. Psychological Bulletin 126, 260–280. https://doi.org/10.1037/0033-2909.126.2.260

Lickliter, R., Hellewell, T.B., 1992. Contextual determinants of auditory learning in bobwhite quail embryos and hatchlings. Developmental Psychobiology 25, 17–31. https://doi.org/10.1002/dev.420250103

Liddell, K., 1976. Smell as a diagnostic marker. Postgraduate medical journal 52, 136–138. http://dx.doi.org/10.1136/pgmj.52.605.136

Lindeberg, T., 2011. Generalized Gaussian Scale-Space Axiomatics Comprising Linear Scale-Space, Affine Scale-Space and Spatio-Temporal Scale-Space. J Math Imaging Vis 40, 36–81. https://doi.org/10.1007/s10851-010-0242-2

Lochy, A., de Heering, A., Rossion, B., 2019a. The non-linear development of the right hemispheric specialization for human face perception. Neuropsychologia 126, 10–19. https://doi.org/10.1016/j.neuropsychologia.2017.06.029

Lochy, A., Schiltz, C., 2019. Lateralized Neural Responses to Letters and Digits in First Graders. Child Development 90, 1866–1874. https://doi.org/10.1111/cdev.13337

Lochy, A., Schiltz, C., Rossion, B., 2019b. The right hemispheric dominance for face perception in preschool children depends on the visual discrimination level. Developmental Science. https://doi.org/10.1111/desc.12914

Loos, H.M., Reger, D., Schaal, B., 2019. The odour of human milk: Its chemical variability and detection by newborns. Physiology & Behavior 199, 88–99. https://doi.org/10.1016/j.physbeh.2018.11.008

Lord, T., Kasprzak, M., 1989. Identification of Self through Olfaction. Percept Mot Skills 69, 219–224. https://doi.org/10.2466/pms.1989.69.1.219

Lübke, K.T., Busch, A., Hoenen, M., Schaal, B., Pause, B.M., 2017. Chemosensory anxiety signals prime defensive behavior in prepubertal girls. Physiol. Behav. 173, 30–33. https://doi.org/10.1016/j.physbeh.2017.01.035

Lübke, K.T., Hoenen, M., Pause, B.M., 2012. Differential processing of social chemosignals obtained from potential partners in regards to gender and sexual orientation. Behavioural Brain Research 228, 375–387. https://doi.org/10.1016/j.bbr.2011.12.018

Lübke, K.T., Pause, B.M., 2015. Always follow your nose: The functional significance of social chemosignals in human reproduction and survival. Hormones and Behavior 68, 134–144. https://doi.org/10.1016/j.yhbeh.2014.10.001

Luisier, A.-C., Petitpierre, G., Bérod, A.C., Garcia-Burgos, D., Bensafi, M., 2018. Effects of familiarization on odor hedonic responses and food choices in children with autism spectrum disorders: Autism. https://doi.org/10.1177/1362361318815252

Lundström, J.N., Boyle, J.A., Zatorre, R.J., Jones-Gotman, M., 2009. The neuronal substrates of human olfactory based kin recognition. Human brain mapping 30, 2571–2580. https://doi.org/10.1002/hbm.20686

Lundström, J.N., Boyle, J.A., Zatorre, R.J., Jones-Gotman, M., 2008. Functional neuronal processing of body odors differs from that of similar common odors. Cerebral Cortex 18, 1466–1474. https://doi.org/10.1093/cercor/bhm178

Lundström, J.N., Mathe, A., Schaal, B., Frasnelli, J., Nitzsche, K., Gerber, J., Hummel, T., 2013. Maternal status regulates cortical responses to the body odor of newborns. Front. Psychol. 4. https://doi.org/10.3389/fpsyg.2013.00597

Lundström, J.N., Olsson, M.J., 2010. Functional Neuronal Processing of Human Body Odors, in: Vitamins & Hormones. Elsevier, pp. 1–23. https://doi.org/10.1016/S0083-6729(10)83001-8

Lundström, J.N., Regenbogen, C., Ohla, K., Seubert, J., 2019. Prefrontal Control Over Occipital Responses to Crossmodal Overlap Varies Across the Congruency Spectrum. Cerebral Cortex 29, 3023–3033. https://doi.org/10.1093/cercor/bhy168

Macfarlane, A., 1975. Olfaction in the development of social preferences in the human neonate. Ciba Found. Symp. 103–117. https://doi.org/10.1002/9780470720158.ch7

Maddock, R.J., 1999. The retrosplenial cortex and emotion: new insights from functional neuroimaging of the human brain. Trends in Neurosciences 22, 310–316. https://doi.org/10.1016/S0166-2236(98)01374-5

Mahon, B.Z., Caramazza, A., 2011. What drives the organization of object knowledge in the brain? Trends in Cognitive Sciences 15, 97–103. https://doi.org/10.1016/j.tics.2011.01.004

Majid, A., Roberts, S.G., Cilissen, L., Emmorey, K., Nicodemus, B., O'Grady, L., Woll, B., LeLan, B., Sousa, H. de, Cansler, B.L., Shayan, S., Vos, C. de, Senft, G., Enfield, N.J., Razak, R.A., Fedden, S., Tufvesson, S., Dingemanse, M., Ozturk, O., Brown, P., Hill, C., Guen, O.L., Hirtzel, V., Gijn, R. van, Sicoli, M.A., Levinson, S.C., 2018. Differential coding of perception in the world's languages. PNAS 115, 11369–11376. https://doi.org/10.1073/pnas.1720419115

Mallet, P., Schaal, B., 1998. Rating and Recognition of Peers' Personal Odors by 9-Year-Old Children: An Exploratory Study. The Journal of General Psychology 125, 47–64. https://doi.org/10.1080/00221309809595576

Malnic, B., Hirono, J., Sato, T., Buck, L.B., 1999. Combinatorial Receptor Codes for Odors. Cell 96, 713–723. https://doi.org/10.1016/S0092-8674(00)80581-4

Mandler, J.M., 2004. The foundations of mind: Origins of conceptual thought. Oxford University Press.

Manesse, C., Fournel, A., Bensafi, M., Ferdenzi, C., 2020. Visual priming influences olfactomotor response and perceptual experience of smells. Chemical Senses. https://doi.org/10.1093/chemse/bjaa008

Mares, I., Ewing, L., Farran, E.K., Smith, F.W., Smith, M.L., 2020. Developmental changes in the processing of faces as revealed by EEG decoding. NeuroImage 211, 116660. https://doi.org/10.1016/j.neuroimage.2020.116660

Mareschal, D., Quinn, P.C., 2001. Categorization in infancy. Trends in Cognitive Sciences 5, 443–450. https://doi.org/10.1016/S1364-6613(00)01752-6

Margalit, E., Jamison, K.W., Weiner, K.S., Vizioli, L., Zhang, R.-Y., Kay, K.N., Grill-Spector, K., 2020. Ultra-high-resolution fMRI of human ventral temporal cortex reveals differential representation of categories and domains. The Journal of Neuroscience 2106–19. https://doi.org/10.1523/JNEUROSCI.2106-19.2020

Marinović, V., Hoehl, S., Pauen, S., 2014. Neural correlates of human–animal distinction: An ERP-study on early categorical differentiation with 4- and 7-month-old infants and adults. Neuropsychologia 60, 60–76. https://doi.org/10.1016/j.neuropsychologia.2014.05.013

Marlier, L., Schaal, B., Soussignan, R., 1998. Neonatal Responsiveness to the Odor of Amniotic and Lacteal Fluids: A Test of Perinatal Chemosensory Continuity. Child Development 69, 611–623. https://doi.org/10.1111/j.1467-8624.1998.00611.x

Martins, Y., Preti, G., Crabtree, C.R., Runyan, T., Vainius, A.A., Wysocki, C.J., 2005. Preference for Human Body Odors Is Influenced by Gender and Sexual Orientation. Psychol Sci 16, 694–701. https://doi.org/10.1111/j.1467-9280.2005.01598.x

Mas, M., Brindisi, M.-C., Chabanet, C., Nicklaus, S., Chambaron, S., 2019. Weight Status and Attentional Biases Toward Foods: Impact of Implicit Olfactory Priming. Front. Psychol. 10. https://doi.org/10.3389/fpsyg.2019.01789

Mattioni, S., Rezk, M., Battal, C., Bottini, R., Cuculiza Mendoza, K.E., Oosterhof, N.N., Collignon, O., 2020. Categorical representation from sound and sight in the ventral occipito-temporal cortex of sighted and blind. eLife 9, e50732. https://doi.org/10.7554/eLife.50732

Maurer, D., Lewis, T.L., 2001. Visual acuity: the role of visual input in inducing postnatal change. Clinical Neuroscience Research 1, 239–247. https://doi.org/10.1016/S1566-2772(01)00010-X

McCarthy, G., Wood, C.C., 1985. Scalp distributions of event-related potentials: an ambiguity associated with analysis of variance models. Electroencephalography and clinical neurophysiology 62, 203–208. https://doi.org/10.1016/0168-5597(85)90015-2

Mcclintock, M.K., 1971. Menstrual Synchrony and Suppression. Nature 229, 244–245. https://doi.org/10.1038/229244a0

McGann, J.P., 2017. Poor human olfaction is a 19th-century myth. Science 356. https://doi.org/10.1126/science.aam7263

McGurk, H., MacDonald, J., 1976. Hearing lips and seeing voices. Nature 264, 746–748. https://doi.org/10.1038/264746a0

Mellier, D., Bezard, S., Caston, J., 1997. Études exploratoires des relations intersensorielles olfaction-douleur. Enfance 50, 98–111. https://doi.org/10.3406/enfan.1997.3049

Mennella, J.A., Beauchamp, G.K., 1993. The Effects of Repeated Exposure to Garlic-Flavored Milk on the Nursling's Behavior. Pediatr Res 34, 805–808. https://doi.org/10.1203/00006450-199312000-00022

Mennella, J.A., Jagnow, C.P., Beauchamp, G.K., 2001. Prenatal and Postnatal Flavor Learning by Human Infants. Pediatrics 107, e88–e88. https://doi.org/10.1542/peds.107.6.e88

Meredith, M.A., Nemitz, J.W., Stein, B.E., 1987. Determinants of multisensory integration in superior colliculus neurons. I. Temporal factors. J. Neurosci. 7, 3215–3229. https://doi.org/10.1523/JNEUROSCI.07-10-03215.1987

Meredith, M.A., Stein, B.E., 1986. Spatial factors determine the activity of muitisensory neurons in cat superior colliculus. Brain Research 365, 350–354. https://doi.org/10.1016/0006-8993(86)91648-3

Meredith, M.A., Stein, B.E., 1983. Interactions among converging sensory inputs in the superior colliculus. Science 221, 389–391. https://doi.org/10.1126/science.6867718

Mezrai, N., Chiao, C.-C., Dickel, L., Darmaillacq, A.-S., 2019. A difference in timing for the onset of visual and chemosensory systems during embryonic development in two closely related cuttlefish species. Developmental Psychobiology 61, 1014–1021. https://doi.org/10.1002/dev.21868

Milinski, M., Croy, I., Hummel, T., Boehm, T., 2013. Major histocompatibility complex peptide ligands as olfactory cues in human body odour assessment. Proceedings of the Royal Society B: Biological Sciences 280, 20122889. https://doi.org/10.1098/rspb.2012.2889

Milton, A., Rowland, A., Stothart, G., Clatworthy, P., Pennington, C.M., Kazanina, N., 2020. Fast Periodic Visual Stimulation indexes preserved semantic memory in healthy ageing. Scientific Reports 10, 13159. https://doi.org/10.1038/s41598-020-69929-5

Mishkin, M., Ungerleider, L.G., 1982. Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys. Behavioural Brain Research 6, 57–77. https://doi.org/10.1016/0166-4328(82)90081-X

Monzalvo, K., Fluss, J., Billard, C., Dehaene, S., Dehaene-Lambertz, G., 2012. Cortical networks for vision and language in dyslexic and normal children of variable socio-economic status. NeuroImage 61, 258–274. https://doi.org/10.1016/j.neuroimage.2012.02.035

Mooney, C.M., 1957. Age in the development of closure ability in children. Canadian Journal of Psychology/Revue canadienne de psychologie 11, 219. https://doi.org/10.1037/h0083717

Moran, D.T., Rowley, J.C., Jafek, B.W., Lovell, M.A., 1982. The fine structure of the olfactory mucosa in man. J. Neurocytol. 11, 721–746. https://doi.org/10.1007/bf01153516

Morgan, S.T., Hansen, J.C., Hillyard, S.A., 1996. Selective attention to stimulus location modulates the steady-state visual evoked potential. PNAS 93, 4770–4774. https://doi.org/10.1073/pnas.93.10.4770

Morrot, G., Brochet, F., Dubourdieu, D., 2001. The Color of Odors. Brain and Language 79, 309–320. https://doi.org/10.1006/brln.2001.2493

Mourad, N., Reilly, J.P., de Bruin, H., Hasey, G., MacCrimmon, D., 2007. A simple and fast algorithm for automatic suppression of high-amplitude artifacts in EEG data, in: 2007 IEEE International Conference on Acoustics, Speech and Signal Processing-ICASSP'07. IEEE, p. I–393. https://doi.org/10.1109/ICASSP.2007.366699

Mujica-Parodi, L.R., Strey, H.H., Frederick, B., Savoy, R., Cox, D., Botanov, Y., Tolkunov, D., Rubin, D., Weber, J., 2009. Chemosensory Cues to Conspecific Emotional Stress Activate Amygdala in Humans. PLOS ONE 4, e6415. https://doi.org/10.1371/journal.pone.0006415

Müller, M.M., Andersen, S., Trujillo, N.J., Valdés-Sosa, P., Malinowski, P., Hillyard, S.A., 2006. Feature-selective attention enhances color signals in early visual areas of the human brain. PNAS 103, 14250–14254. https://doi.org/10.1073/pnas.0606668103

Muntz, W.R.A., 1964. Vision in frogs. Scientific American 210, 110–119. https://doi.org/10.1038/scientificamerican0364-110

Murphy, G.L., 2002. Conceptual combination. The Big Book of Concepts. Cambridge, MA: MIT Press.

Mutic, S., Freiherr, J., Cavazzana, A., Rocha, M., Soares, S.C., Parma, V., 2019. The scent of the other women: Body odor-induced behavioral and physiological effects on face categorization. Physiology & Behavior 210, 112562. https://doi.org/10.1016/j.physbeh.2019.112562

Mutic, S., Parma, V., Brünner, Y.F., Freiherr, J., 2016. You Smell Dangerous: Communicating Fight Responses Through Human Chemosignals of Aggression. Chem Senses 41, 35–43. https://doi.org/10.1093/chemse/bjv058

Nagata, Y., Takeuchi, N., 1990. Measurement of odor threshold by triangle odor bag method. Bulletin of Japan Environmental Sanitation Center 17, 77–89.

Nakato, E., Otsuka, Y., Kanazawa, S., Yamaguchi, M.K., Honda, Y., Kakigi, R., 2011. I know this face: Neural activity during mother'face perception in 7-to 8-month-old infants as investigated by near-infrared spectroscopy. Early human development 87, 1–7. https://doi.org/10.1016/j.earlhumdev.2010.08.030

Natsch, A., 2017. Biochemistry and Genetics of Human Axilla Odor, in: Buettner, A. (Ed.), Springer Handbook of Odor, Springer Handbooks. Springer International Publishing, Cham, pp. 123–124. https://doi.org/10.1007/978-3-319-26932-0_49

Nickerson, R.S., 1973. Intersensory facilitation of reaction time: Energy summation or preparation enhancement? Psychological Review 80, 489–509. https://doi.org/10.1037/h0035437

Nishitani, S., Kuwamoto, S., Takahira, A., Miyamura, T., Shinohara, K., 2014. Maternal Prefrontal Cortex Activation by Newborn Infant Odors. Chem Senses 39, 195–202. https://doi.org/10.1093/chemse/bjt068

Nishitani, S., Miyamura, T., Tagawa, M., Sumi, M., Takase, R., Doi, H., Moriuchi, H., Shinohara, K., 2009. The calming effect of a maternal breast milk odor on the human newborn infant. Neuroscience Research 63, 66–71. https://doi.org/10.1016/j.neures.2008.10.007

Norcia, A.M., Appelbaum, L.G., Ales, J.M., Cottereau, B.R., Rossion, B., 2015. The steady-state visual evoked potential in vision research: A review. Journal of vision 15, 1–16. https://doi.org/10.1167/15.6.4.doi

Novak, L.R., Gitelman, D.R., Schuyler, B., Li, W., 2015. Olfactory-visual integration facilitates perception of subthreshold negative emotion. Neuropsychologia 77, 288–297. https://doi.org/10.1016/j.neuropsychologia.2015.09.005

Oakes, L.M., Horst, J.S., Kovack-Lesh, K.A., Perone, S., 2009. How infants learn categories, in: Learning and the Infant Mind. Oxford University Press, New York, NY, US, pp. 144–171.

Ohla, K., Höchenberger, R., Freiherr, J., Lundström, J.N., 2018. Superadditive and Subadditive Neural Processing of Dynamic Auditory-Visual Objects in the Presence of Congruent Odors. Chem Senses 43, 35–44. https://doi.org/10.1093/chemse/bjx068

Oliva, A., Torralba, A., 2007. The role of context in object recognition. Trends in Cognitive Sciences 11, 520–527. https://doi.org/10.1016/j.tics.2007.09.009

Olofsson, J.K., Ekström, I., Lindström, J., Syrjänen, E., Stigsdotter-Neely, A., Nyberg, L., Jonsson, S., Larsson, M., 2020. Smell-based memory training: Evidence of olfactory learning and transfer to the visual domain. Chem Senses. https://doi.org/10.1093/chemse/bjaa049

Omer, Y., Sapir, R., Hatuka, Y., Yovel, G., 2019. What Is a Face? Critical Features for Face Detection: Perception. https://doi.org/10.1177/0301006619838734

Or, C.C.-F., Retter, T.L., Rossion, B., 2019. The contribution of color information to rapid face categorization in natural scenes. Journal of Vision 19, 20–20. https://doi.org/10.1167/19.5.20

Österbauer, R.A., Matthews, P.M., Jenkinson, M., Beckmann, C.F., Hansen, P.C., Calvert, G.A., 2005. Color of scents: chromatic stimuli modulate odor responses in the human brain. Journal of neurophysiology. https://doi.org/10.1152/jn.00555.2004

Otsuka, Y., Hill, H.C.H., Kanazawa, S., Yamaguchi, M.K., Spehar, B., 2012. Perception of Mooney faces by young infants: The role of local feature visibility, contrast polarity, and motion. Journal of Experimental Child Psychology 111, 164–179. https://doi.org/10.1016/j.jecp.2010.10.014

Otsuka, Y., Nakato, E., Kanazawa, S., Yamaguchi, M.K., Watanabe, S., Kakigi, R., 2007. Neural activation to upright and inverted faces in infants measured by near infrared spectroscopy. Neuroimage 34, 399–406. https://doi.org/10.1016/j.neuroimage.2006.08.013

Palmer, C.J., Clifford, C.W.G., 2020. Face Pareidolia Recruits Mechanisms for Detecting Human Social Attention. Psychological Science 31, 1001–1012. https://doi.org/10.1177/0956797620924814

Parma, V., Bulgheroni, M., Tirindelli, R., Castiello, U., 2014. Facilitation of action planning in children with autism: The contribution of the maternal body odor. Brain and Cognition 88, 73–82. https://doi.org/10.1016/j.bandc.2014.05.002

Parma, V., Bulgheroni, M., Tirindelli, R., Castiello, U., 2013. Body Odors Promote Automatic Imitation in Autism. Biological Psychiatry, Oxytocin and Autism 74, 220–226. https://doi.org/10.1016/j.biopsych.2013.01.010

Parma, V., Gordon, A.R., Cecchetto, C., Cavazzana, A., Lundström, J.N., Olsson, M.J., 2017. Processing of Human Body Odors, in: Buettner, A. (Ed.), Springer Handbook of Odor, Springer Handbooks. Springer International Publishing, Cham, pp. 127–128. https://doi.org/10.1007/978-3-319-26932-0_51

Parma, V., Tirindelli, R., Bisazza, A., Massaccesi, S., Castiello, U., 2012. Subliminally Perceived Odours Modulate Female Intrasexual Competition: An Eye Movement Study. PLOS ONE 7, e30645. https://doi.org/10.1371/journal.pone.0030645

Pascalis, O., De Martin de Viviés, X., Anzures, G., Quinn, P.C., Slater, A.M., Tanaka, J.W., Lee, K., 2011. Development of face processing. Wiley Interdisciplinary Reviews: Cognitive Science 2, 666–675. https://doi.org/10.1002/wcs.146

Pascalis, O., Fort, M., Quinn, P.C., 2020. Development of face processing: are there critical or sensitive periods? Current Opinion in Behavioral Sciences 36, 7–12. https://doi.org/10.1016/j.cobeha.2020.05.005

Pause, B.M., Krauel, K., Sojka, B., Ferstl, R., 1998. Body odor evoked potentials: a new method to study the chemosensory perception of self and non-self in humans. Genetica 104, 285–294. https://doi.org/10.1023/A:1026462701154

Pause, B.M., Lübke, K., Laudien, J.H., Ferstl, R., 2010. Intensified Neuronal Investment in the Processing of Chemosensory Anxiety Signals in Non-Socially Anxious and Socially Anxious Individuals. PLOS ONE 5, e10342. https://doi.org/10.1371/journal.pone.0010342

Pause, B.M., Ohrt, A., Prehn, A., Ferstl, R., 2004. Positive Emotional Priming of Facial Affect Perception in Females is Diminished by Chemosensory Anxiety Signals. Chem Senses 29, 797–805. https://doi.org/10.1093/chemse/bjh245

Peelen, M.V., Downing, P.E., 2017. Category selectivity in human visual cortex: Beyond visual object recognition. Neuropsychologia 105, 177–183. https://doi.org/10.1016/j.neuropsychologia.2017.03.033

Peelen, M.V., Downing, P.E., 2007. The neural basis of visual body perception. Nature Reviews Neuroscience 8, 636–648. https://doi.org/10.1038/nrn2195

Peltola, M.J., Leppänen, J.M., Mäki, S., Hietanen, J.K., 2009. Emergence of enhanced attention to fearful faces between 5 and 7 months of age. Social Cognitive and Affective Neuroscience 4, 134–142. https://doi.org/10.1093/scan/nsn046

Penn, D.J., Oberzaucher, E., Grammer, K., Fischer, G., Soini, H.A., Wiesler, D., Novotny, M.V., Dixon, S.J., Xu, Y., Brereton, R.G., 2007. Individual and gender fingerprints in human body odour. Journal of the Royal society interface 4, 331–340. https://doi.org/10.1098/rsif.2006.0182

Perl, O., Mishor, E., Ravia, A., Ravreby, I., Sobel, N., 2020. Are Humans Constantly but Subconsciously Smelling Themselves? (preprint). PsyArXiv. https://doi.org/10.31234/osf.io/eg9j4

Petrides, M., Alivisatos, B., Frey, S., 2002. Differential activation of the human orbital, mid-ventrolateral, and mid-dorsolateral prefrontal cortex during the processing of visual stimuli. PNAS 99, 5649–5654. https://doi.org/10.1073/pnas.072092299

Peykarjou, S., Hoehl, S., 2013. Three-month-olds' brain responses to upright and inverted faces and cars. Developmental neuropsychology 38, 272–280. https://doi.org/10.1080/87565641.2013.786719

Peykarjou, S., Hoehl, S., Pauen, S., Rossion, B., 2017. Rapid categorization of human and ape faces in 9-month-old infants revealed by fast periodic visual stimulation. Scientific Reports 7, 1–12. https://doi.org/10.1038/s41598-017-12760-2

Peykarjou, S., Pauen, S., Hoehl, S., 2016. 9-month-old infants recognize individual unfamiliar faces in a rapid repetition ERP paradigm. Infancy 21, 288–311. https://doi.org/10.1111/infa.12118

Philpott, C., Wolstenholme, C., Goodenough, P., Clark, A., Murty, G., 2006. Comparison of Subjective Perception with Objective Measurement of Olfaction. Otolaryngology - Head and Neck Surgery 134, 488–490. https://doi.org/10.1016/j.otohns.2005.10.041

Piaget, J., 1952. The origins of intelligence in children. International Universities Press New York.

Platek, S.M., Burch, R.L., Gallup, G.G., 2001. Sex differences in olfactory self-recognition. Physiology & Behavior 73, 635–640. https://doi.org/10.1016/S0031-9384(01)00539-X

Poncelet, J., Rinck, F., Bourgeat, F., Schaal, B., Rouby, C., Bensafi, M., Hummel, T., 2010. The effect of early experience on odor perception in humans: Psychological and physiological correlates. Behavioural Brain Research 208, 458–465. https://doi.org/10.1016/j.bbr.2009.12.011

Poncet, F., Leleu, A., Rekow, D., Damon, F., Durand, K., Schaal, B., Baudouin, J.-Y., 2021. Odor-evoked hedonic contexts influence the categorization of facial expressions in the human brain. Biological Psychology 158. https://doi.org/10.1016/j.biopsycho.2020.108005

Porada, D.K., Regenbogen, C., Seubert, J., Freiherr, J., Lundström, J.N., 2019. Multisensory Enhancement of Odor Object Processing in Primary Olfactory Cortex. Neuroscience 418, 254–265. https://doi.org/10.1016/j.neuroscience.2019.08.040

Porter, R.H., Balogh, R.D., Cernoch, J.M., Franchi, C., 1986. Recognition of kin through characteristic body odors. Chem Senses 11, 389–395. https://doi.org/10.1093/chemse/11.3.389

Porter, R.H., Cernoch, J.M., McLaughlin, F.J., 1983. Maternal recognition of neonates through olfactory cues. Physiology & behavior 30, 151–154. https://doi.org/10.1016/0031-9384(83)90051-3

Porter, R.H., Makin, J.W., Davis, L.B., Christensen, K.M., 1991. An assessment of the salient olfactory environment of formula-fed infants. Physiology & Behavior 50, 907–911. https://doi.org/10.1016/0031-9384(91)90413-I

Porter, R.H., Moore, J.D., 1981. Human kin recognition by olfactory cues. Physiology & Behavior 27, 493–495. https://doi.org/10.1016/0031-9384(81)90337-1

Porter, R.H., Varendi, H., Winberg, J., 2001. The Role of Olfaction in the Feeding Behavior of Human Neonates, in: Marchlewska-Koj, A., Lepri, J.J., Müller-Schwarze, D. (Eds.), Chemical Signals in Vertebrates 9. Springer US, Boston, MA, pp. 417–422. https://doi.org/10.1007/978-1-4615-0671-3_57

Porter, R.H., Winberg, J., 1999. Unique salience of maternal breast odors for newborn infants. Neuroscience & Biobehavioral Reviews 23, 439–449. https://doi.org/10.1016/S0149-7634(98)00044-X

Powell, L.J., Kosakowski, H.L., Saxe, R., 2018. Social Origins of Cortical Face Areas. Trends in Cognitive Sciences 22, 752–763. https://doi.org/10.1016/j.tics.2018.06.009

Prehn-Kristensen, A., Wiesner, C., Bergmann, T.O., Wolff, S., Jansen, O., Mehdorn, H.M., Ferstl, R., Pause, B.M., 2009. Induction of empathy by the smell of anxiety. PloS one 4, e5987. https://doi.org/10.1371/journal.pone.0005987

Preti, G., Cutler, W.B., Garcia, C.R., Huggins, G.R., Lawley, H.J., 1986. Human axillary secretions influence women's menstrual cycles: The role of donor extract of females. Hormones and Behavior 20, 474–482. https://doi.org/10.1016/0018-506X(86)90009-7

Price, J.L., Carmichael, S.T., Carnes, K.M., Clugnet, M.C., Kuroda, M., Ray, J.P., 1991. Olfactory input to the prefrontal cortex, in: Davis, J.L., Eichenbaum, H., Eichenbaum, U.P.H. (Eds.), Olfaction: A Model System for Computational Neuroscience. MIT Press, pp. 101–120.

Proverbio, A.M., Zani, A., Adorni, R., 2008. Neural markers of a greater female responsiveness to social stimuli. BMC Neurosci 9, 56. https://doi.org/10.1186/1471-2202-9-56

Puce, A., Allison, T., Gore, J.C., McCarthy, G., 1995. Face-sensitive regions in human extrastriate cortex studied by functional MRI. Journal of Neurophysiology 74, 1192–1199. https://doi.org/10.1152/jn.1995.74.3.1192

Quek, G.L., Liu-Shuang, J., Goffaux, V., Rossion, B., 2018a. Ultra-coarse, single-glance human face detection in a dynamic visual stream. NeuroImage 176, 465–476. https://doi.org/10.1016/j.neuroimage.2018.04.034

Quek, G.L., Nemrodov, D., Rossion, B., Liu-Shuang, J., 2018b. Selective Attention to Faces in a Rapid Visual Stream: Hemispheric Differences in Enhancement and Suppression of Category-selective Neural Activity. Journal of Cognitive Neuroscience 30, 393–410. https://doi.org/10.1162/jocn_a_01220

Quek, G.L., Peelen, M.V., 2020. Contextual and Spatial Associations Between Objects Interactively Modulate Visual Processing. Cereb Cortex. https://doi.org/10.1093/cercor/bhaa197

Quek, G.L., Rossion, B., 2017. Category-selective human brain processes elicited in fast periodic visual stimulation streams are immune to temporal predictability. Neuropsychologia 104, 182–200. https://doi.org/10.1016/j.neuropsychologia.2017.08.010

Quek, G.L., Rossion, B., Liu-Shuang, J., 2020. Critical information thresholds underlying concurrent face recognition functions. bioRxiv. https://doi.org/10.1101/2020.06.22.163584

Quinn, P.C., 2011. Born to categorize, in: Goswami, U. (Ed.), The Wiley-Blackwell Handbook of Childhood Cognitive Development. Wiley-Blackwell, Oxford, UK, pp. 129–152.

Quinn, P.C., Eimas, P.D., Rosenkrantz, S.L., 1993. Evidence for representations of perceptually similar natural categories by 3-month-old and 4-month-old infants. Perception 22, 463–475. https://doi.org/10.1068/p220463

Quinn, P.C., Lee, K., Pascalis, O., 2019. Face Processing in Infancy and Beyond: The Case of Social Categories. Annual Review of Psychology 70, 165–189. https://doi.org/10.1146/annurev-psych-010418-102753

Quinn, P.C., Westerlund, A., Nelson, C.A., 2006. Neural markers of categorization in 6-month-old infants. Psychol Sci 17, 59–66. https://doi.org/10.1111/j.1467-9280.2005.01665.x

Quinn, P.C., Yahr, J., Kuhn, A., Slater, A.M., Pascalis, O., 2002. Representation of the gender of human faces by infants: A preference for female. Perception 31, 1109–1121. https://doi.org/10.1068/p3331

Quintana, P., Nolet, K., Baus, O., Bouchard, S., 2019. The Effect of Exposure to Fear-Related Body Odorants on Anxiety and Interpersonal Trust Toward a Virtual Character. Chem Senses 44, 683–692. https://doi.org/10.1093/chemse/bjz063

Rakic, P., 1988. Specification of cerebral cortical areas. Science 241, 170–176. https://doi.org/10.1126/science.3291116

Rakison, D.H., Yermolayeva, Y., 2010. Infant categorization. WIREs Cognitive Science 1, 894–905. https://doi.org/10.1002/wcs.81

Rao, R.P.N., Shon, A.P., Meltzoff, A.N., 2007. A Bayesian model of imitation in infants and robots, in: Nehaniv, C.L., Dautenhahn, K. (Eds.), Imitation and Social Learning in Robots, Humans and Animals. Cambridge University Press, Cambridge, pp. 217–248. https://doi.org/10.1017/CBO9780511489808.016

Rattaz, C., Goubet, N., Bullinger, A., 2005. The calming effect of a familiar odor on full-term newborns. Journal of developmental and behavioral pediatrics 26, 86–92. https://doi.org/10.1097/00004703-200504000-00003

Regan, D., 1989. Human brain electrophysiology: Evoked potentials and evoked magnetic fields in science and medicine. Elsevier, New York.

Regenbogen, C., Axelsson, J., Lasselin, J., Porada, D.K., Sundelin, T., Peter, M.G., Lekander, M., Lundström, J.N., Olsson, M.J., 2017. Behavioral and neural correlates to multisensory detection of sick humans. Proceedings of the National Academy of Sciences 114, 6400–6405. https://doi.org/10.1073/pnas.1617357114

Regenbogen, C., Johansson, E., Andersson, P., Olsson, M.J., Lundström, J.N., 2016. Bayesian-based integration of multisensory naturalistic perithreshold stimuli. Neuropsychologia, Special Issue: Synaesthesia and Multisensory Processes 88, 123–130. https://doi.org/10.1016/j.neuropsychologia.2015.12.017

Rekow, D., Baudouin, J.-Y., Brochard, R., Rossion, B., Leleu, A., in prep. Did you spot the face in the clouds? Conscious categorization of illusory faces (face pareidolia) in the human brain.

Rekow, D., Baudouin, J.-Y., Poncet, F., Damon, F., Durand, K., Schaal, B., Rossion, B., Leleu, A., in revision. Smells like real faces: odor-driven face pareidolia in the infant brain.

Rekow, D., Baudouin, J.-Y., Rossion, B., Leleu, A., 2020a. An ecological measure of rapid and automatic face-sex categorization. Cortex 127, 150–161. https://doi.org/10.1016/j.cortex.2020.02.007

Rekow, D., Leleu, A., Poncet, F., Damon, F., Rossion, B., Durand, K., Schaal, B., Baudouin, J.-Y., 2020b. Categorization of objects and faces in the infant brain and its sensitivity to maternal odor: further evidence for the role of intersensory congruency in perceptual development. Cognitive Development 55, 100930. https://doi.org/10.1016/j.cogdev.2020.100930

Rennels, J.L., Davis, R.E., 2008. Facial experience during the first year. Infant Behavior and Development 31, 665–678. https://doi.org/10.1016/j.infbeh.2008.04.009

Retter, T.L., Jiang, F., Webster, M.A., Rossion, B., 2020. All-or-none face categorization in the human brain. NeuroImage 213, 116685. https://doi.org/10.1016/j.neuroimage.2020.116685

Retter, T.L., Rossion, B., 2016. Uncovering the neural magnitude and spatio-temporal dynamics of natural image categorization in a fast visual stream. Neuropsychologia 91, 9–28. https://doi.org/10.1016/j.neuropsychologia.2016.07.028

Reynolds, G.D., Richards, J.E., 2005. Familiarization, attention, and recognition memory in infancy: an event-related potential and cortical source localization study. Dev Psychol 41, 598–615. https://doi.org/10.1037/0012-1649.41.4.598

Reynolds, G.D., Roth, K.C., 2018. The Development of Attentional Biases for Faces in Infancy: A Developmental Systems Perspective. Front. Psychol. 9. https://doi.org/10.3389/fpsyg.2018.00222

Riby, D.M., Brown, P.H., Jones, N., Hanley, M., 2012. Brief Report: Faces Cause Less Distraction in Autism. J Autism Dev Disord 42, 634–639. https://doi.org/10.1007/s10803-011-1266-1

Riby, D.M., Hancock, P.J.B., 2009. Do Faces Capture the Attention of Individuals with Williams Syndrome or Autism? Evidence from Tracking Eye Movements. J Autism Dev Disord 39, 421–431. https://doi.org/10.1007/s10803-008-0641-z

Rice, G.E., Caswell, H., Moore, P., Hoffman, P., Lambon Ralph, M.A., 2018. The Roles of Left Versus Right Anterior Temporal Lobes in Semantic Memory: A Neuropsychological Comparison of Postsurgical Temporal Lobe Epilepsy Patients. Cereb Cortex 28, 1487–1501. https://doi.org/10.1093/cercor/bhx362

Richardson, R., 2002. Extinction of Conditioned Odor Potentiation of Startle. Neurobiology of Learning and Memory 78, 426–440. https://doi.org/10.1006/nlme.2002.4074

Rikowski, A., Grammer, K., 1999. Human body odour, symmetry and attractiveness. Proceedings of the Royal Society of London. Series B: Biological Sciences 266, 869–874. https://doi.org/10.1098/rspb.1999.0717

Ripp, I., Nieden, A.-N. zur, Blankenagel, S., Franzmeier, N., Lundström, J.N., Freiherr, J., 2018. Multisensory integration processing during olfactory-visual stimulation—An fMRI graph theoretical network analysis. Human Brain Mapping 39, 3713–3727. https://doi.org/10.1002/hbm.24206

Rizzolatti, G., Umiltà, C., Berlucchi, G., 1971. Opposite superiorities of the right and left cerebral hemispheres in discriminative reaction time to physiognomical and alphabetical material. Brain: A Journal of Neurology. https://doi.org/10.1093/brain/94.3.431

Roberts, S.C., Gosling, L.M., Spector, T.D., Miller, P., Penn, D.J., Petrie, M., 2005. Body Odor Similarity in Noncohabiting Twins. Chem Senses 30, 651–656. https://doi.org/10.1093/chemse/bji058

Roberts, S.C., Havlícek, J., Petrie, M., 2013. Repeatability of odour preferences across time. Flavour and Fragrance Journal 28, 245–250. https://doi.org/10.1002/ffj.3142

Roberts, S.C., Kralevich, A., Ferdenzi, C., Saxton, T.K., Jones, B.C., DeBruine, L.M., Little, A.C., Havlícek, J., 2011. Body Odor Quality Predicts Behavioral Attractiveness in Humans. Arch Sex Behav 40, 1111–1117. https://doi.org/10.1007/s10508-011-9803-8

Robinson, A.K., Mattingley, J.B., Reinhard, J., 2013. Odors enhance the salience of matching images during the attentional blink. Front. Integr. Neurosci. 7. https://doi.org/10.3389/fnint.2013.00077

Rocha, M., Parma, V., Lundström, J.N., Soares, S.C., 2018. Anxiety Body Odors as Context for Dynamic Faces: Categorization and Psychophysiological Biases. Perception 47, 1054–1069. https://doi.org/10.1177/0301006618797227

Romantshik, O., Porter, R., Tillmann, V., Varendi, H., 2007. Preliminary evidence of a sensitive period for olfactory learning by human newborns. Acta Paediatrica 96, 372–376. https://doi.org/10.1111/j.1651-2227.2006.00106.x

Rosch, E., 1978. Principles of Categorization, in: Rosch, Eleanor, Lloyd, B. (Eds.), Cognition and Categorization. Lawrence Elbaum Associates.

Rosch, E., Mervis, C.B., Gray, W.D., Johnson, D.M., Boyes-Braem, P., 1976. Basic objects in natural categories. Cognitive Psychology 8, 382–439. https://doi.org/10.1016/0010-0285(76)90013-X

Rossion, B., 2018a. Damasio's error - Prosopagnosia with intact within-category object recognition. Journal of Neuropsychology 12, 357–388. https://doi.org/10.1111/jnp.12162

Rossion, B., 2018b. Humans Are Visual Experts at Unfamiliar Face Recognition. Trends in Cognitive Sciences 22, 471–472. https://doi.org/10.1016/j.tics.2018.03.002

Rossion, B., Caharel, S., 2011. ERP evidence for the speed of face categorization in the human brain: Disentangling the contribution of low-level visual cues from face perception. Vision Research 51, 1297–1311. https://doi.org/10.1016/j.visres.2011.04.003

Rossion, B., Curran, T., 2010. Visual expertise with pictures of cars correlates with RT magnitude of the car inversion effect. Perception 39, 173–183. https://doi.org/10.1068/p6270

Rossion, B., Dricot, L., Goebel, R., Busigny, T., 2011. Holistic face categorization in higher order visual areas of the normal and prosopagnosic brain : toward a non-hierarchical view of face perception. Frontiers in human neuroscience 4, 1–30. https://doi.org/10.3389/fnhum.2010.00225

Rossion, B., Gauthier, I., Tarr, M.J., Despland, P., Bruyer, R., Linotte, S., Crommelinck, M., 2000. The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. Neuroreport 11, 69–72. https://doi.org/10.1097/00001756-200001170-00014

Rossion, B., Hanseeuw, B., Dricot, L., 2012. Defining face perception areas in the human brain: A large-scale factorial fMRI face localizer analysis. Brain and Cognition 79, 138–157. https://doi.org/10.1016/j.bandc.2012.01.001

Rossion, B., Jacques, C., 2011. The N170: Understanding the Time Course of Face Perception in the Human Brain, in: Steven, J.L. (Ed.), The Oxford Handbook of Event-Related Potential Components. Oxford University Press, pp. 115–142. https://doi.org/10.1093/oxfordhb/9780195374148.013.0064

Rossion, B., Jacques, C., Jonas, J., 2018. Mapping face categorization in the human ventral occipitotemporal cortex with direct neural intracranial recordings: Intracranial mapping of face categorization. Annals of the New York Academy of Sciences 1426, 5–24. https://doi.org/10.1111/nyas.13596

Rossion, B., Retter, T.L., 2020. Face perception, in: Poeppel, D., Mangun, G.R., Gazzaniga, M.S. (Eds.), The Cognitive Neurosciences. MIT Press, pp. 129–139.

Rossion, B., Retter, T.L., Liu-Shuang, J., 2020. Understanding human individuation of unfamiliar faces with oddball fast periodic visual stimulation and electroencephalography. European Journal of Neuroscience. https://doi.org/10.1111/ejn.14865

Rossion, B., Torfs, K., Jacques, C., Liu-Shuang, J., 2015. Fast periodic presentation of natural images reveals a robust face-selective electrophysiological response in the human brain. Journal of vision 15, 1–18. https://doi.org/10.1167/15.1.18

Rossiter, K.J., 1996. Structure−Odor Relationships. Chem. Rev. 96, 3201–3240. https://doi.org/10.1021/cr950068a

Rousselet, G.A., Macé, M.J.-M., Fabre-Thorpe, M., 2003. Is it an animal? Is it a human face? Fast processing in upright and inverted natural scenes. Journal of Vision 3, 5–5. https://doi.org/10.1167/3.6.5

Royet, J.-P., 2004. Lateralization of Olfactory Processes. Chemical Senses 29, 731–745. https://doi.org/10.1093/chemse/bjh067

Royet, J.-P., Hudry, J., Zald, D.H., Godinot, D., Grégoire, M.C., Lavenne, F., Costes, N., Holley, A., 2001. Functional Neuroanatomy of Different Olfactory Judgments. NeuroImage 13, 506–519. https://doi.org/10.1006/nimg.2000.0704

Royet, J.-P., Koenig, O., Gregoire, M.-C., Cinotti, L., Lavenne, F., Bars, D.L., Costes, N., Vigouroux, M., Farget, V., Sicard, G., Holley, A., Mauguière, F., Comar, D., Froment, J.-C., 1999. Functional Anatomy of Perceptual and Semantic Processing for Odors. Journal of Cognitive Neuroscience 11, 94–109. https://doi.org/10.1162/089892999563166

Rubin, D., Botanov, Y., Hajcak, G., Mujica-Parodi, L.R., 2012. Second-hand stress: inhalation of stress sweat enhances neural response to neutral faces. Scan 7, 208–212. https://doi.org/10.1093/scan/nsq097

Rudden, M., Herman, R., Rose, M., Bawdon, D., Cox, D.S., Dodson, E., Holden, M.T.G., Wilkinson, A.J., James, A.G., Thomas, G.H., 2020. The molecular basis of thioalcohol production in human body odour. Scientific Reports 10, 12500. https://doi.org/10.1038/s41598-020-68860-z

Russell, M.J., 1976. Human olfactory communication. Nature 260, 520–522. https://doi.org/10.1038/260520a0

Russell, M.J., Mendelson, T., Peeke, H.V.S., 1983. Mothers' Identification of their Infant's Odors. Ethology and Sociobiology 4, 29–31.

Sai, F.Z., 2005. The Role of the Mother's Voice in Developing Mother's Face Preference: Evidence for Intermodal Perception at Birth. Infant and Child Development 14, 29–50. https://doi.org/10.1002/icd. 376

Saito, H., Chi, Q., Zhuang, H., Matsunami, H., Mainland, J.D., 2009. Odor Coding by a Mammalian Receptor Repertoire. Sci. Signal. 2. https://doi.org/10.1126/scisignal.2000016

Sarnat, H.B., 1978. Olfactory reflexes in the newborn infant. The Journal of Pediatrics 92, 624–626. https://doi.org/10.1016/S0022-3476(78)80307-2

Sarolidou, G., Axelsson, J., Kimball, B.A., Sundelin, T., Regenbogen, C., Lundström, J.N., Lekander, M., Olsson, M.J., 2020. People expressing olfactory and visual cues of disease are less liked. Philosophical Transactions of the Royal Society B: Biological Sciences 375, 20190272. https://doi.org/10.1098/rstb.2019.0272

Sarrafchi, A., Laska, M., 2017. Olfactory sensitivity for the mammalian blood odor component trans-4, 5-epoxy-(E)-2-decenal in CD-1 mice. Perception 46, 333–342. https://doi.org/10.1177/0301006616653136

Sarrafchi, A., Odhammer, A.M.E., Hernandez Salazar, L.T., Laska, M., 2013. Olfactory Sensitivity for Six Predator Odorants in CD-1 Mice, Human Subjects, and Spider Monkeys. PLoS One 8. https://doi.org/10.1371/journal.pone.0080621

Schaal, B., 2014. Pheromones for Newborns, in: Neurobiology of Chemical Communication. CRC Press/Taylor & Francis, Boca Raton (FL).

Schaal, B., 2010. Mammary odor cues and pheromones: mammalian infant-directed communication about maternal state, mammae, and milk. Vitamins & Hormones 83, 83–136. https://doi.org/10.1016/S0083-6729(10)83004-3

Schaal, B., Durand, K., 2017. Olfaction and gustation, in: Hopkins, B., Geangu, E., Linkenauger, S. (Eds.), The Cambridge Encyclopedia of Child Development. Cambridge University Press, pp. 339–349.

Schaal, B., Durand, K., 2012. The role of olfaction in human multisensory development, in: Bremner, A.J., Lewkowicz, D.J., Spence, C. (Eds.), Multisensory Development. Oxford University Press, Oxford, pp. 29–62.

Schaal, B., Hummel, T., Soussignan, R., 2004. Olfaction in the fetal and premature infant: functional status and clinical implications. Clinics in Perinatology 31, 261–285. https://doi.org/10.1016/j.clp.2004.04.003

Schaal, B., Marlier, L., 1998. Maternal and Paternal Perception of Individual Odor Signatures in Human Amniotic Fluid – Potential Role in Early Bonding? NEO 74, 266–273. https://doi.org/10.1159/000014033

Schaal, B., Marlier, L., Soussignan, R., 2000. Human foetuses learn odours from their pregnant mother's diet. Chemical senses 25, 729–737. https://doi.org/10.1093/chemse/25.6.729

Schaal, B., Marlier, L., Soussignan, R., 1998. Olfaction function in the Human Fetus: Evidence from Selective Neonatal Responsiveness to the odor of amniotic fluid. Behavioral Neuroscience 112, 1438–1449. https://doi.org/10.1037/0735-7044.112.6.1438

Schaal, B., Montagner, H., Hertling, E., Bolzoni, D., Moyse, A., Quichon, R., 1980. Les stimulations olfactives dans les relations entre l'enfant et la mère. Reproduction Nutrition Développement 20, 843–858. https://doi.org/10.1051/rnd:19800510

Schaal, B., Porter, R.H., 1991. "Microsmatic Humans" Revisited: The Generation and Perception of Chemical Signals, in: Slater, P.J.B., Rosenblatt, J.S., Beer, C., Milinski, M. (Eds.), Advances in the Study of Behavior. Academic Press, pp. 135–199. https://doi.org/10.1016/S0065-3454(08)60321-6

Schaal, B., Saxton, T.K., Loos, H., Soussignan, R., Durand, K., 2020. Olfaction scaffolds the developing human from neonate to adolescent and beyond. Philosophical Transactions of the Royal Society B: Biological Sciences 375, 20190261. https://doi.org/10.1098/rstb.2019.0261

Schaal, B., Soussignan, R., Marlier, L., 2002. Olfactory cognition at the start of life: the perinatal shaping of selective odor responsiveness, in: Rouby, C., Schaal, B., Dubois, D., Gervais, R., Holley, A. (Eds.), Olfaction, Taste, and Cognition. Cambridge University Press, New York, pp. 421–440.

Schaeffer, J.P., 1910. The lateral wall of the cavum nasi in man, with especial reference to the various developmental stages. Journal of Morphology 21, 613–707. https://doi.org/10.1002/jmor.1050210405

Schäfer, L., Sorokowska, A., Weidner, K., Croy, I., 2020. Children's Body Odors: Hints to the Development Status. Front. Psychol. 11. https://doi.org/10.3389/fpsyg.2020.00320

Scherf, K.S., Behrmann, M., Humphreys, K., Luna, B., 2007. Visual category-selectivity for faces, places and objects emerges along different developmental trajectories. Developmental Science 10. https://doi.org/10.1111/j.1467-7687.2007.00595.x

Schleidt, M., Genzel, C., 1990. The significance of mother's perfume for infants in the first weeks of their life. Ethology and Sociobiology 11, 145–154. https://doi.org/10.1016/0162-3095(90)90007-S

Schleidt, M., Hold, B., Attili, G., 1981. A cross-cultural study on the attitude towards personal odors. J Chem Ecol 7, 19–31. https://doi.org/10.1007/BF00988632

Schroeder, C.E., Foxe, J., 2005. Multisensory contributions to low-level, 'unisensory' processing. Current Opinion in Neurobiology, Sensory systems 15, 454–458. https://doi.org/10.1016/j.conb.2005.06.008

Scott, L.S., Shannon, R.W., Nelson, C.A., 2006. Neural correlates of human and monkey face processing in 9-month-old infants. Infancy 10, 171–186. https://doi.org/10.1207/s15327078in1002_4

Seghier, M.L., 2013. The Angular Gyrus: Multiple Functions and Multiple Subdivisions. Neuroscientist 19, 43–61. https://doi.org/10.1177/1073858412440596

Seigneuric, A., Durand, K., Jiang, T., Baudouin, J.-Y., Schaal, B., 2010. The nose tells it to the eyes: Crossmodal associations between olfaction and vision. Perception 39, 1541–1554. https://doi.org/10.1068/p6740

Sela, L., Sobel, N., 2010. Human olfaction: a constant state of change-blindness. Experimental Brain Research 205, 13–29. https://doi.org/10.1007/s00221-010-2348-6

Sell, C.S., 2006. On the Unpredictability of Odor. Angewandte Chemie International Edition 45, 6254–6261. https://doi.org/10.1002/anie.200600782

Seo, H.-S., Roidl, E., Müller, F., Negoias, S., 2010. Odors enhance visual attention to congruent objects. Appetite 54, 544–549. https://doi.org/10.1016/j.appet.2010.02.011

Sergeant, M.J.T., Dickins, T.E., Davies, M.N.O., Griffiths, M.D., 2007. Women's Hedonic Ratings of Body Odor of Heterosexual and Homosexual Men. Arch Sex Behav 36, 395–401. https://doi.org/10.1007/s10508-006-9126-3

Sergent, J., Ohta, S., Macdonald, B., 1992. Functional Neuroanatomy of Face and Object Processing. Brain 115, 15–36. https://doi.org/10.1093/brain/115.1.15

Seubert, J., Loughead, J., Kellermann, T., Boers, F., Brensinger, C.M., Habel, U., 2010. Multisensory integration of emotionally valenced olfactory-visual information in patients with schizophrenia and healthy controls. Journal of Psychiatry and Neuroscience 35, 185–194. https://doi.org/10.1503/jpn.090094

Shehadeh, N.H., Kligman, A.M., 1963. The effect of topical antibacterial agents on the bacterial flora of the axilla. Journal of Investigative Dermatology 40, 61–71. https://doi.org/10.1038/jid.1963.10

Shelley, W.B., Hurley, H.J., Nichols, A.C., 1953. Axillary odor: experimental study of the role of bacteria, apocrine sweat, and deodorants. Ama archives of Dermatology and Syphilology 68, 430–446. https://doi.org/10.1001/archderm.1953.01540100070012

Shepherd, G.M., 2006. Smell images and the flavour system in the human brain. Nature 444, 316–321. https://doi.org/10.1038/nature05405

Simion, F., Di Giorgio, E., 2015. Face perception and processing in early infancy: Inborn predispositions and developmental changes. Frontiers in Psychology 6, 1–11. https://doi.org/10.3389/fpsyg.2015.00969

Smallegange, R.C., Verhulst, N.O., Takken, W., 2011. Sweaty skin: an invitation to bite? Trends in parasitology 27, 143–148. https://doi.org/10.1016/j.pt.2010.12.009

Smeets, M.A.M., Rosing, E.A.E., Jacobs, D.M., van Velzen, E., Koek, J.H., Blonk, C., Gortemaker, I., Eidhof, M.B., Markovitch, B., de Groot, J.H.B., Semin, G.R., 2020. Chemical Fingerprints of Emotional Body Odor. Metabolites 10, 84. https://doi.org/10.3390/metabo10030084

Smith, E.E., Medin, D.L., 1981. Categories and concepts. Harvard University Press Cambridge, MA.

Smith, J.P., Forrester, R., 2017. Maternal Time Use and Nurturing: Analysis of the Association Between Breastfeeding Practice and Time Spent Interacting with Baby. Breastfeeding Medicine 12, 269–278. https://doi.org/10.1089/bfm.2016.0118

Smotherman, W.P., Robinson, S.R., 1987. Psychobiology of fetal experience in the rat, in: Krasnego, A., Blass, E.M., Hofer, M.A. (Eds.), Behavioral Biology. Perinatal Development: A Psychobiological Perspective. pp. 39–60.

Snyder-Mackler, N., Burger, J.R., Gaydosh, L., Belsky, D.W., Noppert, G.A., Campos, F.A., Bartolomucci, A., Yang, Y.C., Aiello, A.E., O'Rand, A., Harris, K.M., Shively, C.A., Alberts, S.C., Tung, J., 2020. Social determinants of health and survival in humans and other animals. Science 368. https://doi.org/10.1126/science.aax9553

Somerville, D.A., 1969. The Normal Flora of the Skin in Different Age Groups. British Journal of Dermatology 81, 248–258. https://doi.org/10.1111/j.1365-2133.1969.tb13976.x

Sorokowska, A., Sorokowski, P., Szmajke, A., 2012. Does Personality Smell? Accuracy of Personality Assessments Based on Body Odour. European Journal of Personality 26, 496–503. https://doi.org/10.1002/per.848

Soussignan, R., Schaal, B., Marlier, L., Jiang, T., 1997. Facial and autonomic responses to biological and artificial olfactory stimuli in human neonates: Re-examining early hedonic discrimination of odors. Physiology and Behavior 62, 745–758. https://doi.org/10.1016/S0031-9384(97)00187-X

Spence, C., 2011. Crossmodal correspondences: A tutorial review. Atten Percept Psychophys 73, 971–995. https://doi.org/10.3758/s13414-010-0073-7

Spencer, N.A., McClintock, M.K., Sellergren, S.A., Bullivant, S., Jacob, S., Mennella, J.A., 2004. Social chemosignals from breastfeeding women increase sexual motivation. Hormones and Behavior, Olfaction, Sex, and Behavior 46, 362–370. https://doi.org/10.1016/j.yhbeh.2004.06.002

Starkenmann, C., 2017. Analysis and Chemistry of Human Odors, in: Buettner, A. (Ed.), Springer Handbook of Odor, Springer Handbooks. Springer International Publishing, Cham, pp. 121–122. https://doi.org/10.1007/978-3-319-26932-0_48

Stein, B.E., Meredith, M.A., 1993. The merging of the senses. The MIT Press, Cambridge, MA.

Stein, B.E., Scott Huneycutt, W., Alex Meredith, M., 1988. Neurons and behavior: the same rules of multisensory integration apply. Brain Research 448, 355–358. https://doi.org/10.1016/0006-8993(88)91276-0

Steinberg, C., Dobel, C., Schupp, H.T., Kissler, J., Elling, L., Pantev, C., Junghöfer, M., 2012. Rapid and highly resolving: affective evaluation of olfactorily conditioned faces. Journal of Cognitive Neuroscience 24, 17–27. https://doi.org/10.1162/jocn_a_00067

Stettler, D.D., Axel, R., 2009. Representations of Odor in the Piriform Cortex. Neuron 63, 854–864. https://doi.org/10.1016/j.neuron.2009.09.005

Stevenson, R.A., Bushmakin, M., Kim, S., Wallace, M.T., Puce, A., James, T.W., 2012. Inverse Effectiveness and Multisensory Interactions in Visual Event-Related Potentials with Audiovisual Speech. Brain Topography 25, 308–326. https://doi.org/10.1007/s10548-012-0220-7

Stevenson, R.A., James, T.W., 2009. Audiovisual integration in human superior temporal sulcus: Inverse effectiveness and the neural processing of speech and object recognition. NeuroImage 44, 1210–1223. https://doi.org/10.1016/j.neuroimage.2008.09.034

Stevenson, R.J., Repacholi, B.M., 2003. Age-related changes in children's hedonic response to male body odor. Developmental Psychology 39, 670–679. https://doi.org/10.1037/0012-1649.39.4.670

Sullivan, R.M., Toubas, P., 1998. Clinical Usefulness of Maternal Odor in Newborns: Soothing and Feeding Preparatory Responses. NEO 74, 402–408. https://doi.org/10.1159/000014061

Syrjänen, E., Liuzza, M.T., Fischer, H., Olofsson, J.K., 2017. Do Valenced Odors and Trait Body Odor Disgust Affect Evaluation of Emotion in Dynamic Faces? Perception 46, 1412–1426. https://doi.org/10.1177/0301006617720831

Syrjänen, E., Wiens, S., Fischer, H., Zakrzewska, M., Wartel, A., Larsson, M., Olofsson, J.K., 2018. Background Odors Modulate N170 ERP Component and Perception of Emotional Facial Stimuli. Front. Psychol. 9. https://doi.org/10.3389/fpsyg.2018.01000

Tanaka, J.W., Curran, T., 2001. A Neural Basis for Expert Object Recognition. Psychological Science 12, 43–47. https://doi.org/10.1111/1467-9280.00308

Tanaka, K., 1996. Inferotemporal Cortex and Object Vision. Annual Review of Neuroscience 19, 109–139. https://doi.org/10.1146/annurev.ne.19.030196.000545

Tang, J., Falkmer, M., Horlin, C., Tan, T., Vaz, S., Falkmer, T., 2015. Face Recognition and Visual Search Strategies in Autism Spectrum Disorders: Amending and Extending a Recent Review by Weigelt et al. PLOS ONE 10, e0134439. https://doi.org/10.1371/journal.pone.0134439

Thornhill, R., Chapman, J.F., Gangestad, S.W., 2013. Women's preferences for men's scents associated with testosterone and cortisol levels: Patterns across the ovulatory cycle. Evolution and Human Behavior 34, 216–221. https://doi.org/10.1016/j.evolhumbehav.2013.01.003

Thorpe, S., Fize, D., Marlot, C., 1996. Speed of processing in the human visual system. Nature 381, 520–522. https://doi.org/10.1038/381520a0

Todd, W.A., 1979. Psychosocial problems as the major complication of an adolescent with trimethylaminuria. The Journal of Pediatrics 94, 936–937. https://doi.org/10.1016/S0022-3476(79)80224-3

Troccaz, M., Borchard, G., Vuilleumier, C., Raviot-Derrien, S., Niclass, Y., Beccucci, S., Starkenmann, C., 2009. Gender-Specific Differences between the Concentrations of Nonvolatile (R)/(S)-3-Methyl-3-Sulfanylhexan-1-Ol and (R)/(S)-3-Hydroxy-3-Methyl-Hexanoic Acid Odor Precursors in Axillary Secretions. Chem Senses 34, 203–210. https://doi.org/10.1093/chemse/bjn076

Tsao, D.Y., Moeller, S., Freiwald, W.A., 2008. Comparing face patch systems in macaques and humans. PNAS 105, 19514–19519. https://doi.org/10.1073/pnas.0809662105

Turati, C., Valenza, E., Leo, I., Simion, F., 2005. Three-month-olds' visual preference for faces and its underlying visual processing mechanisms. Journal of Experimental Child Psychology 90, 255–273. https://doi.org/10.1016/j.jecp.2004.11.001

Turkewitz, G., Devenny, D.A., 1993. Developmental Time and Timing. Psychology Press.

Tzourio-Mazoyer, N., de Schonen, S., Crivello, F., Reutter, B., Aujard, Y., Mazoyer, B., 2002. Neural Correlates of Woman Face Processing by 2-Month-Old Infants. NeuroImage 15, 454–461. https://doi.org/10.1006/nimg.2001.0979

Ullman, S., 1995. Sequence Seeking and Counter Streams: A Computational Model for Bidirectional Information Flow in the Visual Cortex. Cereb Cortex 5, 1–11. https://doi.org/10.1093/cercor/5.1.1

Varendi, H., Christensson, K., Porter, R.H., Winberg, J., 1998. Soothing effect of amniotic fluid smell in newborn infants. Early Human Development 51, 47–55. https://doi.org/10.1016/S0378-3782(97)00082-0

Varendi, H., Porter, R.H., 2001. Breast odour as the only maternal stimulus elicits crawling towards the odour source. Acta Paediatrica 90, 372–375. https://doi.org/10.1111/j.1651-2227.2001.tb00434.x

Varendi, H., Porter, R.H., Winberg, J., 1994. Does the newborn baby find the nipple by smell? The Lancet, 2,8928 344, 989–990. https://doi.org/10.1016/S0140-6736(94)91645-4

Verhallen, R.J., Bosten, J.M., Goodbourn, P.T., Bargary, G., Lawrance-Owen, A.J., Mollon, J.D., 2014. An online version of the Mooney Face Test: phenotypic and genetic associations. Neuropsychologia 63, 19–25. https://doi.org/10.1016/j.neuropsychologia.2014.08.011

Vettori, S., Dzhelyova, M., Van der Donck, S., Jacques, C., Steyaert, J., Rossion, B., Boets, B., 2019. Reduced neural sensitivity to rapid individual face discrimination in autism spectrum disorder. NeuroImage: Clinical 21, 101613. https://doi.org/10.1016/j.nicl.2018.101613

Volfart, A., Jonas, J., Maillard, L., Colnat-Coulbois, S., Rossion, B., 2020. Neurophysiological evidence for crossmodal (face-name) person-identity representation in the human left ventral temporal cortex. PLOS Biology 18, e3000659. https://doi.org/10.1371/journal.pbio.3000659

von Kriegstein, K., Kleinschmidt, A., Sterzer, P., Giraud, A.-L., 2005. Interaction of Face and Voice Areas during Speaker Recognition. Journal of Cognitive Neuroscience 17, 367–376. https://doi.org/10.1162/0898929053279577

Wagemans, J., Elder, J.H., Kubovy, M., Palmer, S.E., Peterson, M.A., Singh, M., von der Heydt, R., 2012. A century of Gestalt psychology in visual perception: I. Perceptual grouping and figure–ground organization. Psychological bulletin 138, 1172. https://doi.org/10.1037/a0029333

Wallace, M.T., 2004. The Development of Multisensory Integration., in: Calvert, G., Spence, C., Stein, B.E. (Eds.), The Handbook of Multisensory Processes. MIT Press, Cambridge, Massachusetts, pp. 625–642.

Weisfeld, G.E., Czilli, T., Phillips, K.A., Gall, J.A., Lichtman, C.M., 2003. Possible olfaction-based mechanisms in human kin recognition and inbreeding avoidance. Journal of Experimental Child Psychology 85, 279–295. https://doi.org/10.1016/S0022-0965(03)00061-4

Werchan, D.M., Baumgartner, H.A., Lewkowicz, D.J., Amso, D., 2018. The origins of cortical multisensory dynamics: Evidence from human infants. Developmental Cognitive Neuroscience 34, 75–81. https://doi.org/10.1016/j.dcn.2018.07.002

Wilke, K., Martin, A., Terstegen, L., Biel, S.S., 2007. A short history of sweat gland biology. International Journal of Cosmetic Science 29, 169–179. https://doi.org/10.1111/j.1467-2494.2007.00387.x

Wudarczyk, O.A., Kohn, N., Bergs, R., Goerlich, K.S., Gur, R.E., Turetsky, B., Schneider, F., Habel, U., 2016. Chemosensory anxiety cues enhance the perception of fearful faces – An fMRI study. NeuroImage 143, 214–222. https://doi.org/10.1016/j.neuroimage.2016.09.002

Wyatt, T.D., 2017. Pheromones. Current Biology 27, R739–R743. https://doi.org/10.1016/j.cub.2017.06.039

Wysocki, C.J., Preti, G., 2004. Facts, fallacies, fears, and frustrations with human pheromones. The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology 281A, 1201–1211. https://doi.org/10.1002/ar.a.20125

Xie, W., Richards, J.E., 2016. Effects of interstimulus intervals on behavioral, heart rate, and event-related potential indices of infant engagement and sustained attention. Psychophysiology 53, 1128–1142. https://doi.org/10.1111/psyp.12670

Yamazaki, S., Hoshino, K., Kusuhara, M., 2010. Odor Associated with Aging. Anti-aging medicine 7, 60–65. https://doi.org/10.3793/jaam.7.60

Yarbus, A.L., 1967. Eye Movements During Perception of Complex Objects, in: Yarbus, A.L. (Ed.), Eye Movements and Vision. Springer US, Boston, MA, pp. 171–211. https://doi.org/10.1007/978-1-4899-5379-7_8

Yarmolinsky, D.A., Zuker, C.S., Ryba, N.J.P., 2009. Common Sense about Taste: From Mammals to Insects. Cell 139, 234–244. https://doi.org/10.1016/j.cell.2009.10.001

Yeshurun, Y., Sobel, N., 2010. An Odor is Not Worth a Thousand Words: From Multidimensional Odors to Unidimensional Odor Objects. Annual Review of Psychology 61, 219–241. https://doi.org/10.1146/annurev.psych.60.110707.163639

Yin, R.K., 1969. Looking at upside-down faces. Journal of experimental psychology 81, 141. https://doi.org/10.1037/h0027474

Zarzo, M., 2008. Psychologic Dimensions in the Perception of Everyday Odors: Pleasantness and Edibility. Journal of Sensory Studies 23, 354–376. https://doi.org/10.1111/j.1745-459X.2008.00160.x

Zarzo, M., Stanton, D.T., 2009. Understanding the underlying dimensions in perfumers' odor perception space as a basis for developing meaningful odor maps. Attention, Perception & Psychophysics 71, 225–247. https://doi.org/10.3758/APP.71.2.225

Zatorre, R.J., Jones-Gotman, M., Rouby, C., 2000. Neural mechanisms involved in odor pleasantness and intensity judgments. NeuroReport 11, 2711–2716. https://doi.org/10.1097/00001756-200008210-00021

Zellner, D.A., Bartoli, A.M., Eckard, R., 1991. Influence of color on odor identification and liking ratings. Am J Psychol 104, 547–561. https://doi.org/10.2307/1422940

Zeng, X.-N., Leyden, J.J., Spielman, A.I., Preti, G., 1996. Analysis of characteristic human female axillary odors: Qualitative comparison to males. J Chem Ecol 22, 237–257. https://doi.org/10.1007/BF02055096

Zernecke, R., Haegler, K., Kleemann, A.M., Albrecht, J., Frank, T., Linn, J., Brückmann, H., Wiesmann, M., 2011. Effects of Male Anxiety Chemosignals on the Evaluation of Happy Facial Expressions. Journal of Psychophysiology 25, 116–123. https://doi.org/10.1027/0269-8803/a000047

Zhang, S., Su, F., Li, J., Chen, W., 2018. The Analgesic Effects of Maternal Milk Odor on Newborns: A Meta-Analysis. Breastfeeding Medicine 13, 327–334. https://doi.org/10.1089/bfm.2017.0226

Zheng, Y., You, Y., Farias, A.R., Simon, J., Semin, G.R., Smeets, M.A.M., Li, W., 2018. Human chemosignals of disgust facilitate food judgment. Sci Rep 8, 1–10. https://doi.org/10.1038/s41598-018-35132-w

Zhou, G., Lane, G., Cooper, S.L., Kahnt, T., Zelano, C., 2019. Characterizing functional pathways of the human olfactory system. eLife 8, e47177. https://doi.org/10.7554/eLife.47177

Zhou, L.-F., Meng, M., 2020. Do you see the "face"? Individual differences in face pareidolia. Journal of Pacific Rim Psychology 14. https://doi.org/10.1017/prp.2019.27

Zhou, W., Chen, D., 2009. Fear-Related Chemosignals Modulate Recognition of Fear in Ambiguous Facial Expressions. Psychol Sci 20, 177–183. https://doi.org/10.1111/j.1467-9280.2009.02263.x

Zhou, W., Chen, D., 2008. Encoding human sexual chemosensory cues in the orbitofrontal and fusiform cortices. Journal of Neuroscience 28, 14416–14421. https://doi.org/10.1523/JNEUROSCI.3148-08.2008

Zhou, W., Jiang, Y., He, S., Chen, D., 2010. Olfaction Modulates Visual Perception in Binocular Rivalry. Current Biology 20, 1356–1358. https://doi.org/10.1016/j.cub.2010.05.059

Appendices

I. Appendix 1: More on the unsuspected importance of odors

A. Why smell is unsuspected

1. Visual dominance is an illusion

It is a common saying that vision is the dominant sense in humans, because of its importance and its complexity. With little evidence to support this claim, we propose to consider a view that challenges this statement to realize that this visual dominance could in fact be illusory: we believe we are witnessing it but a change of viewpoint might as well change everything.

We rely on vision because we feel it strongly defines our relationship between our body and the outside world. Indeed, we constantly sample our environment using visual inputs: it is a distant sense as opposed to touch, smell and taste traditionally classified as intimate. It allows us to represent our surroundings from an egocentric point of view. As a consequence, when asked about what sensory deprivation would scare them the most, 73% of people answered vision versus 14 % audition, 11% taste, 1% touch, and 0% olfaction (1,see also 2). Thus, a strong subjective bias seems to exist, partly explained by this empirical importance. Mostly unaware of it, we consider visual information as more accurate and reliable; as illustrated by the fact that people consciously report visual information more, even when presented simultaneously with auditory inputs (e.g., Colavita effect, 3).

The visual system is consensually considered more complex than any other sensory modality based on the fact that the visual cortex corresponds to the largest part of the sensory cortices. However, analogously to the fact that the absolute or relative brain size was unanimously used to classify intelligence across species (4) before neuron density was considered (for instance 5), this criterion might as well have become arbitrary and obsolete. If we considered the number of sensory receptor types instead, vision would be one of the least important sensory modality with only 2 receptor types (rods and cones) whereas the number of expressed olfactory receptor is estimated around 400 types (6). Thanks to methodological improvements allowing live measurements, we now more and more represent brain connectivity and realize that our brain partly functions in a multisensory way (7).

The Matthew effect (8) describes the reinforcing pattern observed in science networking: the most well-known topics/researchers will gain more and more attention and reward over time, making any other attempt of purely innovative investigation risking to be frivolous. This additional bias translates into the scientific literature as the simple consequence that researchers have a natural bias to work on topics they personally find important and interesting. Counting the number of published papers according to each modality shows that over 1500 papers have been published on visual memory whereas less than 200 were published on olfactory memory between 1806 and May 2019 (9,10,1). Moreover, smell philosophers argue that the conception of human perception is biased and build from a visual perspective (11-13), thus directly impacting our theoretical framework and how we describe and think about sensory modalities.

However, this view, placing vision on top, could be relative to a mature-sight perspective embedded in Caucasian culture. Indeed, it is known that vision is slow to mature, poorly stimulated during uterine life, depriving the newborn of accurate inputs and taking several months to become reliable (see I. B.), a transient state which seems incompatible with such a view. Besides, western societies have evolved from oral transmission to a written culture after Gutenberg's invention of printing, making information sampling to no longer rely on oral communication. In fact, even more recent technological advancement have drastically emphasized the importance of visual information in our daily life (television, social networks, even phonecalls have now become videocalls).

These elements make us reconsider the actual importance of vision in our relationship to the world and the way this bias may impact our own representations. Because if there is a bias to consider vision as the most important sense whereas it may not be that critical in maintaining survival in modern western societies, there may also exist a bias regarding other senses, like olfaction. In the next section, I will explore the possible explanations underlying the unsuspected importance of odors in humans, whether cultural, historical or scientific. However speculative, this cognitive bias is challenged by the actual use of odorant at a massive scale in our everyday environment and reflects on our modulated behavior when odors are encountered.

2. A long-lasting depreciation of smell in western culture and a late scientific interest

In parallel to the over-appreciation of vision, olfaction has long been - wrongfully - depreciated. In the late 19th century, anatomists Broca (14) and Turner (15) classified animals according to the relative size of their sensory organ (i.e., the olfactory bulb), neglecting notions of olfactory sensibility and performance. Humans, along with the other primates, were thus labeled "microsmatic" (i.e., "small olfactory organ") with the idea that the olfactory bulb had reduced to favor the development of the frontal lobe, nest of free will and responsible for our controlled behavior when exposed to odors, unlike the typically sniffing behavioral instinct found in other (macrosmatic) animals. The same years, William James (16) commented in The Principles of Psychology "*Taste, smell, as well as hunger, thirst, nausea and other so-called "common" sensations need not be touched on… as almost nothing of psychological interest is known concerning them.*" According to this dominant and scientific view, Freud (17) had associated smell, taste and touch, with a primitive facet of the mind (i.e., oral and anal stages). The intimate sense of smell was thus associated with animal's instinct of sniffing, hence visible odor-driven behaviors had to be refrained (e.g., ostensibly sampling your food before eating, smelling yourself, etc.) in society. These representations had profoundly marked our representations over the 20th century. Even recently, the low number of human gene receptors expressed (e.g., only ? 40% of compared to almost 100% in rodents) was explained as the necessary outcome of the development of trichromatic vision in primates (18).

In sum, human smell would be a remnant of evolutionary inheritance, far from what the civilized modern human has become and no longer decisive for the survival of our species. Or so it was considered until cross-cultural studies underlined the non-universal dimension of this view. Other cultures place odors at the core of their intimate relation to the world: plants used for medical treatments, incense to communicate with the spirits in religious ceremonies. Anthropologists also point out that this cultural difference is reflected in odor lexicon, i.e., the variety of words related to odors and smell, of each of these cultures (19,20). Western cultures have a poorer smell vocabulary in comparison to color descriptors when compared with a Thai dialect (21) or more generally to a Mexican lexicon i.e., Seri, (22). We can however note the effects of training (23,24) and expertise (e.g., in perfumers, 25) on odor labeling performance and brain plasticity in our western culture. In fact, it is argued that even if we are bad at labeling, or simply describing, what we smell, this could also be because we are used to primarily classify odors in the hedonic dimension (i.e., pleasant, neutral, unpleasant, 26).

Overall, this poor consideration of human smell is reflected by our confidence in our olfactory performance (27), it reflects in how we talk about odors and smells in our surroundings and what place we consciously give to the olfactory dimension in our experience of the world. Before, olfactory perception was thought simple: one odorant is binding with its odorant-selective receptor, mirroring the immune system's antibody (28). As we discuss in the introduction, this representation was erroneous. Fortunately, the late scientific interest to go beyond anatomical descriptors mutated into a recent curiosity to fill the blanks of human olfaction, starting during the 1970s with comparative psychology and inspired by work in ethology (see 29,and 30 for influential reviews). Axel & Buck's work have comprehensively revolutionized our understanding of mammalian olfaction, starting with their discovery of odorant receptors (31) uncovering the organization of the olfactory system and awarded by a Nobel Prize in 2005 (32,33). We now understand one odorant is not perceived as a sum of independent molecules but as rich mixtures using a combinatory pattern (11) and now estimate that humans are thus able to discriminate more than one trillion olfactory stimuli (34). This very impressive ability, at first theorized, is piece by piece confirmed empirically as the path to olfactory knowledge is gradually unraveled before us.

3. A significant and useful evolutionary remnant

The vital importance of chemical signals is traced back to the origins of life on Earth, when primitive forms of life, in the form of simple organisms and bacteria, inhabited marine environment, deprived of sound and light (35). In this context, chemical signals could help detecting food, predator and potential mates (36). Millions of years have passed, bringing a load of cellular evolution to obtain the current neural complexity we seek to investigate here. Chemosignals have the advantage of being distantly transported, available when other senses are unavailable (e.g., in the dark, in noisy environment), can be produced quickly with a generally low production cost and can remain in the environment long after being produced (37). For all these reasons, the basic functions of odors have not been extinguished over time and are still valid today and common to all organisms (see 38 for a review). In primates, odor communication serves for food (foraging), safety (individual or kin recognition, territory assessment) and reproduction (mate choice). In humans, if these behaviors are not strictly qualified as odor-driven, they certainly are odor-guided (29,39,40).

In humans, odors are obviously involved in food perception, as they favor nutrient detection and toxin avoidance, anticipate digestion and can thus influence the quantity (e.g., 41,42) and quality (for a review, see 43) of food-intake. Additionally, while chewing food, molecules from the mouth join the nasal cavity by the retronasal pathway and enhance the perception of flavor (e.g., 44). In their recent review, Lübke & Pause (39) present chemosensory communication among humans and its fundamental role in modulating key functions of human survival. In that respect, human chemosignals (see II. B.) play a significant role in reproductive behavior: it modulates mate choice by the identification of the major histocompatibility complex to promote genetic diversity, correlates with physical attractiveness, which may be linked to perceived health (see 45, for a review), and signals hormonal status of fertility as in other social mammals (for a comparative review in ethology, see 46). Chemical cues are also involved in harm avoidance, particularly during the establishment of mother-infant early relationships. By promoting bonding and feeding from the earliest stages of development, it insures phylogenetic and ontogenetic survival by reducing early mortality (e.g., infanticide, malnutrition; 47,48).

It seems thus that odors are still involved in decisive human behaviors, directly impacting reproduction, offspring rearing and the survival of the species. Yet, what these elements also show us is that, as individual, we would not have guessed to rely on chemical cues for these matters. Despite a few examples of an alert function signaling immediate hazard to avoid, olfactory is still not considered important (1,2).

4. A paradox and its explanation

Taken together, the above-mentioned studies show that olfaction has long been - and is still - under-appreciated but that scientists have come to realize that "poor human olfaction is a 19th-century myth" (49), gradually making up for centuries of disregard. Yet today, a paradox remains. When we look at western societies, odors are strikingly very much present: artificially flavored beverage or food, perfume and cosmetics, fragranced cleaning products, air fresheners for your home, car, closet, fridge, bathroom, etc. We seem in fact very connected to our odorous surroundings, so much that essential oils and incense are now also use in private home and not restricted to religious ceremonies, and that odor's effect on mood have been rerouted to influence consumer's practice in stores (50).

Compiling evidence points toward the fact that we do care about our olfactory environment. We might actually rely on our smell a lot more than we think, since there is a bias in - subjectively - considering odors are of no importance, while the use of odors is omnipresent and science is gradually assessing its importance. Sela & Sobel (51) offer an explanation for this phenomenon/paradox. For these authors, the answer lies in the peculiar functioning of this sense: we are mostly unaware of it (i.e., we do not consciously distinguish a stimulus from its olfactory background) because it does not grab our attention.

Human attention is biased by the nature of visual and auditory inputs: it precisely locates the source of an input in space and time, from a continuous sampling from the eyes (52) and ears (53). Smell does not work like this; it is not continuous and does not allow fast and accurate localization of the source. Sampling the olfactory environment is constrained by our breathing, which simply put corresponds to: sniffs interleaved by blanks. As a consequence, olfactory sampling is more susceptible to change blindness, a mechanism mirroring visual perception deceived by temporal breaks (54). Authors argue that this change anosmia prevents from noticing changes in the olfactory space, unless drastic (i.e., alert signal). They also specify that the sniff frequency in humans is lower than in other mammals, classified macrosmatic, which could allow a better awareness of odors in those species and subsequent ostensible behaviors. Olfactory perception would thus mainly be a byproduct of selective attention (55), usually based on temporal and spatial saliency, which are not the main properties of olfactory inputs.

This mechanism would at least partly explain how/why olfaction does not attract attention, translating into the lack of awareness of our olfactory environment and a general underestimation of our performance. Indeed, no correlation is evidenced between subjective assessment and objective measurement of our olfactory performance (27). However, it does not mean we are absolutely bad at smelling odors or we never perceive odors of course. As evidence show we can orient our attention toward olfactory stimulation (56). In fact, our performance seems comparable to the best mammalian smellers, rodents and dogs, we may even outperform them (57,58), provided the tests are adapted and the odorants relevant for each species (30,59,60 for a review).

After having reviewed why we, as species, culture, and individuals, have overlooked the sense of smell for centuries, I propose to shortly consider in the next section how good we actually are at sampling our surroundings using our nose; and to estimate to what extent can odors influence our mood and behavior.

B. Evidence of olfactory importance

1. An impressive performance

Compared to other primates, hominoid species have the greatest olfactory receptor gene loss among their phylogenetic branches (61). Yet, nor the number of active receptor genes or the size of olfactory organs are predictors of olfactory sensitivity. In fact, humans are able to detect odorants with a very low threshold: we can detect as few as 0.2 part per billion of ethyl mercaptan (i.e., odor of rotten egg; 62) corresponding to the equivalent of 3 drops in an Olympic swimming pool. Another reference study on this question gives the lowest detection threshold found to date, with isoamyl mercaptan (onion-like smell), being detected as lower as 0.77 part per trillion. Comparatively to dogs following a scent trail, we would also be able to track a scent by nose (63) and staying in the canine area, dog owners have been shown to identify their dog among other dogs using their smell (64).

Other astonishing performances are obtained by using biologocal odorants: human odors. In an already-mentioned study, humans are performing better than mice at detecting a component of human blood (58). Individual recognition is also achieved by smell alone: whether it is our own t-shirt presented amongst 100 other worn t-shirts (65), kin recognition in siblings (66), mother-infant dyad (67,68), to name a few (see II B.). Children's have a poor performance in naming dangerous products (i.e., 15% of accuracy; 69), but this is constrained by their developing language and vocabulary, which correlate with identification performance (70). Given adapted measures, they are nonetheless very good at classifying odorants according to edibility (i.e., 80%; 69). Sensitivity seems although to remain stable across development (71) and odor identification and labeling improves with practice (23-25,72), even if the "tip of the nose" state (73), describing the evocative power of smell and our poor labeling performance, seems to be an inherent property of human olfactory perception.

2. Living without smelling: a loss of quality of life

An alternative view to understand the importance of olfaction for humans is to observe what are the consequences if smell is reduced (hyposmia) or lost (anosmia). In both cases, the affection can be partial (i.e., affecting some odorants) or total (i.e., affecting all odorants). A third smell abnormality is expressed by a degraded perception happening in the presence or absence of odorant (dysosmia). Their causes can be various, from a simple cold obstructing the respiratory tracts (i.e., reversible) to head trauma, neurodegenerative diseases or congenital defects (see 28 for a review).

As in any sensory impairment or deprivation, people suffering from olfactory abnormalities, even transient, have reported an overall loss in their quality of life. Because of the intimate link between odor and flavor, it impacts feeding behavior and the quality of food-intake by turning to sugars and fats components (i.e., gustatory) to compensate unflavored meals (43,74). It is also often accompanied with a loss of appetite, which sometimes results in social gathering avoidance, since going out with friends is mostly organized around a meal or drinks (75,76). The warning effect of smell is also compromised and patients report a higher proportion of difficulties with cooking (e.g., overcooking), eating spoiled food and not detecting hazardous smells (e.g., gas leaks or smoke) which could lead to household accidents (77,78). Overall, patients report an overall decrease of enjoyment towards food and a jeopardized safety (74 for review).

In addition, smell disorder is associated with a higher proportion of general depression than in the normosmic population (e.g., 75,see 74 for a review). By affecting the daily routine and personal hygiene of patients, the latter are more reluctant to engage in social interactions by fear of smelling bad (e.g., sweat, bad breath), which indeed modifies spontaneous interactions (79). It can thus impact professional relationships as well as intimate ones, where a decreased libido is also reported (75).

In line with the above descriptions of the importance of smell for humans from an evolutionary perspective, consequences of partial or total smell deprivation seem to deeply affect mood and modify behavior. Human olfaction is clearly and strongly involved in feeding, reproduction, warning and the mediation of social interactions.

3. Odors influence our behavior

We are surrounded by odors and their perception, more or less conscious, guides our behavior, influences our mood and can impact our cognitive abilities. We have seen above that olfaction impairment affects food-intake quality. The reverse is also true: odors mediate satiety (Holley, 1999) and the nature of food ingested (e.g., 41). In addition, reports of worse mood were linked with a poorer olfactory environment, suggesting a modulating effect of odors on mood.

Aside from aromatherapy's infatuation (80), literature confirms that odors can influence mood. Ambient odors alter mood either positively (e.g., chocolate or baby powder, 81, e.g., lavender or lemon, 82, e.g., orange, 83) or negatively (i.e., dimethyl sulfide, 82), when diffused in a room with undetectable concentration. Biologically relevant odorants seem to achieve similar effects. The body odor of the romantic partner is shown to reduce subjective report of discomfort in stressful situation (84) and to improve the quality of sleep (85). Also, sex steroids (i.e., androstadienone) reduce sadness in women but increase it and men (86). In other studies, women exposed to masked body odors (i.e., coupled with cedarwood oil) were more inclined to prosocial decisions (87) but felt more anxious if they were exposed to an odorant (trimethylundecylenic aldehyde) which had been previously associated with a stressful task (88). Similarly, Epple & Herz (89) observed that 5-year-old children failing to resolve an impossible maze task in a scented room, had overall a lower performance to a subsequent, very easy, task if they were again exposed to the odor, illustrating a contingency between odor, mood and cognitive abilities (see also, 90). From these observations, studies have shown that contextual odor could help memory performance (e.g., 91,see 92 for a review), modify facial expression discrimination (93,94), attractiveness while smelling body odors (95,but see also 96) or tears (97).

Undetected odors in our environment also induce changes in our behavior. Kirk-Smith & Booth (98) showed that an androstenone-odorized chair in a dentist's waiting room repelled men but attracted women, and Holland (99) evidenced the implicit influence of citrus odor (an aroma commonly used in cleaning product) on the willingness to engage cleaning behaviors. Ambient scent can also be used in malls and restaurants to increase time and money spent by consumers in these places, by providing a pleasant and relaxing atmosphere (100,101), respectively. A relationship linking subjective time of our personal internal clock and the relaxing property of the odor context was indeed recently evidenced by colleagues (102). At last, odors also influence our social interactions, as already mentioned above, showing for instance than malodor elicited differential behaviors (prosocial empathy, 79, or rejection, 103). An emerging line of literature investigates the human chemical cues and their influence on mood and behavior of other individuals; these reports are specifically addressed in the second section of the introduction.

In conclusion, while olfaction has been overlooked and minimized in the past due to a misunderstanding of its ecological importance favoring the accuracy and apparent reliability of vision; a growing interest has recently emerged to catch up with our poor knowledge of olfactory function and influences. Odors are very well present in our environment, we smell more than we think and a lot of our behaviors are (at least partly) guided by odors, whether by attraction or avoidance.

References

1. Hutmacher, F. Why Is There So Much More Research on Vision Than on Any Other Sensory Modality? Front. Psychol. 10, (2019).
2. Classen, C. V., Classen, C., Howes, D. & Synnott, A. Aroma: The cultural history of smell. (Taylor & Francis, 1994).
3. Hirst, R. J., Cragg, L. & Allen, H. A. Vision dominates audition in adults but not children: A meta-analysis of the Colavita effect. Neuroscience & Biobehavioral Reviews 94, 286–301 (2018).
4. Dicke, U. & Roth, G. Neuronal factors determining high intelligence. Philosophical Transactions of the Royal Society B: Biological Sciences 371, 20150180 (2016).
5. Olkowicz, S. et al. Birds have primate-like numbers of neurons in the forebrain. PNAS 113, 7255–7260 (2016).
6. Glusman, G., Yanai, I., Rubin, I. & Lancet, D. The complete human olfactory subgenome. Genome research 11, 685–702 (2001).
7. Ghazanfar, A. & Schroeder, C. Is neocortex essentially multisensory? Trends in Cognitive Sciences 10, 278–285 (2006).
8. Merton, R. K. The Matthew Effect in Science: The reward and communication systems of science are considered. Science 159, 56–63 (1968).
9. Gallace, A. & Spence, C. The cognitive and neural correlates of tactile memory. Psychological Bulletin 135, 380–406 (2009).
10. Gallace, A. & Spence, C. In touch with the future: the sense of touch from cognitive neuroscience to virtual reality. (Oxford University Press, 2014).
11. Barwich, A.-S. A Critique of Olfactory Objects. Front. Psychol. 10, (2019).
12. Keller, A. Philosophy of Olfactory Perception. (Springer International Publishing, 2016). doi:10.1007/978-3-319-33645-9.
13. Smith, B. C. Human Olfaction, Crossmodal Perception, and Consciousness. Chemical Senses 42, 793–795 (2017).
14. Broca, M. P. Recherches sur les centres olfactifs. Revue d'Antropologie 2, (1879).
15. Turner, W. The Convolutions of the Brain: A Study in Comparative Anatomy. J Anat Physiol 25, 105–153 (1890).
16. James, W. Principles of psychology: Briefer course. New York: Holt (1892).
17. Freud, S. Three Essays on Sexuality. Inhibitions, Symptoms and Anxiety 125–243 (1905).
18. Gilad, Y., Wiebe, V., Przeworski, M., Lancet, D. & Pääbo, S. Loss of Olfactory Receptor Genes Coincides with the Acquisition of Full Trichromatic Vision in Primates. PLoS Biology 2, e5 (2004).
19. Majid, A. Cultural Factors Shape Olfactory Language. Trends in Cognitive Sciences 19, 629–630 (2015).
20. Majid, A. et al. Differential coding of perception in the world's languages. PNAS 115, 11369–11376 (2018).
21. Majid, A. & Burenhult, N. Odors are expressible in language, as long as you speak the right language. Cognition 130, 266–270 (2014).
22. O'Meara, C. & Majid, A. How Changing Lifestyles Impact Seri Smellscapes and Smell Language. Anthropological Linguistics 58, 107–131 (2016).
23. Cain, W. S. To know with the nose: keys to odor identification. Science 203, 467–470 (1979).
24. Sulmont-Rossé, C., Issanchou, S. & Köster, E. P. Odor naming methodology: Correct identification with multiple-choice versus repeatable identification in a free task. Chemical senses 30, 23–27 (2005).
25. Delon-Martin, C., Plailly, J., Fonlupt, P., Veyrac, A. & Royet, J.-P. Perfumers' expertise induces structural reorganization in olfactory brain regions. Neuroimage 68, 55–62 (2013).
26. Yeshurun, Y. & Sobel, N. An Odor is Not Worth a Thousand Words: From Multidimensional Odors to Unidimensional Odor Objects. Annual Review of Psychology 61, 219–241 (2010).
27. Philpott, C., Wolstenholme, C., Goodenough, P., Clark, A. & Murty, G. Comparison of Subjective Perception with Objective Measurement of Olfaction. Otolaryngology - Head and Neck Surgery 134, 488–490 (2006).
28. Bartoshuk, L. M. & Beauchamp, G. K. Chemical Senses. Annual Review of Psychology 45, 419–49 (1994).
29. Doty, R. L. Olfactory communication in humans. Chemical Senses 6, 351–376 (1981).
30. Schaal, B. & Porter, R. H. "Microsmatic Humans" Revisited: The Generation and Perception of Chemical Signals. in Advances in the Study of Behavior (eds. Slater, P. J. B., Rosenblatt, J. S., Beer, C. & Milinski, M.) vol. 20 135–199 (Academic Press, 1991).
31. Buck, L. B. & Axel, R. A Novel Multigene Family May Encode Odorant Receptors: A Molecular Basis for Odor Recognition. Cell 65, 175–187 (1991).
32. Axel, R. Scents and Sensibility: A Molecular Logic of Olfactory Perception (Nobel Lecture). Angewandte Chemie International Edition 44, 6110–6127 (2005).
33. Buck, L. B. Unraveling the Sense of Smell (Nobel Lecture). Angewandte Chemie International Edition 44, 6128–6140 (2005).
34. Bushdid, C., Magnasco, M. O., Vosshall, L. B. & Keller, A. Humans Can Discriminate More than 1 Trillion Olfactory Stimuli. Science 343, 1370–1372 (2014).
35. Müller-Schwarze, D. Signal specialization and evolution in mammals. in Advances in chemical signals in vertebrates (eds. Johnson, R. E., Müller-Schwarze, D. & Sorensen, P. W.) 1–14 (Springer Science & Business Media, 1999).
36. Pickenhagen, W. History of odor and odorants. in Springer Handbook of Odor 1–10 (Springer, 2017).
37. Thornhill, R. & Alcock, J. The evolution of insect mating systems. (Harvard University Press, 1983).

38. Wyatt, T. D. Pheromones and animal behaviour: communication by smell and taste. (Cambridge University Press, 2003).
39. Lübke, K. T. & Pause, B. M. Always follow your nose: The functional significance of social chemosignals in human reproduction and survival. Hormones and Behavior 68, 134–144 (2015).
40. Sarafoleanu, C., Mella, C., Georgescu, M. & Perederco, C. The importance of the olfactory sense in the human behavior and evolution. J Med Life 2, 196–198 (2009).
41. Marty, L., Bentivegna, H., Nicklaus, S., Monnery-Patris, S. & Chambaron, S. Non-Conscious Effect of Food Odors on Children's Food Choices Varies by Weight Status. Front. Nutr. 4, (2017).
42. Sulmont-Rossé, C. et al. Impact of Olfactory Priming on Food Intake in an Alzheimer's Disease Unit. Journal of Alzheimer's Disease 66, 1497–1506 (2018).
43. Lee, J. et al. Nutritional implications of taste and smell dysfunction. in Handbook of olfaction and gustation (ed. Doty, R. L.) 829–864 (Wiley Online Library, 2015).
44. Frank, R. A. & Byram, J. Taste–smell interactions are tastant and odorant dependent | Chemical Senses | Oxford Academic. Chemical Senses 13, 445–455 (1988).
45. Havlícek, J., Fialová, J. & Roberts, S. C. Individual Variation in Body Odor. in Springer Handbook of Odor (ed. Buettner, A.) 125–126 (Springer International Publishing, 2017). doi:10.1007/978-3-319-26932-0_50.
46. Goldberg, J. Les sociétés animales. (Delachaux et Niestlé, 1998).
47. Edmond, K. M., Kirkwood, B. R., Amenga-Etego, S., Owusu-Agyei, S. & Hurt, L. S. Effect of early infant feeding practices on infection-specific neonatal mortality: an investigation of the causal links with observational data from rural Ghana. The American journal of clinical nutrition 86, 1126–1131 (2007).
48. Edmond, K. M. et al. Delayed breastfeeding initiation increases risk of neonatal mortality. Pediatrics 117, e380–e386 (2006).
49. McGann, J. P. Poor human olfaction is a 19th-century myth. Science 356, (2017).
50. Nibbe, N. & Orth, U. R. Odor in Marketing. in Springer Handbook of Odor (ed. Buettner, A.) 141–142 (Springer International Publishing, 2017). doi:10.1007/978-3-319-26932-0_56.
51. Sela, L. & Sobel, N. Human olfaction: a constant state of change-blindness. Experimental Brain Research 205, 13–29 (2010).
52. DeValois, R. L. & DeValois, K. K. Spatial vision. in Encyclopedia of the human brain (ed. Ramachandran, V. S.) vol. 4 419–431 (Academic Press, 2002).
53. Bregman, A. S. Auditory scene analysis: The perceptual organization of sound. (MIT press, 1994).
54. Rensink, R. A., O'Regan, J. K. & Clark, J. J. To See or not to See: The Need for Attention to Perceive Changes in Scenes. Psychol Sci 8, 368–373 (1997).
55. Posner, M. I. Orienting of Attention. Quarterly Journal of Experimental Psychology 32, 3–25 (1980).
56. Spence, C., McGlone, F. P., Kettenmann, B. & Kobal, G. Attention to olfaction. Exp Brain Res 138, 432–437 (2001).
57. Sarrafchi, A., Odhammer, A. M. E., Hernandez Salazar, L. T. & Laska, M. Olfactory Sensitivity for Six Predator Odorants in CD-1 Mice, Human Subjects, and Spider Monkeys. PLoS One 8, (2013).
58. Sarrafchi, A. & Laska, M. Olfactory sensitivity for the mammalian blood odor component trans-4, 5-epoxy-(E)-2-decenal in CD-1 mice. Perception 46, 333–342 (2017).
59. Shepherd, G. M. The Human Sense of Smell: Are We Better Than We Think? PLoS Biol 2, (2004).
60. Walker, J. C. & Jennings, R. A. Comparison of Odor Perception in Humans and Animals. in The Human Sense of Smell (eds. Laing, D. G., Doty, R. L. & Breipohl, W.) 261–280 (Springer, 1991). doi:10.1007/978-3-642-76223-9_13.
61. Niimura, Y., Matsui, A. & Touhara, K. Acceleration of Olfactory Receptor Gene Loss in Primate Evolution: Possible Link to Anatomical Change in Sensory Systems and Dietary Transition. Molecular Biology and Evolution 35, 1437–1450 (2018).
62. Whisman, M. L., Goetzinger, J. W., Cotton, F. O. & Brinkman, D. W. Odorant evaluation: a study of ethanethiol and tetrahydrothiophene as warning agents in propane. Environ Sci Technol 12, 1285–1288 (1978).
63. Porter, J. et al. Mechanisms of scent-tracking in humans. Nat Neurosci 10, 27–29 (2007).
64. Wells, D. L. & Hepper, P. G. The Discrimination of Dog Odours by Humans. Perception 29, 111–115 (2000).
65. Lord, T. & Kasprzak, M. Identification of Self through Olfaction. Percept Mot Skills 69, 219–224 (1989).
66. Porter, R. H. & Moore, J. D. Human kin recognition by olfactory cues. Physiology & Behavior 27, 493–495 (1981).
67. Porter, R. H., Cernoch, J. M. & McLaughlin, F. J. Maternal recognition of neonates through olfactory cues. Physiology & behavior 30, 151–154 (1983).
68. Schaal, B. et al. Les stimulations olfactives dans les relations entre l'enfant et la mère. Reproduction Nutrition Développement 20, 843–858 (1980).
69. De Wijk, R. A. & Cain, W. S. Short Note Odor Identification by Name and by Edibility: Life-Span Development and Safety. Hum Factors 36, 182–187 (1994).
70. Richman, R. A., Post, E. M., Sheehe, P. R. & Wright, H. N. Olfactory performance during childhood. I. Development of an odorant identification test for children. The Journal of Pediatrics 121, 908–911 (1992).
71. Schaal, B. Le développement de la sensibilité olfactive: de la période foetale à la puberté. Rencontres IPSEN en ORL 105–125 (1999).
72. Hummel, T., Guel, H. & Delank, W. Olfactory Sensitivity of Subjects Working in Odorous Environments. Chem Senses 29, 533–536 (2004).
73. Lawless, H. & Engen, T. Associations to odors: Interference, mnemonics, and verbal labeling. Journal of Experimental Psychology: Human Learning and Memory 3, 52–59 (1977).
74. Hummel, T. & Nordin, S. Olfactory disorders and their consequences for quality of life. Acta Oto-Laryngologica 125, 116–121 (2005).
75. Tennen, H., Affleck, G. & Mendola, R. Coping with smell and taste disorders. in Smell and taste in health and disease (ed. Getchell, T. V.) 787–802 (Raven Press, 1991).

76. Van Toller, S. Assessing the impact of anosmia: review of a questionnaire's findings. Chemical senses 24, 705–712 (1999).
77. Miwa, T. et al. Impact of olfactory impairment on quality of life and disability. Archives of Otolaryngology–Head & Neck Surgery 127, 497–503 (2001).
78. Santos, D. V., Reiter, E. R., DiNardo, L. J. & Costanzo, R. M. Hazardous events associated with impaired olfactory function. Archives of otolaryngology–head & neck surgery 130, 317–319 (2004).
79. Camps, J., Stouten, J., Tuteleers, C. & van Son, K. Smells like cooperation? Unpleasant body odor and people's perceptions and helping behaviors. Journal of Applied Social Psychology 44, 87–93 (2014).
80. Herz, R. S. Aromatherapy facts and fictions: a scientific analysis of olfactory effects on mood, physiology and behavior. International Journal of Neuroscience 119, 263–290 (2009).
81. Knasko, S. C. Pleasant Odors and Congruency: Effects on Approach Behavior. Chem Senses 20, 479–487 (1995).
82. Knasko, S. C. Ambient odor's effect on creativity, mood, and perceived health. Chem Senses 17, 27–35 (1992).
83. Lehrner, J., Eckersberger, C., Walla, P., Pötsch, G. & Deecke, L. Ambient odor of orange in a dental office reduces anxiety and improves mood in female patients. Physiology & Behavior 71, 83–86 (2000).
84. Granqvist, P. et al. The scent of security: Odor of romantic partner alters subjective discomfort and autonomic stress responses in an adult attachment-dependent manner. Physiology & Behavior 198, 144–150 (2019).
85. Hofer, M. K. & Chen, F. S. The Scent of a Good Night's Sleep: Olfactory Cues of a Romantic Partner Improve Sleep Efficiency: Psychological Science (2020) doi:10.1177/0956797620905615.
86. Bensafi, M., Brown, W. M., Khan, R., Levenson, B. & Sobel, N. Sniffing human sex-steroid derived compounds modulates mood, memory and autonomic nervous system function in specific behavioral contexts. Behavioural Brain Research 152, 11–22 (2004).
87. Cecchetto, C., Lancini, E., Bueti, D., Rumiati, R. I. & Parma, V. Body odors (even when masked) make you more emotional: behavioral and neural insights. Scientific Reports 9, (2019).
88. Kirk-Smith, M. D., Van Toller, C. & Dodd, G. H. Unconscious odour conditioning in human subjects. Biological psychology 17, 221–231 (1983).
89. Epple, G. & Herz, R. S. Ambient odors associated to failure influence cognitive performance in children. Developmental Psychobiology 35, 103–107 (1999).
90. Rodionova, E. & Minor, A. The effects of low-level exposure to peppermint and lavender scents on school-task performance in elementary-school children. Chemical Senses 30, E36 (2005).
91. Cecchetto, C. et al. Human body odor increases familiarity for faces during encoding-retrieval task. Human Brain Mapping (2020) doi:https://doi.org/10.1002/hbm.24920.
92. Larsson, M., Arshamian, A. & Kärnekull, C. Odor-based context dependent memory. in Springer handbook of odor 105–106 (Springer, 2017).
93. Leleu, A. et al. The Odor Context Facilitates the Perception of Low-Intensity Facial Expressions of Emotion. PloS ONE 10, 1–19 (2015).
94. Leleu, A. et al. Contextual odors modulate the visual processing of emotional facial expressions : An ERP study. Neuropsychologia 77, 366–379 (2015).
95. Roberts, S. C. et al. Body Odor Quality Predicts Behavioral Attractiveness in Humans. Arch Sex Behav 40, 1111–1117 (2011).
96. Foster, J. D. Beauty Is Mostly in the Eye of the Beholder: Olfactory Versus Visual Cues of Attractiveness. The Journal of Social Psychology 148, 765–774 (2008).
97. Gelstein, S. et al. Human Tears Contain a Chemosignal. Science 331, 226–230 (2011).
98. Kirk-Smith, M. D. & Booth, D. A. Effects of androstenone on choice of location in other's presence. Olfaction and Taste VII. IRL Press, London 397–400 (1980).
99. Holland, R. W., Hendriks, M. & Aarts, H. Smells Like Clean Spirit: Nonconscious Effects of Scent on Cognition and Behavior. Psychol Sci 16, 689–693 (2005).
100. Chebat, J.-C., Morrin, M. & Chebat, D.-R. Does Age Attenuate the Impact of Pleasant Ambient Scent on Consumer Response? Environment and Behavior 41, 258–267 (2009).
101. Guéguen, N. & Petr, C. Odors and consumer behavior in a restaurant. International Journal of Hospitality Management 25, 335–339 (2006).
102. Baccarani, A., Laflamme, V., Grondin, S. & Brochard, R. 2020. The Relaxing and Stimulating Effects of Odors on Time Perception and their Modulation by Expectancy. Attention, Perception & Psychophysics, 1-15.
103. Todd, W. A. Psychosocial problems as the major complication of an adolescent with trimethylaminuria. The Journal of Pediatrics 94, 936–937 (1979).

II. Appendix 2: Supporting information of Study 1

From Leleu et al., 2020, *Dev Sc*
Reproduced with permission from John Wiley and Sons
(License 4815470420405 delivered on April 24th 2020).

Appendix 2A

EEG preprocessing and frequency-domain analysis

All EEG analyses were carried out using Letswave 6 (http://nocions.github.io/letswave6) running on Matlab 2012 (MathWorks, USA). Left and right mastoid electrodes (M1 and M2) were removed from the montage (Figure S2) before processing since they were noisy or artifact-ridden for most infants. EEG data were first bandpass filtered at 0.1 – 100 Hz (butterworth filter, 4th order) and then resampled to 200 Hz to reduce file size and processing time. Data were cropped according to each sequence in 36-sec segments starting from the fade-in. To reduce very high-amplitude artefacts, each segment was processed using the Artifact Blocking algorithm (Fujioka et al., 2011; Mourad et al., 2007) windowed on the overall segment with a large threshold of ± 500 µV. For one infant, a remaining noisy channel (Fpz) was then rebuilt using linear interpolation from the two nearest electrodes (Fp1 and Fp2). Data were then re-referenced according to a common average reference. EEG segments were further cropped in shorter epochs starting from the first full contrast face image in the stimulation sequence (i.e., just after the fade-in) and lasting 32 secs (i.e., exactly thirty-two 1 Hz cycles).

To increase signal-to-noise ratio (SNR), two data-driven criteria were used for each infant to remove sequences with no general response of the visual system to the rapid stream of stimulation (Barry-Anwar et al., 2018; de Heering and Rossion, 2015; Peykarjou et al., 2017), or with atypical scalp-wide power at the 1-Hz face-selective rate compared with the other sequences. A fast Fourier transform (FFT) was first applied to every epoch and amplitude spectra were extracted for all electrodes with a frequency resolution of 1/32 = 0.03125 Hz. For the first criterion, *Z*-scores were calculated for each channel and each frequency bin as the difference between the signal amplitude and the mean noise amplitude (estimated from the 20 surrounding bins, 10 on each side, excluding the two immediately adjacent and the two most extreme (minimum and maximum) bins) divided by the standard deviation (SD) of the noise. Since a general response of the infant visual system has been previously observed over medial occipital sites to both meaningful or meaningless (i.e., phase-scrambled) fast trains of images (de Heering and Rossion, 2015), sequences were kept for further analysis when at least two Z-scores were greater than 1.64 ($p < .05$, one-tailed, signal > noise) or at least one Z-score was larger than 2.32 ($p < .01$, one-tailed) over medial occipital electrodes (Oz, POz, O1, O2) for the 6-Hz base frequency or its first harmonic (i.e., integer multiple = 12 Hz) as a general marker of adequate looking at the stimulation screen. For the second criterion, FFT amplitude spectra were pooled across all channels and amplitude at the 1-Hz face-selective frequency was corrected by subtracting the mean noise amplitude. Here, mean noise was estimated using 6 instead of 20 frequency bins since EEG power is high in the low-frequency range and non-linearly decreases as frequency increases (Fransson et al., 2013). Accordingly, considering too many frequency bins would overestimates the background noise (and therefore underestimates the face-selective response) because the power spectrum is steeper for lower than for higher frequency bins around the 1-Hz target frequency. A sequence was considered atypical when its noise-corrected amplitude was above or below 2 SDs of the mean of all sequences retained after application of the first criterion. Once these two criteria were applied, between 4 and 15 sequences were kept per infant for an overall rejection of 10 out of 145 sequences. On average, 3.72 ± 0.35 (SEM) and 4 ± 0.41 sequences were respectively retained for the control and the body odor conditions with no significant difference between them, $t_{17} = 1.05$, $p = .31$. Finally, to reduce EEG activity non phase-locked to the stimuli, sequences were separated according to the odor conditions and averaged in the time-domain to obtain one single 32-sec epoch per condition for each infant. FFT was applied and amplitude spectra were extracted for each electrode.

Statistical analysis

Statistical analysis was conducted on both brain responses to the 6-Hz base rate of image presentation and the 1-Hz selective rate of face presentation in two consecutive steps: 1/ channels with significant responses were identified in grand-averaged data using *Z*-scores (i.e., using amplitude variance across frequency bins (e.g., de Heering and Rossion, 2015; Rossion et al., 2015); 2/ odor conditions were compared over identified channels using T-tests calculated on noise-corrected amplitudes (i.e., using amplitude variance across individual infants).

For 1/, the aim was to determine whether each brain response was significantly larger than surrounding noise level ($Z > 1.64$, $p < .05$, one-tailed, signal > noise). Given that such responses were isolated in the infant brain using a similar paradigm with some infants installed in a car seat and others seated on their mother's lap (de Heering and Rossion, 2015), we first estimated significant responses for the frequencies of interest and their harmonics (i.e., integer multiples) regardless of the odor condition in an attempt to replicate de Heering & Rossion's findings. FFT data were averaged across conditions for each infant and amplitude over each channel was normalized by dividing by the square root of the sum of squared amplitudes of all channels (McCarthy and Wood, 1985) at each frequency bin. Normalization was intended to identify the main electrodes over which a response is recorded by scaling differences between electrodes on the global magnitude of the response across the scalp. After normalization, data were grand-averaged across infants and *Z*-scores were calculated for each electrode. We expected significant common (6 Hz and harmonics) and face-selective (1 Hz and harmonics) visual responses mainly over channels Oz and P7/8 respectively (de Heering and Rossion, 2015). We thus considered a medial occipital region-of-interest (ROI) centered on Oz and including contiguous channels (POz, O1, O2) for the common visual response, and two lateral posterior ROIs centered on P7 and P8 and including contiguous channels (O1/2, P3/4, C5/6) for the face categorization response (Figure S2). Harmonics were considered for further analysis until *Z*-scores over one channel were no longer significant (Tables S1 and S4). For each response, individual normalized amplitudes were then summed for significant harmonics and *Z*-scores were calculated on these summed amplitudes for each infant (Tables S2 and S5) as well as for the grand-averaged data (Table S4 for the common visual response) to estimate the significance of the overall responses distributed on several harmonics. For visualization purpose, each response was also quantified in a single value expressed in microvolts by summing noise-corrected amplitudes (before normalization) across significant harmonics (Retter and Rossion, 2016). Thereafter, we determined which electrodes presented significant responses separately for each odor condition. Individual datasets for each condition were first normalized on the global power of both conditions combined as previously calculated. Normalized amplitudes were then summed across significant harmonics and *Z*-scores were finally computed on grand-averaged data.

For 2/, the aim was to analyze the difference in amplitude between the two odor conditions for each brain response. Individual summed responses expressed in non-normalized noise-corrected amplitudes were extracted for the relevant channels identified in step 1/. Analysis was performed using T-tests comparing the two conditions (significance threshold: $p < .05$, two-tailed, maternal odor ≠ control odor) and individual data were grand-averaged for visualization. To explore the significance of the odor effect (maternal odor minus control odor) on the face-selective response in every infant brain, uncorrected normalized amplitudes obtained in the control odor condition were subtracted from those recorded in the maternal odor condition for each individual dataset. *Z*-scores were calculated at each electrode within the ROIs for significance testing of the difference between odor conditions ($Z > 1.96$ or < -1.96, $p < .05$, two-tailed, maternal odor ≠ control odor; Table S3). According to the results of the group-level analysis showing a significantly larger face categorization response over right posterior regions in the presence of maternal odor cues (see Results), the significance of each individual odor effect was also estimated using one-tailed *Z*-scores ($Z > 1.64$, $p < .05$, maternal odor > control odor; Table S3).

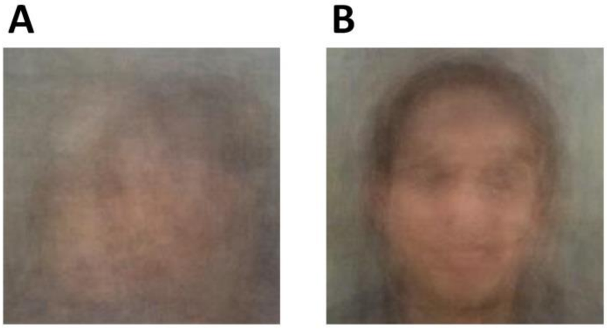


Figure S1. Mean face images from the present study and the study of de Heering & Rossion (2015). (A) In the present study, faces were off-centered to increase physical variability and avoid the presence of a clear facial configuration in the mean face image obtained by averaging the 66 faces used as stimuli. (B) A face pattern is more clearly visible in the mean face image obtained from the 48 centered faces used in the study of de Heering & Rossion (2015).

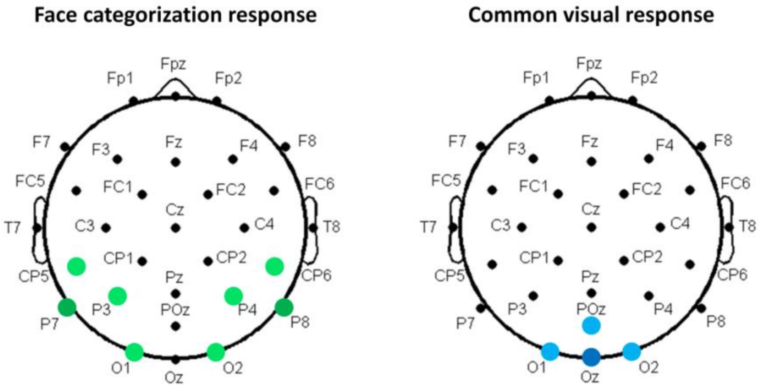


Figure S2. 30-channel montage used for EEG processing and regions-of-interest (ROIs) used for data analysis. EEG was recorded from 32 channels positioned according to the 10-10 classification system, but left and right mastoid electrodes (M1 and M2, not shown) were removed before processing due to noisy signal. After preprocessing, frequency-domain analysis of the face categorization response (left) was conducted within right and left lateral ROIs including the occipito-temporal channels P8 and P7 (dark green) and contiguous channels (light green). The common visual response (right) was analyzed within a medial occipital ROI including Oz (dark blue) and contiguous channels (light blue).

Table S1. Electrodes showing a significant face categorization response for the grand-averaged data combined across odor conditions. Z-scores were calculated on normalized amplitudes for each electrode within the lateral ROIs (Figure S2) and for each harmonic (i.e., integer multiple) of the 1-Hz rate of face presentation but no electrode showed a consistent response across several harmonics. The face categorization response was thus quantified only from the signal recorded at 1 Hz. Z-scores in bold are significant according to a threshold of $Z > 1.64$ (*$p < .05$, one-tailed, signal > noise).

		Averaged odor conditions		
	Electrode	**1 Hz**	**2 Hz**	**3 Hz**
Left hemisphere	**CP5**	-0.49	0.27	-0.91
	P3	-1.10	0.66	0.12
	P7	**1.91***	0.70	0.20
	O1	-2.32	0.32	0.71
Right hemisphere	**CP6**	**4.26***	-0.95	-0.16
	P4	-0.43	-1.33	0.98
	P8	**4.79***	-0.25	0.24
	O2	0.16	0.52	0.32

Table S2. Electrodes showing a significant face categorization response for individual infant data combined across odor conditions. Z-scores were calculated on normalized amplitudes at the 1-Hz rate of face presentation for each infant and for each electrode within the lateral ROIs (Figure S2). The face categorization response is significant for 13 out of 18 infants, mainly over the right-hemispheric channels CP6 and P8 (10 infants with a significant response over CP6 and/or P8). Z-scores in bold are significant according to a threshold of $Z > 1.64$ (*$p < .05$, one-tailed, signal > noise).

Averaged odor conditions								
	Left hemisphere				**Right hemisphere**			
Infant	**CP5**	**P3**	**P7**	**O1**	**CP6**	**P4**	**P8**	**O2**
IN01	-1.46	-1.10	0.74	**2.86***	-1.85	-2.12	-0.31	**3.81***
IN02	-0.89	1.61	0.99	-0.46	0.27	0.87	-1.14	0.87
IN03	-0.70	-1.94	1.30	-0.99	**2.04***	-0.62	**2.12***	-1.94
IN04	-1.08	-1.24	-0.48	1.41	0.61	1.42	-0.79	0.30
IN05	**1.65***	-0.74	0.85	-1.90	**2.69***	-1.21	-1.42	-0.62
IN06	0.81	**2.10***	1.34	-1.05	0.18	-2.25	**2.12***	-1.90
IN07	1.20	1.22	-0.17	-2.37	0.05	0.55	**3.55***	-0.34
IN08	-0.53	-2.10	0.70	1.15	0.49	0.14	0.46	1.34
IN09	-1.05	-1.34	-0.87	-0.72	1.04	-0.52	**3.46***	-0.29
IN10	-1.42	**1.75***	0.74	-0.88	-0.72	**2.14***	0.12	-2.26
IN11	**1.65***	-1.17	**3.92***	-0.55	-0.55	0.06	**4.69***	-0.60
IN12	**1.76***	-0.47	-0.44	0.50	**2.48***	-0.91	-0.74	0.24
IN13	0.43	-2.05	-0.68	-1.62	1.10	-0.34	0.48	-0.91
IN14	-0.22	**1.74***	0.74	0.79	**1.90***	-0.23	0.95	0.82
IN15	-0.10	0.13	0.87	-1.38	1.03	-0.11	-0.84	**3.00***
IN16	-2.31	-0.19	1.46	-0.93	0.77	1.13	**4.36***	-0.01
IN17	1.11	-0.16	-2.31	-0.44	**2.97***	-0.08	-1.62	**1.79***
IN18	-0.44	-0.07	-1.41	-1.46	1.35	0.18	0.69	-2.65

Table S3. Electrodes showing a significant effect of maternal odor (i.e., maternal odor minus control odor) for individual infant data. *Z*-scores were calculated on the difference between normalized amplitudes for the maternal body odor and the control odor conditions at the 1-Hz rate of face presentation for each infant and for each electrode within the lateral ROIs (Figure S2). The odor effect on the face categorization response is significant (*Z* > 1.96 or < -1.96, * *p* < .05, two-tailed, maternal odor ≠ control odor, depicted in bold and in italic for negative *Z*s) over at least one electrode for 12 out of 18 infants (9 infants with a larger response in the maternal odor context). According to one-tailed significance testing of a larger face-selective response in the maternal odor context (*Z* > 1.64, *p* < .05, depicted in bold), 12 out of 18 infants present a significant effect, mainly over the right-hemispheric channels CP6, P8 and O2 (7 infants).

	Left hemisphere				Right hemisphere			
Infant	**CP5**	**P3**	**P7**	**O1**	**CP6**	**P4**	**P8**	**O2**
IN01	-0.44	-1.29	0.27	0.54	-1.07	-0.62	**1.97***	**2.83***
IN02	1.62	**3.04***	0.31	1.18	-0.80	0.97	-0.41	1.58
IN03	0.26	-0.59	1.06	0.62	**1.90**	**1.81**	-1.50	**1.86**
IN04	1.51	0.02	1.04	**2.81***	0.96	0.31	0.41	1.49
IN05	-0.52	1.61	***-2.23****	0.57	***-2.54****	-1.90	0.88	**1.73**
IN06	0.80	0.28	0.84	0.70	0.92	-0.10	-1.14	0.48
IN07	0.40	-0.23	***-2.23****	-0.46	-0.40	0.25	0.93	-0.01
IN08	1.08	0.80	**2.07***	**2.63***	1.47	-0.71	1.12	-0.49
IN09	1.25	**1.96***	1.58	-0.77	-1.38	-1.26	1.03	1.34
IN10	0.18	-0.57	-0.66	0.43	1.19	1.21	-0.33	-0.16
IN11	0.56	**1.82**	***-3.21****	0.43	-0.09	-0.36	**2.10***	0.69
IN12	-1.45	**2.48***	***-3.42****	**3.45***	0.98	0.11	-1.48	**2.26***
IN13	0.67	**1.70**	-0.07	0.51	-1.76	-1.31	0.63	0.80
IN14	-1.16	1.31	***-2.44****	-0.49	-0.85	-0.83	1.30	0.18
IN15	1.21	-0.83	0.92	0.10	**4.28***	-0.10	0.18	1.48
IN16	-0.44	1.30	-0.79	0.16	-0.33	-1.10	0.22	-0.35
IN17	-1.10	-0.81	0.76	1.19	0.75	0.41	-0.73	**3.42***
IN18	-1.69	-0.54	1.28	-0.09	0.18	-0.74	-0.86	1.03

Table S4. Electrodes showing a significant common visual response for the grand-averaged data combined across odor conditions. *Z*-scores were calculated on normalized amplitudes for each electrode within the medial occipital ROI (Figure S2) and for each harmonic (i.e., integer multiple) of the 6-Hz base rate of fast periodic stimulation with a consistent response across the six first harmonics. The common visual response was thus quantified from the summed amplitudes of these six harmonics (i.e., sum 6-36 = from 6 Hz to 36 Hz). *Z*-scores in bold are significant according to a threshold of *Z* > 1.64 (**p* < .05, one-tailed, signal > noise).

	Averaged odor conditions								
Electrode	**6 Hz**	**12 Hz**	**18 Hz**	**24 Hz**	**30 Hz**	**36 Hz**	**42 Hz**	**48 Hz**	**sum 6-36**
O1	**7.26***	**7.03***	**9.26***	**8.73***	**2.46***	0.78	**1.85***	-0.08	**11.14***
POz	**2.48***	**2.44***	1.23	**3.90***	**3.26***	-1.57	-0.17	-2.24	**4.42***
Oz	**17.79***	**10.75***	**13.97***	**14.75***	**8.84***	**2.80***	1.49	-0.28	**17.39***
O2	**8.39***	**10.43***	**9.97***	**7.57***	**9.13***	**2.52***	1.17	-0.28	**14.14***

Table S5. Electrodes showing a significant common visual response for individual infant data combined across odor conditions. *Z*-scores were calculated for each infant and for each electrode within the medial occipital ROI (Figure S2) on the summed normalized amplitudes across significant harmonics (i.e., from 6 to 36 Hz) of the 6-Hz base rate of stimulation. All infants present a significant response over channel Oz. *Z*-scores in bold are significant according to a threshold of $Z > 1.64$ (*$p < .05$, one-tailed, signal > noise).

	Averaged odor conditions			
Infant	**O1**	**POz**	**Oz**	**O2**
IN01	**9.37***	1.40	**9.44***	**5.05***
IN02	0.18	**8.74***	**7.82***	-0.17
IN03	-1.10	-2.32	**10.29***	**11.36***
IN04	**10.63***	**3.55***	**7.28***	0.05
IN05	0.55	-0.53	**2.49***	**2.25***
IN06	**2.70***	**7.48***	**7.11***	**6.66***
IN07	1.42	0.65	**9.57***	**4.90***
IN08	**2.75***	-1.81	**12.76***	**8.25***
IN09	**7.62***	-3.72	**8.96***	**2.00***
IN10	**5.67***	0.15	**5.15***	1.26
IN11	**4.74***	-0.40	**4.41***	**4.58***
IN12	**8.86***	-2.68	**8.87***	**8.23***
IN13	**3.52***	**8.43***	**4.57***	1.00
IN14	**6.77***	-3.31	**13.77***	-0.01
IN15	0.48	**4.49***	**10.84***	**4.98***
IN16	1.45	-3.09	**12.66***	**8.74***
IN17	**6.75***	-2.09	**17.12***	**11.39***
IN18	1.13	**2.44***	**4.27***	**1.74***

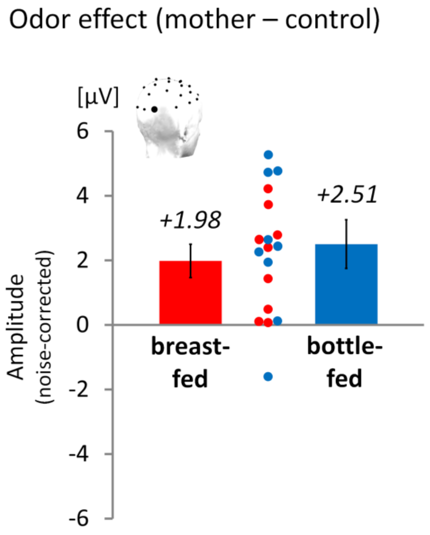


Figure S3. Individual odor effects on the face categorization response depending on infants' feeding experience. Odor effect (i.e., maternal odor minus control odor) on the face-selective response plotted over channel O2 for individual and mean noise-corrected amplitudes (error bar represents standard error of the mean) depending on infants' feeding experience (red: breast-fed, N = 9 infants; blue: bottle-fed, N = 9 infants). The odor effect is large for each feeding status (breast-fed: M = +1.98 ± 0.51 (*SEM*) µV; bottle-fed: M = +2.51 ± 0.75 µV) with no significant difference between them (t_{16} = 0.57, p = .57). However, this observation should be reinforced with larger sample sizes.

III. Appendix 3: Supporting information of Study 2

From Rekow et al., 2020, *Cog Dev*

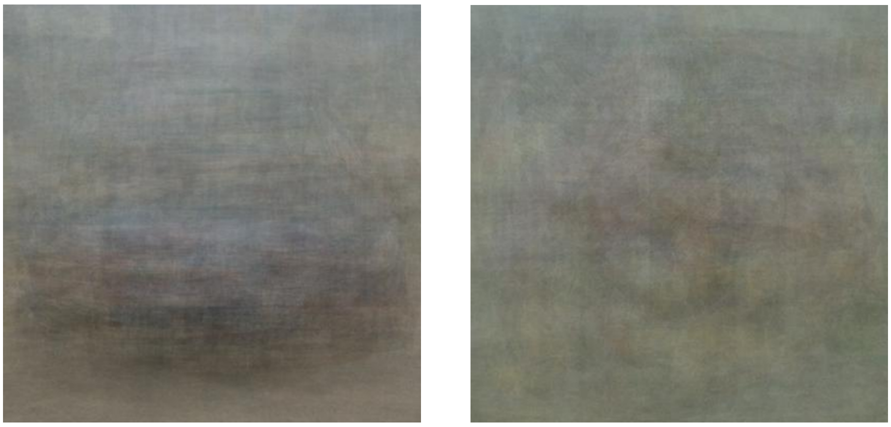


Figure S1. Mean images of cars and other objects. Left: Mean image obtained by averaging the 66 pictures of cars used as stimuli. Cars were off-centered when cropping images to increase physical variability and avoid a systematic configuration in the images. **Right:** Mean image obtained from 66 images of objects picked randomly among the 170 images used as base stimuli. These images depict living (e.g., plants, animals) and non-living (man-made objects) entities.

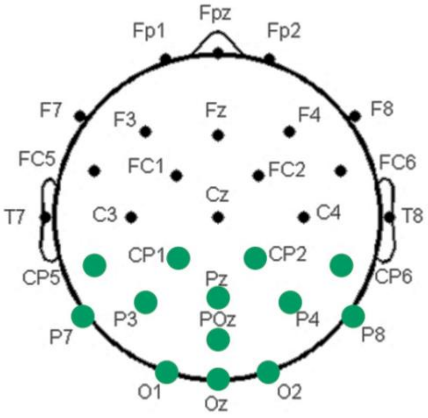


Figure S2. Thirty-channel montage of EEG acquisition and 13-posterior channel array used for analysis. EEG was acquired from a 32-channel headcap, configured according to the 10-10 classification system. Left and right mastoid electrodes (M1 and M2, not shown) were excluded from processing and analysis. After preprocessing, frequency-domain analysis was conducted on the 13 posterior channels highlighted in green.

Table S1. Individual infant data showing a significant car categorization response over posterior electrodes combined across odor conditions. *Z*-scores were calculated on normalized amplitudes for each infant and for each posterior electrode at the 1-Hz rate of car presentation. The response emerges over posterior scalp regions with 15 out of 18 infants presenting a significant response over at least one posterior electrode. *Z*-scores in bold are significant ($Z > 1.64$, $p < .05$, one-tailed, signal > noise).

	Averaged odor conditions												
	Left hemisphere					**Midline**			**Right hemisphere**				
Infant	**CP1**	**CP5**	**P3**	**P7**	**O1**	**POz**	**Pz**	**Oz**	**CP2**	**CP6**	**P4**	**P8**	**O2**
INF01	-1.44	0.87	1.46	**1.67**	**2.16**	-1.91	-2.77	**1.95**	0.65	-1.06	-0.94	0.89	**2.53**
INF02	-0.80	1.21	-0.41	-0.59	-2.18	-1.26	0.34	-1.74	0.67	0.97	0.36	**2.42**	1.35
INF03	1.16	-0.95	0.92	-0.20	0.84	1.26	1.54	1.06	-0.03	-0.90	-0.01	-0.37	0.97
INF04	-1.01	-0.83	**1.84**	0.95	0.52	-0.73	-0.49	0.41	-1.06	**2.59**	**2.01**	-1.05	0.30
INF05	1.56	0.10	0.41	-1.67	-0.55	1.14	-1.17	0.35	-0.17	0.86	-1.41	0.49	0.24
INF06	-0.51	0.81	-1.43	**3.88**	-0.38	-0.33	-0.75	-0.63	-0.82	-0.57	-2.19	-1.21	-0.60
INF07	0.12	0.64	**2.14**	1.12	-0.16	0.23	0.11	0.85	-0.60	-0.29	-1.93	0.04	1.23
INF08	-1.31	0.20	0.06	**2.02**	-1.39	0.48	-2.25	0.37	-0.81	**1.74**	0.57	-0.53	**2.88**
INF09	-0.29	-0.35	1.49	-0.82	0.77	0.91	1.58	-1.60	-2.05	-1.68	0.91	0.96	-0.66
INF10	-2.11	**1.89**	0.13	1.36	-1.96	0.18	0.67	1.44	**2.04**	-0.31	1.40	-0.93	**1.98**
INF11	-0.78	-2.21	-0.35	-2.95	1.29	0.39	**3.64**	-1.66	-0.66	1.25	-1.34	-2.69	1.30
INF12	**2.12**	-0.65	0.49	0.54	**2.82**	0.18	-1.65	-0.13	-0.67	0.28	0.51	0.54	-0.24
INF13	0.57	-1.28	-0.48	-0.22	-0.08	1.59	-1.00	-0.49	0.14	-0.63	-2.15	0.36	**2.06**
INF14	-1.13	-0.09	-0.74	-0.97	-0.62	**2.14**	0.63	-1.50	**3.13**	-1.20	1.19	0.84	-1.10
INF15	-0.13	**2.43**	-2.16	-0.57	-0.40	0.19	-0.12	-1.12	0.45	-0.25	1.34	-0.45	-1.08
INF16	-1.17	-1.07	-0.65	-0.23	-1.86	0.79	**2.13**	-0.90	-0.47	**2.99**	**3.56**	0.17	0.44
INF17	-0.35	-0.39	1.03	**2.29**	0.87	-1.18	-2.40	0.26	-2.07	-0.41	-1.21	-0.34	0.25
INF18	0.77	-0.63	-0.97	-1.29	0.19	-1.36	-0.15	0.57	0.94	-0.10	-1.20	**2.09**	0.42

Table S2. Individual infant data showing a significant general visual response over posterior electrodes combined across odor conditions and summed harmonics. For each infant and for each posterior electrode, *Z*-scores were calculated on the summed normalized amplitudes across significant harmonics (i.e., integer multiples of 6 Hz from 6 to 36 Hz) of the 6-Hz rate of stimulation. The general visual response emerges over middle occipital scalp regions with every infant presenting a significant response over channels Oz and O2. Z-scores in bold are significant ($Z > 1.64$, $p < .05$, one-tailed, signal > noise).

	Averaged odor conditions and summed harmonics												
	Left hemisphere					**Midline**			**Right hemisphere**				
Infant	**CP1**	**CP5**	**P3**	**P7**	**O1**	**POz**	**Pz**	**Oz**	**CP2**	**CP6**	**P4**	**P8**	**O2**
INF01	0.23	-1.00	0.48	**2.16**	**2.50**	**2.24**	-0.31	**5.61**	-2.08	0.33	0.14	0.11	**2.28**
INF02	-1.56	1.31	-1.70	-3.17	**5.50**	-0.12	-1.93	**5.56**	-0.95	-3.39	-2.38	-3.14	**2.67**
INF03	0.19	0.40	-0.40	-1.30	**4.96**	**3.41**	0.99	**5.44**	**1.99**	-1.71	**2.34**	-1.40	**5.78**
INF04	-3.78	-1.49	0.75	-1.19	**2.86**	-0.80	-0.55	**2.43**	-2.27	-2.89	-2.86	-1.92	**2.17**
INF05	-0.23	-1.65	-2.78	-2.99	**2.88**	**7.63**	-2.78	**7.75**	-1.56	-3.16	-3.27	-4.85	**7.26**
INF06	-2.28	-3.25	-0.47	-1.73	**7.25**	**2.55**	-2.47	**8.04**	-4.23	1.25	-0.95	-1.09	**7.61**
INF07	-4.74	-1.77	-1.87	-2.41	**8.23**	-2.18	-3.26	**6.98**	-1.60	-0.18	0.36	-2.28	**3.63**
INF08	-3.92	-2.74	-2.25	-1.31	-2.35	**4.79**	-4.48	**6.11**	-1.97	-2.66	-2.38	-3.00	**6.91**
INF09	-2.39	-1.91	-4.41	-0.88	**2.88**	0.83	-1.84	**5.40**	-3.49	0.71	-0.84	-1.33	**5.57**
INF10	0.04	0.26	-0.87	-1.86	1.58	-1.73	-1.87	**8.04**	-0.81	-0.59	**1.95**	-0.69	**9.15**
INF11	-0.51	-1.92	-0.38	-2.72	**5.34**	**3.07**	-2.79	**9.75**	-2.07	-3.41	-2.65	-3.42	**9.63**
INF12	-2.12	-0.52	-0.98	-2.14	**2.57**	**1.76**	-1.00	**6.64**	0.35	-3.36	-0.96	-1.05	**2.73**
INF13	-4.06	-1.64	**1.78**	-1.95	0.00	1.51	-0.63	**10.08**	-1.94	0.39	-0.31	**1.93**	**7.13**
INF14	-1.19	-1.87	-4.35	-1.41	1.54	-1.07	-3.28	**3.77**	-1.91	-0.21	-2.02	-1.13	**5.68**
INF15	-1.22	-1.17	-0.13	-1.03	**2.62**	-0.95	-0.28	**6.70**	-1.36	-0.90	-0.35	-1.13	**7.63**
INF16	-2.75	-3.31	-2.92	-3.41	**6.61**	**2.76**	-3.97	**7.45**	-3.71	-2.07	-1.38	0.63	**7.97**
INF17	-4.66	-3.59	-3.68	-3.09	**6.17**	**3.56**	-4.59	**6.17**	-4.14	-2.17	-0.88	-2.46	**6.00**
INF18	-2.82	-0.63	-1.32	-3.50	-3.05	**6.06**	-1.11	**10.52**	-1.91	-1.28	0.13	-2.06	**9.57**

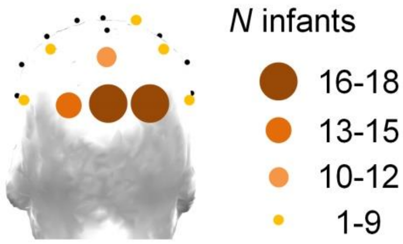


Figure S3. Repartition of significant electrodes at individual level for the general visual response. Head map (back view) showing the density of significant individual *Z*-scores ($Z > 1.64$, $p < .05$, signal > noise) over the 13 posterior channels for the general visual response. Circle size and color illustrate the number of infant with a significant response at the corresponding channel.

Is there a neural signature of online category learning for cars?

Unfamiliar visual categories can be learned during the course of an experiment, the so-called *online category learning* (e.g., Eimas and Quinn, 1994). Accordingly, we tested whether the neural categorization response to cars was different between the beginning (i.e., first half of stimulation sequences) and the end of the experiment (i.e., second half of sequences). Using the same procedures as in the main analysis, we compared the car categorization response for the first and second halves of the experiment instead of the odor contexts. The amplitude of the response over O2 did not significantly increase between the first and the second halves of the experiment (+0.47 ± 1.02 (*SEM*) µV; $t_{17} = 0.46$, $p = .65$). However, while the response recorded at the beginning of the experiment was not significant over any posterior channel, even O2 ($Z = 0.29$, $p = .39$), it became highly significant only over O2 at the end of the experiment ($Z = 2.60$, $p = .005$), suggesting that infants progressively learn to categorize cars during testing (Figure S4). This complementary analysis encourages future studies to investigate more closely online category learning at the neural level using FPVS-EEG.

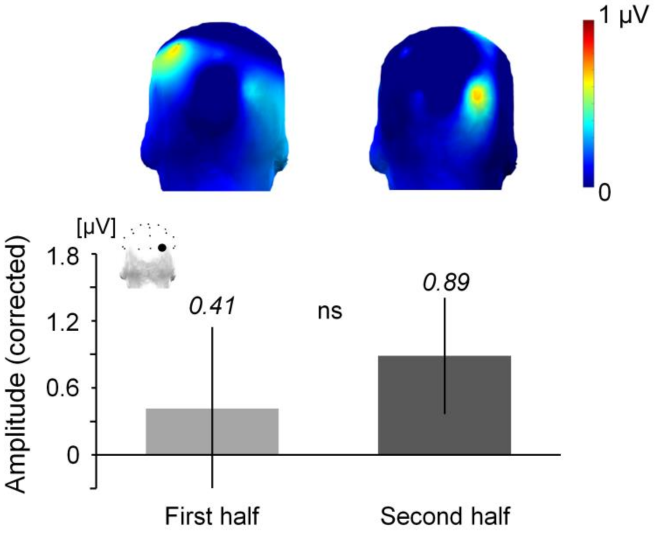


Figure S4. The car categorization response at the beginning *vs.* end of the experiment. Top: 3-D topographical head maps (back view) of the amplitude (noise corrected) of the neural categorization response to cars at the beginning (first half of sequences) and the end (second half of sequences) of the experiment. **Bottom:** Corresponding amplitudes over O2 for the first and second halves of sequences. Error bars represent standard errors of the mean ; ns: $p > .05$.

IV. Appendix 4: Supporting information of Study 3

Supporting information

Supplementary Materials and Methods

EEG preprocessing and frequency-domain analysis

EEG analyses were performed on Letswave 6 (https://www.letswave.org/) running on Matlab 2017 (MathWorks, USA). Both mastoid electrodes were removed from processing because they were noisy for most infants (Figure S1). Following preprocessing steps were highly similar to previous FPVS-EEG infant studies (de Heering and Rossion, 2015; Leleu et al., 2020; Peykarjou et al., 2017). To each individual datasets, we first applied a Butterworth filter (4th order, cutoff: 0.1–100 Hz) and resampled datasets to 200 Hz. Sequences were then cropped from the beginning of fade-in into 36-s-long segments. For each segment, the artifact blocking algorithm (Fujioka et al., 2011; Mourad et al., 2007) was applied to reduce artifacts with a threshold of ± 250 µV. Datasets were then re-referenced to a common average reference. Segments were further cropped into 32-s epochs starting from the end of the fade-in, and thus comprised exactly thirty-two 1-Hz cycles.

Next, we rejected unusable epochs based on two data-driven criteria to increase signal-to-noise ratio (SNR). A fast Fourier transform (FFT) was first applied to all individual datasets and the amplitude spectra was extracted for all electrodes using a high frequency resolution of 1/32 s = 0.03125 Hz. The first criterion consisted in identifying the epochs failing to elicit a reliable general visual response of the visual system at the base rate frequency and its second harmonic (i.e., 6 Hz and 12 Hz responses), used as a measure of infant visual attention (de Heering and Rossion, 2015; Leleu et al., 2020; Peykarjou et al., 2017). Z-scores were calculated for each channel as the difference between the signal amplitude and the mean noise amplitude (noise was estimated from the 10 surrounding bins of each side, excluding the two most extremes and immediately adjacent), divided by the standard deviation of the noise. A sequence was excluded if among the 4 middle occipital electrodes (i.e., centered on Oz and including neighboring electrodes POz, O1, and O2), less than two Z-scores reached significance ($Z > 1.64$, $p < .05$, one-tailed, signal > noise), or none using a more conservative threshold ($Z > 2.32$, $p < .01$). One epoch was rejected for three infants. The second criterion was used to identify if some sequences were atypical compared to the other sequences for each infant based on the scalp-wide power of the 1-Hz response. The response was first corrected by subtracting the mean noise, estimated here from 6 adjacent bins (i.e., using a broader range would provide an overestimation of the noise at this low frequency, considering the high noise amplitude of the lowest frequency bins, (Fransson et al., 2013)). The root mean square amplitude across channels was then calculated for each sequence. Sequences were removed if their root mean square noise-corrected amplitude at 1 Hz was atypical, i.e., above ± 2 SDs of the mean of all sequences. At this step, seven epochs were excluded in total across infants. Overall, the application of these criteria rejected 10 out of 180 epochs, corresponding to an epoch attrition of 1.7% and 4% per criterion, respectively. The mean number of remaining epochs per infant was 8.5 ± 1.6 (SD), with 4.2 ± 0.8 epochs in the baseline condition and 4.3 ± 1 in the maternal odor condition (no difference across conditions, $t_{19} = 0.46$, $p = .64$). Finally, these remaining sequences were averaged by odor condition in the time domain and for each individual infant.

To analyze both responses (i.e., 1 Hz and 6 Hz), datasets were considered in the frequency-domain after calculating an FFT. Statistical analyses followed a two-step procedure quite similar to (Leleu et al., 2020): (a) identification of responsive channels for both the facelike categorization and the general visual responses using *Z*-scores which compared the signal at the target frequencies to their surrounding noise; (b) comparison of odor conditions for both responses using repeated-measures ANOVAs on the noise-corrected amplitude at identified channels.

For (a), responsive channels were identified using *Z*-scores calculated at group level and for each condition. Individual datasets were first normalized across conditions and at each frequency bin by dividing the amplitude of each channel by the square root of the sum of squared amplitudes of all channels (McCarthy and Wood, 1985). This step scales differences between electrodes based on the global magnitude of the response across the scalp to identify the main electrodes over which a response is recorded. For each condition, datasets were then grand-averaged across infant and *Z*-scores were calculated for every electrode. Target channels were defined a priori according to previous studies using the same design with human faces (de Heering and Rossion, 2015; Leleu et al., 2020). The general visual response (6 Hz and harmonics) was expected over Oz, POz, O1 and O2. The facelike categorization response (1 Hz and harmonics) was expected over one left (P7) and three right (P8, CP6, O2) occipito-temporal channels. We considered the response from each target frequency and its harmonics until *Z*-scores over the same channel ceased to be significant ($Z > 1.64$, $p < .05$, one-tailed, signal > noise). To determine whether each response would spread over neighboring locations, contiguous electrodes were also explored using a more conservative significance threshold ($Z > 2.32$, $p < .01$). Figure S1 depicts all analyzed channels. Individual amplitudes were summed for the respective number of harmonics per response, and normalized before *Z*-scores were calculated for grand-averaged data to estimate the significance of the overall responses for each odor condition. For visualization purpose, responses were quantified in a single amplitude value (μV) by summing (non-normalized) noise-corrected amplitudes across harmonics. For (b), we compared the summed noise-corrected amplitude obtained for the two odor conditions separately for each brain response using repeated-measures ANOVAs. For the facelike categorization response, significant channels identified in (a) and their contra-lateral channels (even if non-significant) were used to define two homologous occipito-temporal regions. The analysis included *Electrode* (T7/8, P7/8, CP5/6), *Hemisphere* (left, right) and *Odor* (maternal, baseline) as within-subject factors. For the general visual response, we used *Electrode* (POz, O1, Oz, O2) and *Odor* (maternal, baseline) as within-subject factors. Mauchly's test for sphericity violation was performed and Greenhouse-Geisser correction for degrees of freedom is reported (epsilon: ε) whenever sphericity was violated. Significant effects or interactions were further analyzed by paired *t*-tests.

To investigate the lateralization of the facelike-selective response, we also computed a lateralization index that estimates the hemispheric asymmetry reported to the overall response obtained across both hemispheres. For each infant, we first averaged the uncorrected response amplitudes measured over the three occipito-temporal channels previously considered in each hemisphere to obtain one value per hemisphere and per odor context. Then, for each odor context, we subtracted the left-hemispheric response from the right-hemispheric response and divided by the sum of the two responses (i.e., [right − left] / [right + left]). This index thus reflects the advantage for one hemisphere expressed in %, with positive and negative values indicating right- and left-lateralized responses, respectively. Mean indexes in each odor context were also calculated across left- and right-lateralized infants, and across all infants. Their significance was determined with *t*-tests against 0, and the difference between the two odor contexts was also estimated with a paired *t*-test.

In a final step, we aimed at determining whether the strength of the maternal odor effect (maternal minus baseline) is mainly driven by infants without facelike categorization in the baseline odor context. To remove individual differences in the global power of the response, we first normalized individual noise-corrected amplitudes of both the facelike categorization response in the control odor condition and the difference between the responses measured in the maternal and control odor conditions using the square root of the sum of squared amplitudes of all channels (McCarthy and Wood, 1985). Next, we calculated a *Spearman*'s correlation between these two variables for channel P8 because this channel leads to a significant facelike-selective response in the baseline odor context (see Results). Then, we estimated the significance of individual responses over P8 in this odor context using *Z*-scores ($Z > 1.64$, $p < .05$, one-tailed, signal > noise). We finally compared the mean responses obtained in each odor context when infants with a significant facelike categorization response in the baseline odor context are removed or not.

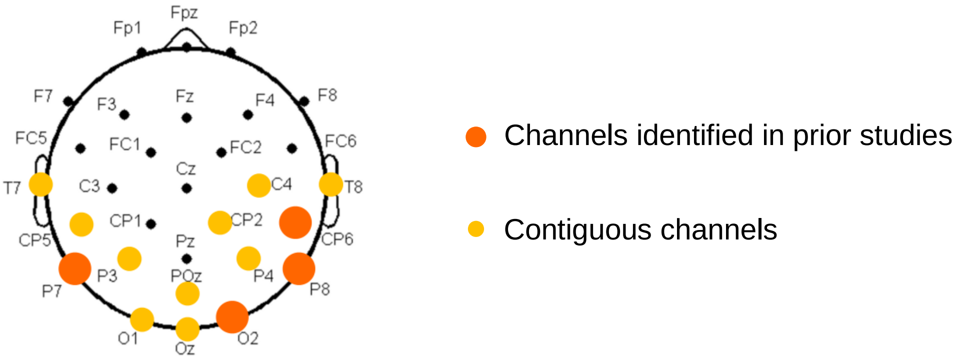
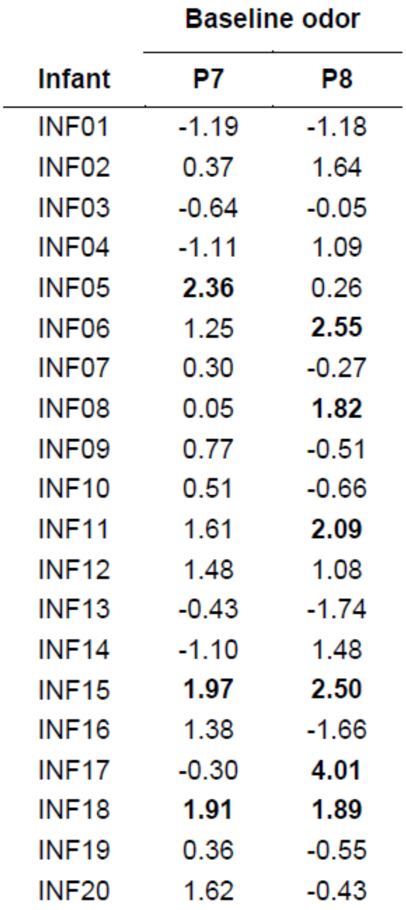


Figure S1. Thirty-channel montage of EEG acquisition and channels considered for analysis. EEG was acquired from a 32-channel headcap, configured according to the 10-10 classification system. Left and right mastoid electrodes (M1 and M2, not shown) were removed from processing and analysis. Frequency-domain analysis was conducted on the 14 colored posterior channels. P8, CP6, O2 and P7 (orange) were analyzed according to previous infant studies that identified a face categorization over them in equivalent age groups (de Heering and Rossion, 2015; Leleu et al., 2020). We also considered contiguous channels (yellow).

Table S1. Electrodes showing a significant facelike categorization response for each odor condition. *Z*-scores were calculated on normalized amplitudes for the first two harmonics of the facelike categorization response (1 Hz and 2 Hz). Electrodes where a face categorization response was reported in previous studies (de Heering and Rossion, 2015; Leleu et al., 2020) are indicated by orange rows and were considered significant according to a standard threshold ($Z > 1.64$, $p < .05$, one-tailed, signal > noise). A more conservative significance threshold was applied for the contiguous electrodes ($Z > 2.32$, $p < .01$). Electrodes with a significant response from the first harmonic in the present study are shown in bold.

	Baseline odor		Maternal odor	
Channel	**1 Hz**	**2 Hz**	**1 Hz**	**2 Hz**
C4	1.45	0.97	-1.90	-1.33
CP2	0.02	2.74	-0.69	-0.04
T8	-0.99	-1.87	**2.33**	1.10
P4	-1.38	-1.88	0.85	0.81
P8	**2.75**	-1.77	**1.88**	-1.49
CP6	-1.08	0.61	**2.05**	-0.02
O2	-0.78	-1.75	-0.37	-0.21
POz	-0.03	-1.30	0.39	1.21
Oz	-0.74	-0.80	-2.04	-1.37
CP5	-0.49	0.42	0.31	1.20
T7	-0.74	0.84	0.19	2.72
P3	-4.28	-0.70	1.97	2.23
P7	**1.76**	0.29	-0.61	0.44
O1	0.29	-1.62	-2.55	-3.73

Table S2. Z-scores of the facelike categorization response for each infant in the baseline odor condition. Individual Z-scores of the facelike categorization response were calculated for the two electrodes yielding significance at group level in the baseline odor condition (i.e., P7 and P8). Electrodes where a significant facelike-selective response was observed are shown in bold (*Z* > 1.64, *p* < .05, one-tailed, signal > noise).



	Baseline odor	
Infant	**P7**	**P8**
INF01	-1.19	-1.18
INF02	0.37	1.64
INF03	-0.64	-0.05
INF04	-1.11	1.09
INF05	**2.36**	0.26
INF06	1.25	**2.55**
INF07	0.30	-0.27
INF08	0.05	**1.82**
INF09	0.77	-0.51
INF10	0.51	-0.66
INF11	1.61	**2.09**
INF12	1.48	1.08
INF13	-0.43	-1.74
INF14	-1.10	1.48
INF15	**1.97**	**2.50**
INF16	1.38	-1.66
INF17	-0.30	**4.01**
INF18	**1.91**	**1.89**
INF19	0.36	-0.55
INF20	1.62	-0.43

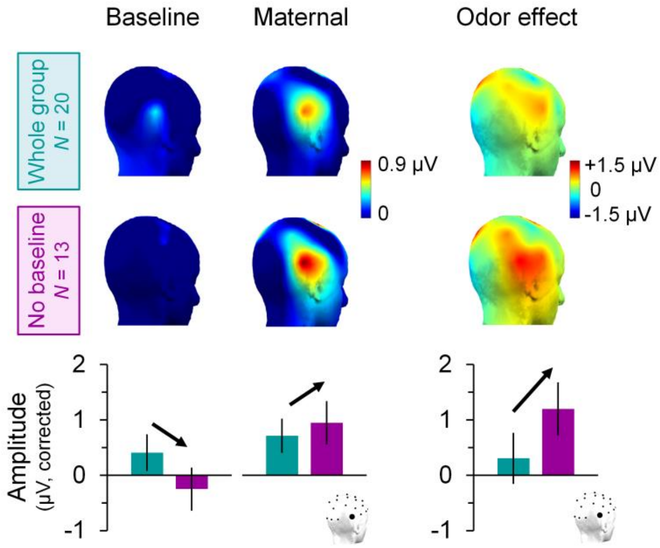


Figure S2. Odor-driven categorization of face pareidolia in infants without a baseline response. This figure is similar to Figure 4B in the main article, except for the inclusion of an additional infant in the "No baseline" group (i.e., INF05 whose baseline response is significant over P7; see Table S2). After removing the infants with a significant baseline response over P7 and/or P8 (Table S2), the mean baseline response across the 13 remaining infants (purple) has a noise-corrected amplitude of -0.25 ± 0.39 µV. The facelike-selective response measured in the maternal odor context is of 0.94 ± 0.39 µV, and the odor effect is large and significant (+1.20 ± 0.48 µV, $t_{12} = 2.51$, $p = .028$).

V. Appendix 5: Complementary study

Did you spot the face in the clouds? Conscious categorization of illusory faces (face pareidolia) in the human brain

Diane Rekow [a], Jean-Yves Baudouin [b], Renaud Brochard [a], Bruno Rossion [c,d], Arnaud Leleu [a]

[a] Laboratoire Éthologie Développementale et Psychologie Cognitive, Centre des Sciences du Goût et de l'Alimentation, Université Bourgogne Franche-Comté, CNRS, Inrae, AgroSup Dijon, F-21000 Dijon, France
[b] Laboratoire Développement, Individu, Processus, Handicap, Éducation (DIPHE), Département Psychologie du Développement, de l'Éducation et des Vulnérabilités (PsyDÉV), Institut de psychologie, Université de Lyon (Lumière Lyon 2), 69676 Bron cedex, France
[c] Université de Lorraine, CNRS, CRAN, F-54000, Nancy, France
[d] Université de Lorraine, CHRU-Nancy, Service de Neurologie, F-54000, Nancy, France

Abstract

Whether the subjective experience of a sensory input – *perceptual awareness* – emerges from its categorization, is a matter of debate. To address this issue, we use a visual illusion, *face pareidolia*, as a proxy to relate the neural categorization of a variety of facelike objects to conscious face perception. In Experiment 1, scalp electroencephalogram (EEG) is recorded while natural images of nonface objects are displayed at 6 Hz and human faces or facelike objects are interleaved once per second (at 1 Hz). Participants perform a cross-detection task and report after testing whether they perceived illusory faces or not. We identify a neural categorization response to facelike objects with a clear facelike right occipito-temporal topography at 1 Hz and harmonics (i.e., integer multiples) in the EEG frequency spectrum. Critically, its amplitude predicts well above chance whether a given participant consciously perceived illusory faces. In Experiment 2, stimulation rate varies (stimulus durations: 17 ms, 33 ms, 50 ms, 67 ms, 83 ms) while facelike or nonface objects are always displayed at 1 Hz in sequences of nonface objects. Participants report after each sequence whether they perceived illusory faces to compare the responses to aware and unaware facelike objects in each single brain. At the shortest durations, behavioral and neural categorization responses are correlated and already larger for sequences containing facelike objects than only nonface objects. Differentiating aware and unaware sequences reveals that neural facelike categorization emerges exclusively when participants report illusory faces. Collectively, these experiments characterize a brain signature of face pareidolia, i.e., the perceptual awareness of an illusory face across variable naturalistic objects, and demonstrate that neural categorization reliably reflects the subjective experience of an input rather than its objective content.

A. Introduction

A fundamental issue in cognitive (neuro)science is how the brain deals with sensory ambiguity to produce our meaningful subjective experience of the environment, or perceptual awareness. A body of research indicates that perceptual awareness emerges from the categorization of unconscious sensory inputs (1–4). Categorization is the ability to produce discrete selective responses to one piece of information (i.e., a category) that generalizes to different instances of that information (across exemplars and/or exposure conditions). Category-selective responses are thus good candidates for the emergence of conscious perception from the organization of the myriad inputs that continuously reaches our senses into more stable and unified percepts (5). However, some studies have challenged this view by showing greater association between category-selective neural responses and the objective content of a stimulus than its subjective report, casting some doubt on the direct relationship between neural categorization and perceptual awareness (6–8).

One elegant way to address this issue would be to rely on stimuli that elicit different conscious per-cepts from similar objective contents. Visual illusions are clear examples of such a dissociation (9). For instance, the so-called phenomenon of bistability, whereby a unique stimulus elicits the spontaneous alternation between two conscious percepts, reveals distinct neural responses associated with each perceptual interpretation (10,11,12 for review). Illusory perception therefore constitutes a powerful approach to relate perceptual awareness to neural categorization. Yet, since illusions are generally tested with restricted sets of artificial and homogenous stimuli, evidence of a neural response that would incorporate both selectivity to the illusory percept and generalizability across a wide range of inputs, is missing. To fill this gap in knowledge, here we characterize a neural categorization response to a variety of naturalistic objects according to the conscious perception of an illusory face, namely face pareidolia.

Face pareidolia refers to the spontaneous perception of a face in an object despite the absence of natural facial features (see examples in Figure 1A), leading to the most remarkable example of ubiquitous illusory percept in the human species. Prior studies have documented how nonface stimuli perceived as faces elicit activity within face-selective regions in the ventral occipito-temporal cortex (13–16), or a facelike electroencephalographic (EEG) response over right occipito-temporal scalp sites (17–19). Facelike neural activity is generally identified when stimuli are reported as faces by human observers (20–23). However, as for other illusions, previous studies are limited in their ability to unequivocally relate the conscious perception of an illusory face to neural face categorization for several reasons. First, only a few exemplars of homogenous facelike stimuli is used. This prevents the measurement of a response that generalizes across variable inputs. Second, stimuli are displayed in isolation (i.e., the background is removed), artificially increasing facelikeness by delineating a global face shape and potentially confounding facelikeness with low physical differences across stimuli (see 24 for a discussion). Finally, facelike objects are rarely contrasted to other objects from the same categories. This is a critical issue to carefully control for shared neural responses and isolate a subjective facelike percept emerging from a subset of similar objective contents.

Hence, in the present study, we provide a direct neural categorization response reflecting the con-scious perception of a face in a large set of naturalistic facelike stimuli contrasted to other stimuli depicting similar objects (Figure 1A). We employ fast periodic visual stimulation (FPVS) coupled with a frequency-tagging approach in scalp EEG (25 for review), which successfully isolated a valid measure of rapid and automatic face categorization (e.g., 26–28) that is not accounted for by physical cues (28,29). In two experiments, we present natural images of nonface objects at a rapid base rate and facelike objects are interspersed at a lower rate (Figure 1B & 1C). This periodic mode of stimulation allows the dissociation of two brain responses at predefined frequencies in the EEG amplitude spectrum: a general visual response to the rapid stream of stimuli, and a categorization response to facelike stimuli. The general response captures the neural activity elicited by both facelike and nonface objects, while the categorization response reflects the selective activity elicited by facelike objects and its generalization across them. In other words, the categorization response is clearly facelike-selective in that it emerges only if stimuli depicting similar objective contents (i.e., facelike and non-face stimuli) elicit dissimilar neural activity, whereas stimuli depicting dissimilar objective contents (i.e., facelike stimuli) elicit similar neural activity according to their facelikeness.

In Experiment 1, we present 27 participants with 40-second-long sequences at a 6-Hz base rate (i.e., 6 images per second, ≈ 167 ms per image) and facelike objects or human faces are interleaved every 6 stimuli (i.e., at 1 Hz; Figure 1B). The general visual response is thus tagged at 6 Hz and harmonics (i.e., integer multiples) and categorization responses at 1 Hz and harmonics. We compare the categorization responses to illusory and human faces to evidence the facelikeness of the former. Importantly, participants perform an orthogonal cross-detection task and are queried after the experiment whether they noticed facelike objects to dissociate them according to their subjective experience of face pareidolia. In Experiment 2, another 22 participants are presented with 16-second-long sequences at 5 different base rates (60 Hz, 30 Hz, 20 Hz, 15 Hz, 12 Hz), such that stimulus duration varies from 17 to 83 ms. Facelike or nonface objects are always interspersed at 1 Hz and participants report after each sequence if they have perceived illusory faces to contrast their brain responses according to awareness. Overall, through these two experiments, we demonstrate that a category-selective response generated by a wide range of stimuli in the human brain directly reflects the conscious (illusory) percept they elicit rather than their objective content.

B. Materials and Methods

1. Experiment 1

a. Participants

Twenty-seven participants (12 females, 6 left-handed (3 females), mean age: 22.5 ± 2.9 (*SD*) years, range: 19–31 years) took part in the experiment and were compensated for their participation. All reported normal/corrected-to-normal visual acuity, and none reported a history of neurological/psychiatric disorder. They provided written informed consent prior to the experiment. Testing was conducted in accordance with the Declaration of Helsinki and approved by a French ethics committee (CPP Sud-Est III - 2016-A02056-45).

Since we aimed at exploring the relationship between facelike neural categorization and conscious illusory face perception, and since participants performed an orthogonal task (see below), we asked them three questions after testing to determine whether they perceived facelike objects. We first asked whether they noticed something particular during the experiment. If participants did not mention illusory faces, we then asked whether they noticed something about the stimuli. Note that all participants reported here the presence of human faces but none detected their periodicity. Again, if participants did not mention illusory faces, we finally questioned them about the presentation of facelike objects. Based on this interview, participants were split in two groups, one group that mentioned illusory faces in at least one question (i.e., *aware* group, $N = 13$, 5 females, 2 left-handed (1 female), mean age: 23.2 ± 3.5 years, range: 19–31 years), and another group that did not (i.e., *unaware* group, $N = 14$, 7 females, 4 left-handed (2 females), mean age: 21.9 ± 2.3 years, range: 19–27 years). The two groups did not significantly differ in age ($T_{25} = 1.21$, $p = .24$), sex ($X^2_1 = .55$, $p = .36$), and handedness ($X^2_1 = .41$, $p = .68$).

b. Stimuli

Stimuli were color natural images of 86 human faces (43 females), 86 facelike objects and 430 non-face objects cropped to a square and sized to 300 × 300 pixels. All stimuli were embedded in their original scenes and differed in size, viewpoint, lighting and background so that their physical charac-teristics were widely variable (examples in Figure 1A, full set available upon request from the authors). In addition, human faces varied largely in age, sex, race and expression. Face and nonface images were adapted from previous studies (e.g., 26–28) or

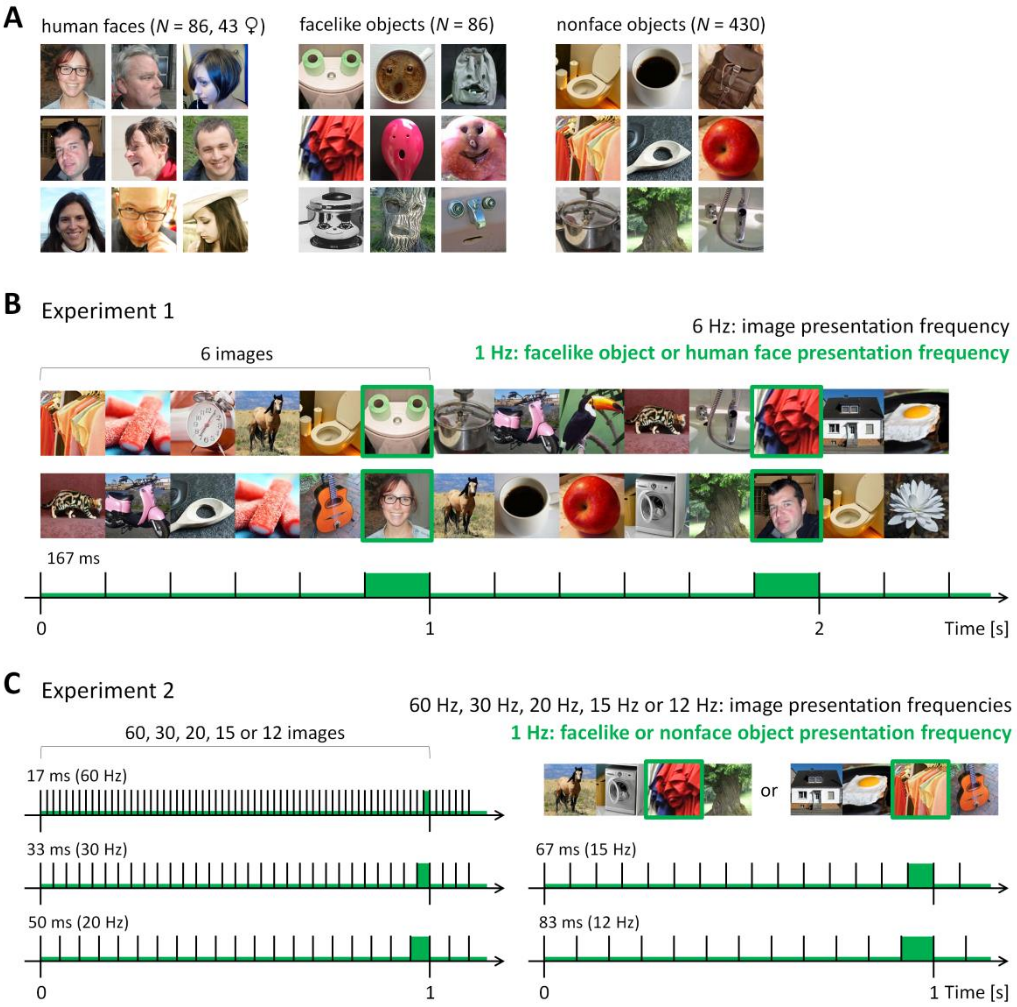


Figure 1. Measuring face pareidolia in the human brain. A. Examples of variable unsegmented natural images of human faces (N = 86, 43 females), facelike objects (*N* = 86) and nonface objects (*N* = 430) used as stimuli. **B.** Examples of ≈ 2 seconds (/40) of fast periodic visual stimulation at a 6-Hz image presentation frequency (i.e., 6 images per second, ≈ 167 ms per image without inter-stimulus interval) used in Experiment 1. Facelike objects or human faces are inserted at 1 Hz (i.e., every 6th stimulus). Two brain responses are thus tagged and identified in the EEG frequency spectrum: a general response (6 Hz and harmonics, i.e. integer multiples) capturing the visual processing of all cues rapidly changing at each image-onset; a categorization response (1 Hz and harmonics) reflecting the visual categorization of facelike objects or human faces (i.e., discrimination from nonface objects and generalization across exemplars). Participants perform an orthogonal cross-detection task and are asked after testing whether they noticed illusory faces. **C.** Examples of ≈ 1 second (/16) of stimulation at the 5 different image presentation frequencies (60 Hz, 30 Hz, 20 Hz, 15 Hz, 12 Hz; stimulus duration: 17 ms, 33 ms, 50 ms, 67 ms, 83 ms) used in Experiment 2. Facelike or nonface objects are always interspersed at 1 Hz. Participants report after each stimulation sequence whether they perceived illusory faces.

collected from the Internet. Nonface objects were various biological and manufactured objects with several exemplars (i.e., between 3 and 20) in each category (listed in Supplementary Materials and Methods). Facelike images were selected among a large set of 224 pictures collected from the Internet when searching for 'face pareidolia'. Selection was made according to the images judged as the most facelike in a pretest (Supplementary Materials and Methods & Figure S1). Critically, facelike images depicted various object categories (between 1 and 5 exemplars in each category) matching some of those used for nonface objects (listed in Supplementary Materials and Methods). Hence, facelike objects differed from nonface objects only in their overall facelike appearance (Figure 1A). Face and facelike stimuli were both divided in two sets of 43 pictures. For human faces, one set contained 22 females and the other one 21 females. For facelike images, at least one exemplar of each object category was allocated to each set. These two sets ensured that all face and facelike stimuli were presented to every participant (see *Procedure*). During the experiment, stimuli were displayed at the center of a 24-inch LED screen (60 Hz refresh rate, resolution: 1920 × 1080 pixels) on a mid-level grey background (i.e., 128/255 in greyscale). From a viewing distance of 57 cm, they subtended approximately 8.3° of visual angle.

c. Procedure

The procedure was adapted from previous face categorization experiments using EEG frequency-tagging (e.g., 26–28). Images were presented at a fast base rate of 6 Hz (i.e., 6 images per second, ≈ 167 ms per image) without inter-stimulus interval (forward- and backward-masking; Figure 1B). In each stimulation sequence, nonface objects were used as base stimuli. In different sequences, human faces or facelike objects were periodically inserted every 6th stimulus (i.e., at 6/6 = 1 Hz; 1 second between two human faces or facelike objects).

After electrode-cap placement, participants were seated in a light- and sound-isolated cabin in front of the stimulation screen. Their head was maintained on a chinrest at a distance of 57 cm from the screen. Stimulation sequences started with a 2-second fade-in of increasing contrast modulation depth (0 to 100%), followed by the full-contrast stimulation lasting 40 seconds and then followed by a 2-second fade-out of decreasing contrast modulation depth (100 to 0%). Both fade-in and fade-out were used to reduce eye-blinks and movements elicited by the sudden onset or offset of flickering stimuli. Sequences were flanked by variable pre- and post-stimulation intervals of 0.5–1.5 seconds of uniform grey background. For both face and facelike stimuli, each set of 43 images was used in half of the stimulation sequences while the 430 nonface objects were used in all sequences. Each experimental condition (i.e., category at 1 Hz) was repeated 6 times (i.e., 3 times for each stimulus set), resulting in 12 sequences throughout the experiment. They were divided in 3 blocks of 4 sequences, each block presenting two sequences per condition (i.e., one per stimulus set). Blocks and sequences within blocks were randomly presented across participants. In each sequence, stimuli were randomly selected from their respective sets.

d. Orthogonal behavioral task

An orthogonal behavioral task was designed to ensure that participants paid full attention to the stimulation. During each sequence, they were asked to detect 8 brief (200 ms) random appearances of a 300 × 300 pixels large white cross on the images by pressing the spacebar of a keyboard with both index fingers as quickly as possible. A minimum interval of 2 seconds was introduced between two cross-onsets. Both accuracy and RTs for correct detections (ranging between 100 and 1000 ms) were submitted to a repeated-measures ANOVA with *Category* (human faces *vs.* facelike objects) as a within-subject factor and *Group* (aware *vs.* unaware) as a between-subject factor.

e. EEG acquisition and preprocessing

Scalp electroencephalogram (EEG) was continuously acquired from a 64-channel BioSemi Active-Two amplifier system (BioSemi, The Netherlands) with Ag/AgCl electrodes located according to the 10–10 classification system. During recording, the Common Mode Sense (CMS) active electrode was used as reference and the Driven Right Leg (DRL) passive electrode was used as ground. Electrode offset was held below ± 15 µV for each electrode and EEG was sampled at 1024 Hz.

All EEG analyses were carried out in Letswave 6 (https://www.letswave.org/) running on Matlab 2017 (MathWorks, USA). For each participant, continuous datasets were first bandpass filtered at 0.1–100 Hz using a Butterworth filter (4th order) and then downsampled to 256 Hz. Datasets were segmented into 45-second epochs for each stimulation sequence (12 per participant, 2 conditions × 6 repetitions), including 1 second before the fade-in and 1 second after the fade-out. An Independent Component Analysis (ICA) with a square mixing matrix was computed (53) to isolate and remove components corresponding to eye-blinks (i.e., one component recorded over Fp channels per participant) and to additional artifacts recorded over frontal and temporal channels (mean number across participants: 2.3, range: 0–4, no significant difference between groups of participants, $T_{25} = 0.91$, $p = .37$). Remaining noisy or artifact-ridden channels were replaced using linear interpolation from the 4 neighboring channels (mean number across participants: 0.9, range: 0–5, no significant difference between groups of participants, $T_{25} = 0.16$, $p = .88$). EEG epochs were then re-referenced to the average of the 64 channels.

f. EEG frequency-domain analysis

In line with previous face categorization studies (e.g., 26–28), our paradigm was designed to tag two different brain responses at two predefined frequencies within a single stimulation sequence, and to quantify them in the EEG amplitude spectrum using frequency-domain analysis: (a) a general response at 6 Hz and harmonics (i.e., integer multiples) elicited by the stream of images (i.e., both nonface and face/facelike images) and capturing the visual response to low- (e.g., local contrast) and higher-level (e.g., object shape) cues rapidly changing 6 times per second; (b) a categorization response at 1 Hz and harmonics reflecting the differential response to face or facelike stimuli. Thanks to the rapid and periodic mode of stimulation, this response indexes single-glance visual categorization of human faces and facelike objects implying discrimination from nonface objects and generalization across category exemplars despite widely variable images. It is not accounted for by low-level cues (28,29) and it is immune to temporal predictability elicited by periodicity (54). Note that the 1-Hz rate of face or facelike presentation allows enough time between image-onsets (i.e., 1 second) for the full face categorization response to develop (≈ 450 ms in duration, 27).

For each participant, the 6 epochs recorded for each condition were averaged to reduce EEG activity non-phase-locked to the stimuli, thus resulting in a single 45-second epoch per condition. Epochs were then precisely cropped from the onset of the full-contrast stimulation to 40 seconds so as to contain an exact integer number of 1-Hz cycles (i.e., 40 cycles, 10240 time bins). A fast Fourier transform (FFT) was applied to every epoch and amplitude spectra were extracted for all channels with a high frequency resolution of 1/40 = 0.025 Hz. Thanks to this high resolution, 40 frequency bins were extracted every 1-Hz step, allowing unambiguous identification of the tagged brain responses and estimation of noise amplitude from surrounding frequency bins. Given our objective to identify a selective response to facelike objects that reflects their categorization as faces, we considered the EEG data recorded for sequences containing human faces as a reference to determine the range of harmonics (i.e., tagged frequencies and their integer multiples) and regions-of-interest (ROIs) for further analysis.

The range of harmonics (Table S1) for the brain responses to the 6-Hz stimulation and the 1-Hz face presentation was defined from the FFT amplitude spectra averaged across channels and participants (Figure 2A). *Z*-scores were calculated as the difference between the amplitude at the target frequency bin and the mean amplitude of the surrounding noise (≈ ± 0.3 Hz: estimated from 20 frequency bins, 10 on each side, excluding the immediately adjacent and the 2 most extreme (minimum and maximum) bins) divided by the standard deviation of the noise. Harmonics were included until *Z*-scores were no longer significant (i.e., $Z > 1.64$, $p < .05$, one-tailed, signal > noise). For the general response, all harmonics were significant (i.e., 8 harmonics, from 6 Hz to 48 Hz, harmonics were not considered beyond the 50 Hz response elicited by AC power). For the face categorization response, harmonics reached significance up to 26 Hz (i.e., 26th harmonic). The overall responses were then condensed by summing amplitudes across significant harmonics (excluding harmonics corresponding to the general response (i.e., 6 Hz, 12 Hz, 18 Hz, 24 Hz) for the categorization response) for each category, channel and participant. Henceforth, mentions of the general and categorization responses to either human or illusory faces will refer to these amplitudes summed across harmonics.

To quantify the magnitude of each brain response in a value expressed in microvolts (μV), we isolated the response from noise level by subtracting out the mean amplitude of the surrounding frequency bins, leading to notional corrected amplitudes of zero in the absence of response. Corrected amplitudes were used to define the ROIs, and the ROIs were used to conduct group-level statistical analyses and significance estimation of individual brain responses. The strength of each brain response within ROIs (Figure 2B & 2C) was also estimated with signal-to-noise ratios (SNR) computed by dividing the uncorrected response amplitude by the mean surrounding noise.

In line with previous studies (26,28), both categorization and general responses in the human face condition present a right hemisphere advantage, but the categorization response is laterally distributed over occipito-temporal regions (Figure 2B) while the general response is located over the middle occipital cortex (Figure 2C). Accordingly, we defined two symmetrical occipito-temporal ROIs for the face categorization response and one middle occipital ROI for the general visual response by considering the channels with the maximal group-level corrected amplitudes. For the face categorization response, the largest amplitude was observed over P10 (4.27 μV), followed by PO8 (3.81 μV), PO7 (3.37 μV), P8 (3.27 μV), P9 (2.96 μV) and P7 (2.93 μV). We thus defined homologous right and left occipito-temporal ROIs (respectively rOT and lOT), each comprising 3 contiguous channels (r/lOT: P10/9, PO8/7, P8/7). For the general visual response, the strongest amplitudes were recorded over O2 (3.50 μV), PO8 (3.32 μV), Oz (3.10 μV) and O1 (3.04 μV). The single middle occipital ROI thus encompassed these 4 neighboring channels.

Statistical analyses were conducted separately for the categorization and general responses. In addition, for each response, two separate analyses were also consecutively performed. The first one evaluated the response elicited by facelike objects compared to human faces with the whole participant sample for an initial characterization of the neural signature of illusory face perception. We ran a repeated-measures ANOVA on individual corrected amplitudes with *Category* (human faces *vs*. facelike objects) as a within-subject factor. The within-subject factor *Hemisphere* (rOT *vs*. lOT) was also included for the categorization response. The second analysis aimed at determining whether the neural patterns identified in the first analysis depend on the perceptual awareness of illusory faces. For this purpose, repeated-measures ANOVAs were conducted for each stimulus category with *Group* (aware *vs*. unaware) as a between-subject factor. In all analyses, post-hoc comparisons were conducted for significant effects using *T*-tests and the false discovery rate (FDR) procedure was applied to adjust *p*-values for multiple comparisons (55). Since corrected amplitudes should not differ from zero in the absence of response, significance of the grand-averaged brain responses was estimated by identifying whether the 95% confidence interval (*CI*, calculated across participants) around the mean response amplitude did not include zero.

Finally, two other analyses were carried on to estimate the significance of the brain responses in every individual participant and to determine whether the topographies of the categorization responses to facelike objects and human faces are reliable and comparable. For the first analysis, the significance of individual responses within ROIs was estimated using *Z*-scores (see above). For the second analysis, the 6 epochs (i.e., time series) recorded for sequences presenting human faces or facelike objects were split according to stimulus sets, resulting in 2 × 3 epochs for both conditions. Epochs were then averaged and following processing steps were similar to those previously described in order to isolate both general and categorization responses to either human faces or facelike objects expressed in summed corrected amplitudes separately for each stimulus set. After grand-averaging individual responses, we computed Pearson's correlations between the categorization responses obtained for each set using the 64 channels as observations. We thus estimated the topographical reliability of the categorization response across stimulus sets for both categories. Correlations were also calculated between both categorization responses to determine whether their scalp distributions are close. As a control index expected to reveal a lower topographical similarity, the correlation between the categorization response and the general response recorded for sequences containing facelike objects was finally computed.

2. Experiment 2

a. Participants

We tested 22 participants (15 females, 1 left-handed (female), mean age: 21.4 ± 4 (*SD*) years, range: 18–33 years) who did not participate in Experiment 1. They reported normal/corrected-to-normal visual acuity and no history of neurological/psychiatric disorder. They provided written informed consent prior to the experiment and were compensated. Testing was conducted in accordance with the Declaration of Helsinki and approved by a French ethics committee (CPP Sud-Est III - 2016-A02056-45).

b. Stimuli

Stimuli were the 80 facelike objects judged as the most facelike in the pretest conducted before Experiment 1 (*Supplementary Materials and Methods* & Figure S1) and the 430 nonface objects used in Experiment 1 (examples in Figure 1A). An additional set of 15 facelike images (judged as the most facelike after the 80 first ones) was also used before testing to illustrate which kind of stimuli participants must detect (see *Explicit behavioral task*). The 80 facelike stimuli used for testing were divided in five sets of 16 pictures. Nonface objects were divided in one set of 350 stimuli always used as base stimuli, and five sets of 16 stimuli for sequences containing only nonface objects (see *Procedure*). Stimulus resolution and size, screen parameters, and viewing distance were identical to Experiment 1.

c. Procedure

The procedure was adapted from a recent EEG frequency-tagging study investigating face categorization at various stimulus durations (4). Images were presented without inter-stimulus interval (forward and backward-masking) at five stimulation frequencies depending on the sequence: 60 Hz, 30 Hz, 20 Hz, 15 Hz and 12 Hz (i.e., stimulus-onset asynchrony = stimulus duration: 17 ms, 33 ms, 50 ms, 67 ms, 83 ms; Figure 1C). These frequencies were chosen according to the screen refresh rate (i.e., 60 Hz), such that stimulus durations were 1, 2, 3, 4 or 5 frames. In every sequence, nonface objects were used as base stimuli. Facelike objects were interspersed at 1 Hz in half of the sequences. Thus, for instance, at 60 Hz, facelike objects appeared every 60 images, while at 12 Hz they appeared every 12 images (Figure 1C). Facelike stimuli were replaced by nonface objects in the other half of the sequences. This led to 10 conditions: 2 categories (facelike objects or nonface objects) × 5 stimulus durations (17 ms, 33 ms, 50 ms, 67 ms, 83 ms; corresponding to 5 stimulation rates: 60 Hz, 30 Hz, 20 Hz, 15Hz, 12 Hz).

Stimulation sequences started with a 0.5-second pre-stimulation interval, followed by a 1.833-second fade-in of increasing contrast modulation depth (0 to 100%). Then, the full-contrast stimulation lasted 15.167 seconds before a 1-second fade-out of decreasing contrast modulation depth (100 to 0%) and a 0.5-second post-stimulation interval. For both facelike and nonface objects interleaved at 1 Hz, each set of 16 images was used in half of the stimulation sequences. The 350 nonface objects used as base stimuli were presented in all sequences. Each experimental condition was repeated 10 times, resulting in 100 sequences throughout the experiment. They were divided in 10 blocks of 10 sequences, each block presenting one sequence per condition. Blocks and sequences within blocks were randomly presented across participants. Stimuli were randomly selected from their respective sets.

d. Explicit behavioral task

Contrary to Experiment 1, perceptual awareness of illusory faces was expected to vary for each participant, as a function of stimulus duration (i.e., stimulation frequency). Hence, participants were explicitly instructed to attend to the stimuli and to detect facelike objects. After electrode-cap setup, participants were told that rapid sequences of natural images depicting objects will be presented at variable rates and that they will have to report orally after each sequence whether it contained some objects resembling faces. Fifteen facelike images were presented one by one for illustration (not used thereafter). Participants were informed that some sequences will contain several facelike objects and some will not. They were also informed that because images will be presented at rapid rates, false alarms could be frequent. Accordingly, they were asked to report illusory face perception if and only if they noticed several facelike exemplars throughout the sequence. The number of facelike reports after a sequence (out of 10) was submitted to a repeated-measures ANOVA with *Category* (facelike objects *vs.* nonface objects) and *Stimulus duration* (17 ms *vs.* 33 ms *vs.* 50 ms *vs.* 67 ms *vs.* 83 ms) as within-subject factors. Note that this dependent variable corresponds to the number of hits and false alarms for sequences presenting facelike objects and nonface objects, respectively. Mauchly's test for sphericity violation was performed and Greenhouse-Geisser correction (epsilon: ε) for degrees of freedom was applied whenever sphericity was violated. Post-hoc comparisons were conducted using *T*-tests and the FDR procedure was applied to adjust *p*-values (55). Comparison with chance level (i.e., 5 reports) was estimated by identifying whether the 95% *CI* around the mean number of reports did not include five.

e. EEG acquisition and preprocessing

EEG acquisition and preprocessing steps were identical to Experiment 1, except for data segmentation into 20-second epochs for each stimulation sequence (100 per participant, 10 conditions × 10 repetitions), including 1 second before the fade-in and 1 second after the fade-out. Following ICA, the mean number of removed components across participants was 2.7 (range: 1–5). The mean number of interpolated channels was 0.5 (range: 0–3).

f. EEG frequency-domain analysis

As in Experiment 1, the facelike categorization response was tagged at 1 Hz and harmonics. In contrast, contrary to Experiment 1, the general visual response was tagged at different frequencies depending on the sequence (i.e., 60 Hz, 30 Hz, 20 Hz, 15 Hz, 12 Hz and their respective harmonics). For each participant, the 10 epochs recorded for each condition were averaged in the time domain, leading to a single 20-second segment per condition. Epochs were cropped from the onset of the full-contrast stimulation to 16 seconds (4096 time bins). An FFT was applied and amplitude spectra were extracted with a frequency resolution of 1/16 = 0.0625 Hz, leading to 16 frequency bins every 1-Hz step.

For the categorization response, harmonics were included up to the 26th harmonic (i.e., 26 Hz) according to Experiment 1. For the general visual response elicited at variable frequencies up to 60 Hz, we considered harmonics until this frequency for each condition. In other words, only the first harmonic (i.e., 60 Hz) was included for the general response to a 60 Hz-stimulation stream, two harmonics (i.e., 30 Hz and 60 Hz) for the response to a 30 Hz-stimulation, three harmonics (i.e., 20 Hz, 40 Hz, 60 Hz) for a 20 Hz-stimulation, four harmonics (i.e., 15 Hz, 30 Hz, 45 Hz, 60 Hz) for a 15 Hz-stimulation and five harmonics (i.e., 12 Hz, 24 Hz, 36 Hz, 48 Hz, 60 Hz) for a 12 Hz-stimulation. The overall responses were summed across harmonics, excluding those corresponding to the stimulation frequencies and their harmonics (i.e., 12 Hz, 15 Hz, 20 Hz, 24 Hz) for the categorization response. The general and categorization responses will refer to these summed amplitudes thereafter.

The magnitude of each brain response was quantified in mean corrected amplitudes within the ROIs defined in Experiment 1 (i.e., right and left occipito-temporal [r/lOT: P10/9, PO8/7, P8/7] for the categorization response and middle occipital [PO8, O2, Oz, O1] for the general response). To estimate the baseline noise level in a similar frequency range as in Experiment 1 (≈ ± 0.3 Hz), we considered the mean amplitude of 6 surrounding frequency bins (3 on each side), excluding the adjacent bins and the most extreme (minimum and maximum) bins. Statistical analyses were carried on individual corrected amplitudes separately for the categorization and general responses using repeated-measures ANOVAs with *Category* (facelike objects *vs*. nonface objects) and *Stimulus duration* (17 ms *vs.* 33 ms *vs.* 50 ms *vs.* 67 ms *vs.* 83 ms) as within-subject factors. The factor *Hemisphere* (rOT *vs*. lOT) was also included for the categorization response. Mauchly’s test for sphericity violation was performed and Greenhouse-Geisser correction (epsilon: ε) for degrees of freedom was applied whenever sphericity was violated. Post-hoc comparisons were conducted using *T*-tests with FDR-adjusted *p*-values (55). As in Experiment 1, significance of the grand-averaged brain responses was estimated by determining whether the 95% *CI* around the mean amplitude did not include zero. Grand-averaged corrected amplitudes were normalized by their scalp-wide power (56) to illustrate the topography of each brain response regardless of its magnitude.

To evaluate the relationship between the behavioral report of illusory faces and the amplitude of the facelike-selective response, we computed Pearson’s correlations between individual data for both measures and for each stimulus duration. We calculated the same correlation for the average of the two shortest durations (i.e., 17 and 33 ms), which lead to mid-level amplitude of the categorization response and mid-level number of facelike reports, and did the same for the two (i.e., 50 and 67 ms) or three (i.e., 50, 67 and 83 ms) following durations, which lead to larger neural responses and near-ceiling behavioral responses. Finally, we computed the correlations after having divided each measure by its value at the longest duration (i.e., 83 ms) to correct for individual differences in ceiling-level responses. In other words, this latter measurement is free from the between-subject variability observed when performance is at ceiling (see 4 for a discussion).

In a last step, we determined whether the facelike categorization response emerges as a function of participants’ report of illusory faces for the combination of the two shortest durations (i.e., 17 and 33 ms). However, because these durations do not have the same number of sequences for which facelike objects were reported (see *Results* and Figure 4A), we first selected 12 participants out of 22 to equate this number across durations (= 69), and also to reduce the difference between the number of reported and unreported sequences for each duration (i.e., 69 *vs*. 51; $\chi^2 = 2.7$, $p = .10$). Then, for each participant, we averaged preprocessed epochs (i.e., in the time domain) across durations separately for reported (i.e. *aware*) and unreported (i.e., *unaware*) sequences. Following processing steps were identical as in the main analysis to obtain one brain response for aware sequences, and one response for unaware sequences. Individual summed corrected amplitudes were submitted to a repeated-measures ANOVA with *Awareness* (aware *vs*. unaware) and *Hemisphere* (rOT *vs*. lOT) as within-subject factors. Significance of the grand-averaged brain responses was estimated by determining whether the 95% *CI* did not include zero. For illustration, the difference between aware and unaware sequences was also computed for each participant.

C. Results

1. Experiment 1: characterizing the conscious categorization of illusory faces

At 1 Hz and harmonics, we identified two brain responses selectively reflecting the categorization of human faces and facelike objects from variable natural images (Figure 2A). Summed across harmonics (Figure 2B), both categorization responses are of high signal-to-noise ratio (SNR ≈ 3 and 1.5 respectively for human faces and facelike objects; i.e., 200% and 50% of signal increase) and significantly above noise level (i.e., 95% confidence intervals (*CI*) do not include 0), despite a larger response to human faces (3.44 ± 0.45 (95% *CI*) µV) than facelike objects (0.72 ± 0.19 µV; 21% of the face categorization response; $F_{1,26} = 175$, $p < .001$, $\eta_p^2 = 0.87$). Importantly, the two categorization responses present close topographies over the occipito-temporal cortex and a right hemisphere advantage (main effect of *Hemisphere*: $F_{1,26} = 7.77$, $p = .009$, $\eta_p^2 = 0.23$). The face categorization response is about 23% larger over the right (rOT; 3.78 ± 0.55 µV) than the left occipito-temporal region (lOT; 3.09 ± 0.48 µV) while the facelike categorization response is about 66% larger over rOT (0.91 ± 0.31 µV) than lOT (0.55 ± 0.21 µV). When considering the categorization responses over the whole scalp, about 11.6% and 16.4% of the face and facelike categorization responses, respectively, are concentrated over rOT (representing less than 5% of the overall channels, i.e., 3 out of 64).

Using channels as observations, we confirmed the close topographies of the two categorization responses with a very high correlation ($R = 0.92$). In comparison, the correlation between the facelike categorization response and the more central general visual response ($R = 0.64$) is significantly lower ($p < .001$). We also split EEG data according to stimulus sets (see *Materials and Methods*) and computed correlations between the responses obtained for each set. We observed that both categorization responses to human faces ($R = 0.99$) and facelike objects ($R = 0.91$) are highly reliable across measurements.

It is worth noting that the visual categorization responses to human and illusory faces are automatically elicited since participants did not explicitly process the two categories but performed an orthogonal cross-detection task with high accuracy (99.3 ± 0.5%) and speed (406 ± 11 ms) without any difference between categories (both *F*s < 1). Similarly, the general visual response recorded at 6 Hz (Figure 2A) and harmonics over the middle occipital cortex (Figure 2C) is not modulated by the stimulus category presented at 1 Hz (human faces: 3.24 ± 0.53 µV; facelike objects: 3.34 ± 0.57 µV; $F < 1$).

Critically, after differentiating participants who overtly reported facelike objects (*aware* group, $N = 13$) and those who did not (*unaware* group, $N = 14$), the categorization response to facelike objects (Figure 3A) is 153% larger for the aware (1.06 ± 0.22 µV) than the unaware group (0.42 ± 0.20 µV; $F_{1,25} = 21.3$, $p < .001$, $\eta_p^2 = 0.46$). In contrast, the face categorization response is not significantly different between participants ($F < 1$), albeit descriptively larger for the aware (3.61 ± 0.73 µV; +10.5%) than the unaware group (3.27 ± 0.63 µV). Likewise, the amplitude of the general visual response (Figure 3B) does not differ between groups (aware: 3.34 ± 0.85 µV; unaware: 3.25 ± 0.82 µV; $F < 1$), who did not differ at the behavioral cross-detection task (aware: 99.5 ± 0.4%, 406 ± 15 ms; unaware: 99.1 ± 0.9%, 406 ± 17 ms; both *F*s < 1).

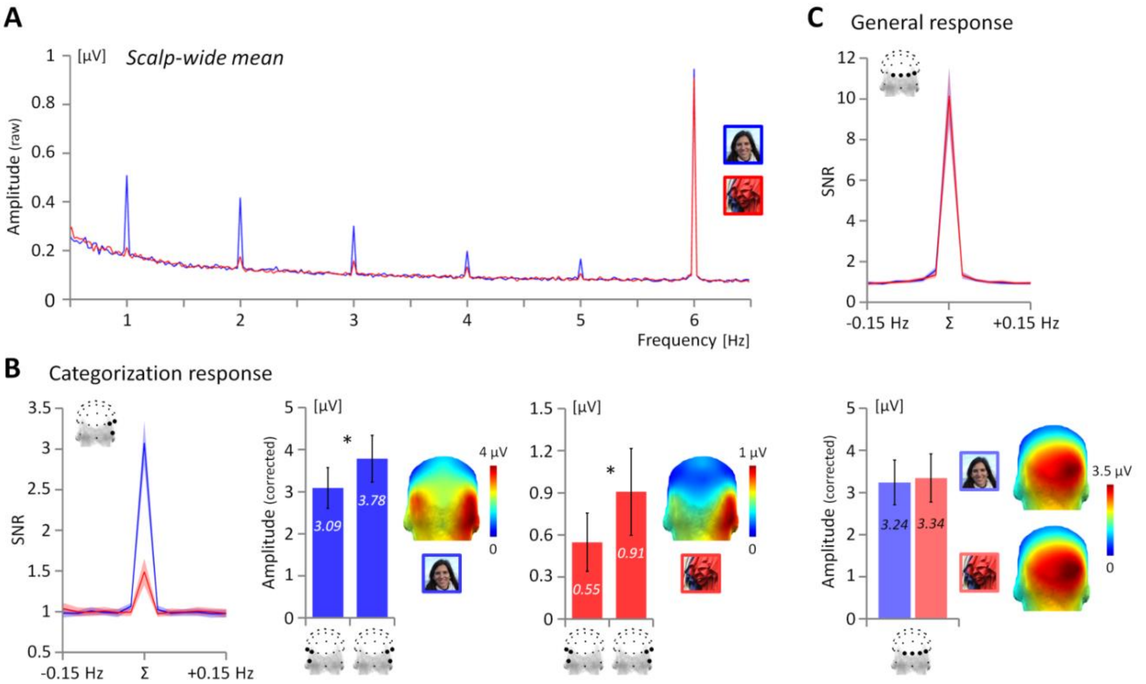


Figure 2. Brain responses elicited in sequences presenting human faces (blue) or facelike objects (red) among nonface objects. A. Grand-averaged FFT amplitude spectra (across 64 channels). Both types of stimulation sequences elicit a large response at the 6-Hz image presentation frequency (i.e., general response to all images). Though stronger to human faces, responses are clearly visible (i.e., of higher amplitude than surrounding frequency bins) at the 1-Hz human/illusory face presentation frequency and its harmonics (i.e., integer multiples, here 2 Hz, 3 Hz, 4 Hz, 5 Hz). **B.** Left: Grand-averaged signal-to-noise ratio (SNR) of the categorization responses to human faces (SNR ≈ 3) and facelike objects (SNR ≈ 1.5) summed across significant harmonics (Σ) for the right occipito-temporal region-of-interest (ROI) and compared with surrounding frequencies (± 0.15 Hz, SNR ≈ 1, signal ≈ noise). Middle and right: Grand-averaged summed corrected amplitude of the categorization responses over the left and right occipito-temporal ROIs (* $p < .05$). **C.** Top: Grand-averaged SNR of the general response to sequences presenting human faces or facelike objects (SNR ≈ 10 for both) summed across significant harmonics (Σ) for the middle occipital ROI. Bottom: Grand-averaged summed corrected amplitude of the general response over the middle occipital ROI. For both categorization (B) and general (C) responses, topographies are illustrated by head maps (posterior view). Shaded areas or error bars represent 95% confidence intervals.

Next, we estimated the significance of individual categorization responses (Figure 3C) using Z-scores contrasting the amplitude of the response (i.e., signal) from surrounding noise level ($Z > 1.64$, $p < .05$, one-tailed, signal > noise). Every individual participant presents a strongly significant categorization response to human faces (all Zs > 11.64, all ps < .001). In contrast, while the categorization response to illusory faces is significant in every aware participant (all Zs > 4.15, all ps < .001), it is significant in only half of the participants (i.e., 7 out 14) from the unaware group (all Zs > 3.07, all ps < .002, other half: from $Z = –0.24$, $p = .59$ to $Z = 1.53$, $p = .063$). By ranking the amplitude of individual categorization responses, we observed that 11 out of the 13 largest responses to facelike objects (i.e., above the median response of participant #23: 0.75 µV) belong to aware participants. In other words, EEG data predicts well above chance ($p = .011$) whether a given participant consciously perceives face pareidolia (accuracy = 85%). Predictability is not above chance ($p = .29$) if based on the response to human faces (8 out of the 13 largest responses (62%) belong to aware participants).

2. Experiment 2: Perceived vs. unperceived illusory faces in a single brain

Experiment 1 provides a clear demonstration that variable objects resembling faces are categorized as faces by the human brain, in association with participants' report of face pareidolia after testing. However, given that participants were differentiated *a posteriori* from this single

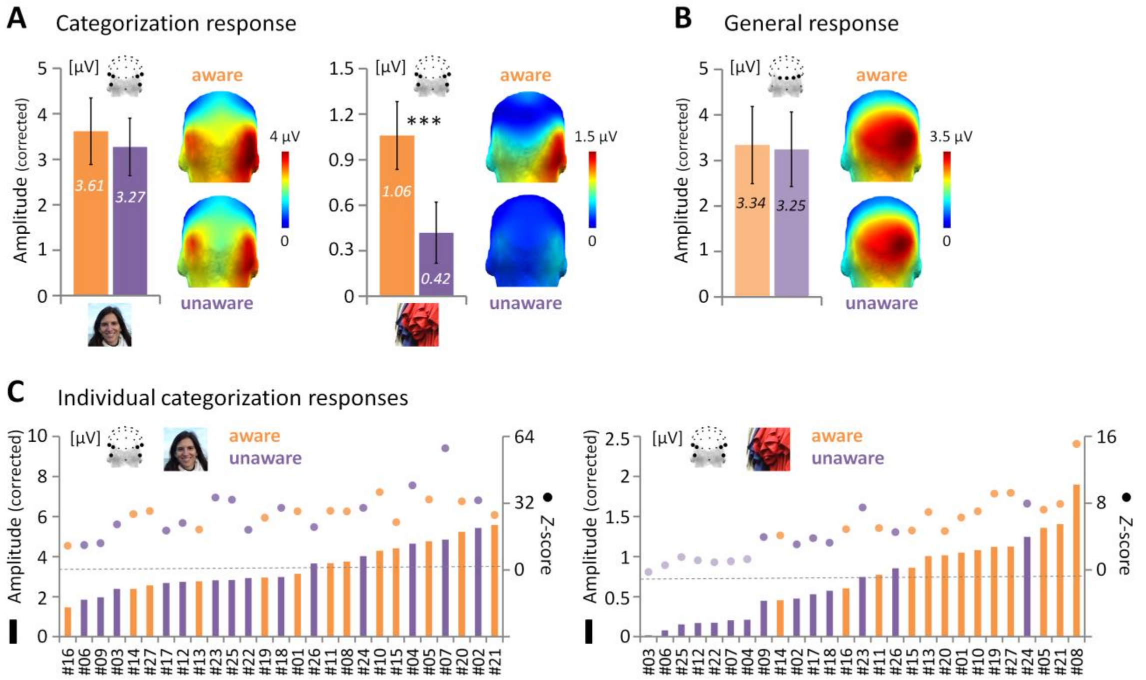


Figure 3. Categorization and general responses according to the perceptual awareness of illusory faces. A. Grand-averaged summed corrected amplitude of the categorization responses to human faces (left) and facelike objects (right) averaged across left and right occipito-temporal regions-of-interest (ROIs) for the aware (orange) and unaware (purple) groups (*** $p < .001$). **B.** Grand-averaged summed corrected amplitude of the general response over the middle occipital ROI for the aware (orange) and unaware (purple) groups (categories collapsed). For both categorization (A) and general (B) responses, topographies are illustrated by head maps (posterior view) and error bars represent 95% confidence intervals. **C.** Individual categorization responses to human (left) and illusory (right) faces for participants from the aware (orange) and unaware (purple) groups. Bars and dots respectively depict summed corrected amplitudes (ranked in ascending order) and *Z*-scores. Lighter dots represent non-significant *Z*-scores ($Z < 1.64$, $p > .05$, one-tailed, signal > noise). The dashed grey line depicts the mean corrected amplitude across participants.

report that summarizes the experience of almost 3000 stimulation cycles including more than 250 facelike stimuli, we conducted a second experiment to directly compare the brain responses to perceived and unperceived facelike objects in a within-subject design. Another 22 participants were explicitly instructed to report if they perceived illusory faces after each of a hundred 16-sec-long sequences. Half of the sequences presented facelike objects among nonface objects and the other half presented only nonface objects. Facelike stimuli were always displayed at 1 Hz, but they lasted 17 ms, 33 ms, 50 ms, 67 ms or 83 ms depending on the sequence (i.e., 5 stimulation frequencies: 60 Hz, 30 Hz, 20 Hz, 15 Hz and 12 Hz; Figure 1C) to manipulate the conscious perception of illusory faces.

At 17 ms, face pareidolia are not reported above chance, with a mean number of reports of 4.8 ± 1.4 (95% *CI*) out of 10 for sequences containing facelike objects (Figure 4A). Facelike reports then increase above chance at 33 ms (7.0 ± 0.9 reports) and reach near-ceiling accuracy from 50 ms (9.0 ± 0.6 reports) to 83 ms (9.6 ± 0.4 reports) with no difference between 50 ms and 83 ms (all *p*s > .05). In contrast, illusory face perception in sequences containing only nonface objects is lower than chance for all durations (from 2.2 ± 1.2 reports at 17 ms to 1.0 ± 0.5 reports at 83 ms, significant difference between 50 ms and 67 ms, $p = .044$), so that the number of accurate facelike reports (i.e., hits) is greater than the number of erroneous perceptions (i.e., false alarms), even at the shortest 17-ms duration (main effect of *Category*: $F_{1,21} = 238$, $p < .001$, $\eta_p^2 = 0.92$). In other words, despite the very high constraints put on the visual system at the highest stimulation rate, participants were able to tell apart the two types of sequences (i.e., with or without facelike objects), this difference between the number of hits and false alarms increasing as a function of stimulus duration (*Category* × *Stimulus duration* interaction: $F_{2.5,52.3} = 37.5$, $\varepsilon = 0.62$, $p < .001$, $\eta_p^2 = 0.64$).

At the neural level, the response measured at 1 Hz and harmonics over the occipito-temporal regions identified in Experiment 1 (Figure 4B) is also always larger for sequences containing facelike stimuli than only nonface objects (main effect of *Category*: $F_{1,21} = 57.8$, $p < .001$, $\eta_p^2 = 0.73$). Albeit very low at the 17-ms stimulus duration (0.17 ± 0.09 µV), the response to facelike objects is greater than noise level (i.e., 95% *CI* does not include 0) and increases with stimulus duration (until 0.74 ± 0.17 µV at 83 ms, all *p*s < .03), contrary to the response to nonface objects (mean amplitude across durations: 0.01 ± 0.05 µV). The difference between the responses to facelike objects and nonface objects thereby increases with duration (*Category* × *Stimulus duration* interaction: $F_{4,84} = 6.64$, $p < .001$, $\eta_p^2 = 0.24$). A right hemisphere advantage is visible at most durations for the selective response to illusory faces (Figure 4D), but it did not reach significance ($F < 1$). Like the facelike categorization response, the general visual response (Figure 4C) is larger than noise at all durations (lowest amplitude: 0.03 ± 0.02 µV at 17 ms) and increases with stimulus duration (until 1.5 ± 0.36 µV at 83 ms, $F_{1.4,29.7} = 57.5$, $\varepsilon = 0.35$, $p < .001$, $\eta_p^2 = 0.73$). However, this middle occipital activity (Figure 4D) elicited by the rapid stream of stimuli is not different between sequences containing facelike and nonface objects

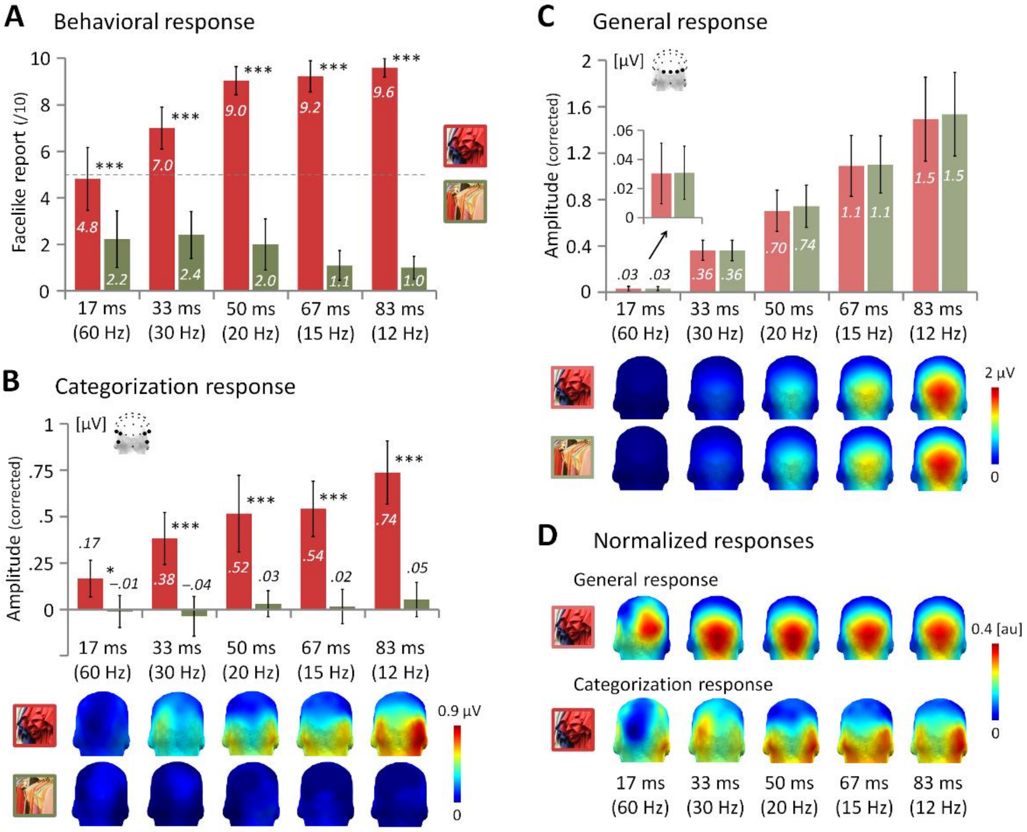


Figure 4. Behavioral and neural responses according to stimulus category and duration. Mean number of facelike reports out of 10 (**A**), grand-averaged summed corrected amplitude of the categorization response over occipito-temporal ROIs (**B**) and of the general response over the middle occipital ROI (**C**) for sequences presenting facelike objects (red) or only nonface objects (green) and for the five stimulus durations (* $p < .05$, *** $p < .001$, error bars represent 95% confidence intervals). In (A), the dashed grey line represents chance level (i.e., 5 reports). For both categorization (B) and general (C) responses, topographies are illustrated by head maps (posterior view). **D.** Topographical head maps of normalized general and categorization responses to sequences containing facelike objects illustrate their spatial distribution across stimulus durations (au: arbitrary unit).

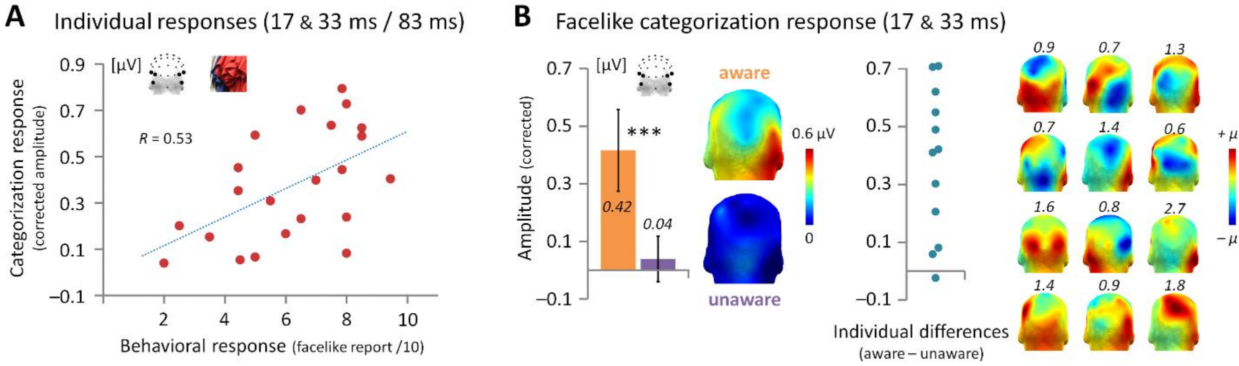


Figure 5. The facelike categorization response predicts the conscious perception of an illusory face. A. Correlation between individual summed corrected amplitudes of the facelike-selective response over occipito-temporal ROIs and the number of facelike reports weighted by their ceiling-level value at the 83-ms duration for the combination of the 17- and 33-ms durations. **B.** Left: grand-averaged summed corrected amplitude of the facelike categorization response over occipito-temporal ROIs for 12 representative participants (see *Materials and Methods*) depending on their report of illusory faces (aware: orange *vs*. unaware: purple; *** $p < .001$) for the combination of the 17- and 33-ms durations. Error bars represent 95% confidence intervals. Topographies are illustrated by head maps (posterior view). Right: dots depict individual differences between the facelike-selective responses to reported and unreported face pareidolia. Topographies are illustrated by head maps (posterior view) with each individual scale indicated above the map.

($F_{1,21} = 1.59$, $p = .22$).

The increase of both neural and behavioral responses to facelike objects as stimulus duration increases suggests a relationship between these measures, in line with participants' awareness of face pareidolia. Thus, we evaluated whether participants reporting facelike stimuli in more sequences present with larger facelike-selective responses. For each duration individually, no correlations between neural activity and behavior reached significance despite marginal relationships at 17 ms ($R = 0.39$, $p = .071$) and 33 ms ($R = 0.38$, $p = .074$). When these two shortest durations are combined, neural and behavioral responses become significantly associated ($R = 0.48$, $p = .024$), while correlations are still not significant for the combination of the two (i.e., 50 and 67 ms; $R = 0.26$, $p = .25$) or three following durations (i.e., from 50 to 83 ms; $R = 0.32$, $p = .14$). After weighting the responses by their value at the longest 83-ms duration to correct for ceiling-level neural activity and behavioral performance, the relationship between the facelike categorization response and the number of facelike reports becomes slightly stronger at 17-33 ms ($R = 0.53$, $p = .011$; Figure 5A) but drops close to zero at 50-67 ms ($R = -0.01$, $p = .97$). This reveals that the amplitude of the selective response to facelike objects is related to their overt report for the two most challenging stimulus durations.

Accordingly, we finally explored whether the advent of the facelike-selective response at the 17- and 33-ms durations directly depends on participants' report of illusory faces. We considered the data of 12 representative participants (see *Materials and Methods*) and differentiated their facelike categorization responses between sequences wherein they perceived facelike objects (*aware*) and those wherein they did not (*unaware*). Strikingly, the selective response to facelike stimuli is significantly above noise level only for aware sequences (0.42 ± 0.14 µV; Figure 5B) and leads to a larger neural activity compared to unaware sequences (0.04 ± 0.08 µV; $F_{1,11} = 26.5$, $p < .001$, $\eta_p^2 = 0.71$). Descriptively, 11 out of the 12 participants have a larger categorization response when they report facelike objects, such that the sign of the difference between the two conditions predicts whether a given participant was aware of the illusory faces with an accuracy of 92%. The topography of this difference reveals an advantage for aware sequences over posterior scalp regions in every individual participant (Figure 5B). This demonstrates that the neural categorization response to facelike objects emerges when these stimuli are consciously perceived as faces.

D. Discussion

Through two experiments, we identify a facelike-selective neural response reflecting conscious face perception emerging from a variety of naturalistic nonface objects, i.e., a signature of face pareidolia in the human brain. This response is isolated in individual participants and predicts perceptual awareness with high accuracy, either between groups of aware vs. unaware participants (Experiment 1), or between stimulation sequences according to participants' report of face pareidolia (Experiment 2). Hence, thanks to the advantages of FPVS and EEG frequency-tagging to measure categorization in the brain, and to the ability of visual illusions to dissociate conscious perception from the physical input, the present study provides a clear illustration that category-selective neural responses relate to the subjective experience of a stimulus rather than its objective content.

Face pareidolia is ubiquitous in humans. It has been widely used by painters (e.g. Giuseppe Arcimboldo, 1527 – 1593) or photographers (e.g., 30), and more than 70% of pictures represent a face when searching "pareidolia" on the web (estimation made in July 2020 with the first 100 different pictures in Google Images). Accordingly, going beyond previous efforts with scalp EEG (e.g., 17,18,22), the first major achievement of the present study is to provide a rich and valid measure of face pareidolia under the variable viewing conditions in which it takes place in the natural visual environment. The use of various natural views of facelike objects contrasted to equally variable nonface stimuli also makes unlikely the contribution of low physical variability between facelike objects (see 24), and implies figure-ground segregation, an integral part of object perception (31), as illustrated by some bistable illusions (e.g., Rubin's vase illusion; 32). In addition, the facelike-selective response reflects spontaneous face pareidolia, that is, the automatic perception (i.e., unintentional, difficult to suppress) of an illusory face at a glance. It is also worth reminding that the facelike categorization response is a direct differential response (i.e., without post-hoc subtraction), such that it would have been absent if facelike objects were not differentiated from nonface objects, as observed in Experiment 2 when only nonface objects are displayed. The response is objective (i.e., recorded at a pre-experimentally defined frequency and its harmonics), and highly sensitive and reliable, as estimated in Experiment 1. These properties are critical to identify unambiguous individual brain responses, estimate their significance, and relate them to participants' report of face pareidolia.

In Experiment 1, we also clarify how similar is the categorization of illusory faces to the categorization of genuine human faces, both quantitatively and qualitatively. Consistent with previous studies using the same paradigm, we observed that the categorization of human faces elicits a large re-sponse of about 4 µV over the occipito-temporal cortex, with a right hemisphere advantage (e.g., 26,27). The facelike categorization response has a similar topography with a great right-hemispheric dominance, but is about 20% of the face-selective response in amplitude (35% when considering only aware participants). At least three non-mutually exclusive interpretations can explain this observation. First, the two responses may be generated by the same face-selective regions distributed along the ventral visual pathway (29,33–35), with a weaker activation overall for facelike objects. Such diminished responsiveness could be due to the absence of some cues pertaining to natural faces in facelike stimuli. For instance, while both shape and color information are important cues for visual recognition (36,37), color does not inform about facelikeness in facelike objects. A second interpretation may be that only a subset of face-selective regions contributes to the facelike categorization response. Previous studies have associated the perception of an illusory face with the lateral part of the middle fusiform gyrus (13,15,16,20), sometimes considered as a hub for the perception of a global face configuration (38,39). Relatedly, the facelike-selective response is strongly right-lateralized, the right hemisphere being particularly involved in the perception of a global facelike configuration (16,17). However, no hemispheric asymmetry was found in Experiment 2, probably due to the explicit instruction to attend to illusory faces (see 40). A last interpretation may be that facelike stimuli either elicit a full response within the whole face-selective network when they are perceived as faces, or they do not elicit a face-selective response at all when they are not perceived as faces, leading to a lower response in average. In other words, neural categorization could be strictly identical for facelike objects and human faces, but artificially appear weaker for facelike objects due to more occasional occurrences. Interestingly for our purpose, this explanation concurs with the view that neural categorization emerges all at once from the linear accumulation of sensory information and reflects perceptual awareness (2–4).

In that respect, the second major achievement of the present study is to characterize to what extent the neural categorization of facelike objects reflects conscious illusory face perception, extending prior work on the association between a neural response to simple facelike stimuli and their perceptual interpretation as a face (20–23). In Experiment 1, we observed a strong categorization response to facelike objects in participants who reported face pareidolia after testing compared to a weak response in those who did not, and revealed that individual facelike categorization responses predict this association. More strikingly, this relationship was confirmed in a single group of participants in Experiment 2, with a significant correlation between the facelike-selective response and the number of illusory face reports at the shortest stimulus durations (i.e., 17 and 33 ms). As a result, when directly comparing aware and unaware sequences at these two challenging durations, the facelike-selective response is observed only when face pareidolia are reported, with a conspicuous difference between the two types of sequences in each individual participant. Hence, given that the response varies greatly as a function of perceptual awareness despite identical stimuli, and given that these stimuli are directly contrasted to other stimuli depicting the same object categories, our study yields clear evidence that neural categorization is a signature of conscious perception (2–4).

The strict absence of facelike categorization response to unreported face pareidolia in Experiment 2 points toward an all-or-none neural categorization function in response to sensory information gradually accumulating in early visual areas, as mentioned above. However, in Experiment 1, although the large difference between aware and unaware participants indicates that the bulk of the response reflects conscious illusory face perception, the response is not completely abolished for unaware participants. This suggests that a residual selective response to facelike objects can be observed in the absence of overt report. One explanation may be that some cues elicit a differential response between facelike and nonface objects, albeit non-sufficient to trigger full categorization. For instance, facelike objects all depict "eyelike" or "mouthlike" features (e.g., Figure 1A), sometimes considered critical features to perceive a nonface stimulus as a face (e.g., 41). Similarly, some image statistics covary with facelikeness, such as more contrast (i.e., higher spatial frequencies) in the upper part of the image. This visual property is well-known to already attract attention in newborns, as a necessary precursor to develop efficient face perception (e.g., 42,43 for review). Moreover, the presence of human faces in this experiment could have primed face-related cues in facelike stimuli. Alternatively, since aware and unaware participants were differentiated a posteriori following a single awareness assessment at the end of the experiment, the small response for unaware participants could be due to a confound such as the criteria to define an illusory face. In this context, it should be noted that both the general visual response elicited by the rapid stream of stimulation and the efficiency at the cross-detection task do not differ between participants, making unlikely the contribution of visual attention as a confound. Whatever the potential confounds at stake, we eliminated them in Experiment 2, which reveals a striking difference between aware and unaware responses to facelike objects in a single group of participants.

By manipulating stimulus duration, Experiment 2 additionally provides important information about the optimal conditions for face pareidolia to arise within a fast train of forward- and backward-masked stimuli. Albeit at chance level at the shortest 17-ms duration, facelike reports are higher for sequences containing facelike objects than only nonface objects at every duration, and the facelike categorization response is larger than noise at every duration. This means that participants were already able to perceive some illusory faces at 17 ms, in agreement with a minimal duration of ap-proximately 13–17 ms to behaviorally or neurally categorize human faces in rapid streams of natural images (4,44), or other visual objects in various experimental designs (2,45–47). Facelike reports then in-crease at 33 ms and reach ceiling at 50 ms, while the amplitude of the facelike-selective response increases until the longest 83-ms duration. Moreover, individual behavioral and neural responses become uncorrelated at 50 ms and 67 ms, especially when they are weighted by their values at 83 ms (i.e., normalization by ceiling-level individual differences). This dissociation between behavioral and neural responses from 50 ms is not surprising given that a single behavioral response was recorded after each sequence, summarizing the experience of at least 192 stimuli, sometimes including 16 facelike objects. Therefore, participants could have reported illusory face perception from a few facelike stimuli, such that accuracy rapidly reached ceiling at the intermediate 50-ms duration, but the number of categorized stimuli within a sequence could still increase at 67 ms and 83 ms. This accords with previous studies showing that various factors, such as the overlap of sensory information with forward and backward stimuli, lead to the categorization of only a fraction of stimuli at short presentation times (e.g., 45). Interestingly, the number of false alarms only decreases at 67 ms and above, and remains significantly higher than zero. Thus, the explicit instruction to detect facelike stimuli among other stimuli within rapid sequences depicting many object categories made participants incline to falsely report facelike objects, even at ceiling-level stimulus durations. Importantly, however, false alarms are not associated with a significant neural categorization response. Since erroneous perceptions can be driven by any stimulus within a sequence of nonface stimuli, they do not occur periodically and do not translate at 1 Hz and harmonics in the EEG spectrum.

In sum, by using a widely variable set of naturalistic facelike objects contrasted to another variable set of the same object categories, we measure a rich neural categorization response to the facelike stimuli that is intimately related to their conscious perception as faces. Coupling a visual illusion, which dissociates the subjective stimulus experience from its physical content, and EEG frequency-tagging, which measures categorization in the brain with objectivity, sensitivity, reliability and validity, is thus a powerful approach to characterize the neural underpinnings of perceptual awareness. In doing so, we corroborate the view that perceptual awareness emerges from categorical responses to unconscious sensory inputs (1–4). Ultimately, since visual categorization is subtended by a set of category-selective regions in the ventral occipito-temporal cortex, as already shown with the present paradigm (29,33,48), it is tempting to consider these regions as the direct neural substrates of perceptual awareness, a long-standing issue in cognitive neuroscience (49–51,52 for reviews). We acknowledge that much research must be carried out to further clarify this issue that goes beyond the scope of the present study.

Acknowledgments

The authors are grateful to Romain Patrux and Lucas Ronat for help in data collection. This work was supported by grants from the "Conseil Régional Bourgogne Franche-Comté" (PARI grant), the FEDER (European Funding for Regional Economic Development), the French "Investissements d'Avenir" program (project ISITE-BFC, contract ANR-15-IDEX-0003), and the French National Research Agency (ANR, contract ANR-19-CE28-0009).

Supporting information

Supplementary Materials and Methods

Stimulus selection

We used a variety of biological[1] and manufactured objects[2] as nonface stimuli, including between 3 and 20 exemplars for each category. Facelike stimuli matched several object categories[3], with 1 to 5 exemplars for each category. Facelike stimuli were selected among 224 images collected from the Internet when searching for 'face pareidolia'. Selection was made according to the images judged as the most facelike in a pretest also including 224 nonface images selected from the main set. We told 142 participants (111 females, 15 left-handed (12 females), mean age: 18.9 ± 1.5 years, range: 17–26 years) that natural images depicting objects will be presented with some of them resembling faces. In a two forced-choice facelike categorization task (i.e., facelike *vs.* non-facelike), participants responded as fast as possible for each image (i.e., 464 trials) using two keys with their left and right index fingers (dominant finger for the facelike response). Each trial began with a fixation cross displayed at the center of a monitor for 467 ms, followed by the test image for 133 ms (Figure S1). Hence, while stimuli were not forward- and backward-masked as in the main experiment, they were presented for a brief duration that constrained participants to judge facelikeness at first glance. Stimuli were followed by an inter-trial interval of 1.2 s. Facelike and nonface images were presented randomly in 8 blocks of 56 trials. For each facelike image, we calculated the percentage of facelike responses across participants and mean response time (RT, only for facelike responses ranging between 100 and 1000 ms). In average across facelike images, the percentage of facelike responses was 83.5 ± 14.3% (*SD*) (range: 23% – 96%) and mean RT was 473 ± 33 ms (range: 416 – 621 ms). To combine both measures and exclude speed-accuracy trade-offs, we calculated inverse efficiency (i.e., RT divided by accuracy) for each image. It ranged from 445 (i.e., judged as the most facelike) to 2299 (i.e., judged as the less facelike). Based on these data, we selected the 86 facelike images judged as the most facelike (range: 445 – 508).

---

[1] birds, cats, cells, dogs, eggs, flowers, fruits, horses, plants, trees, vegetables.

[2] bags, bells, belts, blocks, bowls, boxes, brushes, cameras, candies, canoes, car parts, casings, chairs, clocks, clothes, cookers, crates, cups, electric devices, glasses, graters, guitars, houses, jars, lamps, latches, lids, mail boxes, metallic devices, pant pockets, pastries, pipes, plaques, plastic devices, plates, robots, scooters, spoons, staplers, taps, telephones, trashes, washing machines, toilets, yoghurts.

[3] bags, bells, belts, blocks, bowls, boxes, brushes, candies, canoes, car parts, casings, cells, clocks, clothes, cookers, crates, cups, electric devices, eggs, fruits, glasses, graters, houses, jars, latches, lids, mail boxes, metallic devices, pant pockets, pastries, pipes, plants, plaques, plastic devices, plates, robots, scooters, spoons, staplers, taps, trashes, trees, vegetables, washing machines, toilets, yoghurts.

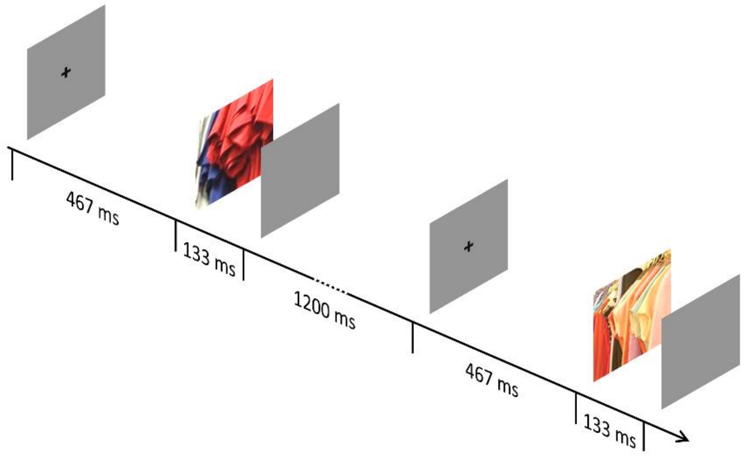


Figure S1. Experimental design for facelike stimulus selection. Participants were presented with 464 trials starting with a fixation cross for 467 ms, followed by the stimulus for 133 ms and an inter-trial interval of 1200 ms. Participants were instructed to categorize the stimulus as facelike or non-facelike as fast as possible after stimulus-onset.

Table S1. Significance of the frequency-tagged responses and their harmonics (i.e., integer multiples). To define the general (6 Hz and harmonics) and categorization (1 Hz and harmonics) responses in Experiment 1, we determined the range of significant harmonics using *Z*-scores (amplitude at the target frequency minus mean amplitude of the surrounding noise (20 frequency bins, 10 on each side, excluding the immediately adjacent and the 2 most extreme bins) divided by the standard deviation of the noise) calculated on the mean EEG amplitude spectrum across channels and participants for sequences containing human faces. Significant Z-scores ($Z > 1.64$, $p < .05$, one-tailed, signal > noise) are indicated in bold. Harmonics were considered until Z-scores were no longer significant for both the general (blue) and categorization (red) responses.

Frequency [Hz]	*Z*-score	Frequency [Hz]	*Z*-score
1	**16.4**	25	**2.33**
2	**49.9**	26	**4.33**
3	**53.5**	27	1.56
4	**24.8**	28	-0.23
5	**21.8**	29	**4.31**
6	**198**	30	**34.9**
7	**37.8**	31	-0.76
8	**33.4**	32	1.57
9	**30.8**	33	**2.06**
10	**18.5**	34	1.33
11	**15.4**	35	0.13
12	**58.1**	36	**22.9**
13	**13.9**	37	-0.29
14	**9.33**	38	0.04
15	**9.12**	39	-1.37
16	**9.23**	40	**1.67**
17	**6.92**	41	**2.32**
18	**80.8**	42	**25.7**
19	**7.29**	43	-0.28
20	**3.04**	44	**1.75**
21	**2.52**	45	0.29
22	**3.16**	46	**1.84**
23	**2.87**	47	0.64
24	**31.5**	48	**16.7**

References

1. de Gardelle, V., Charles, L. & Kouider, S. Perceptual awareness and categorical representation of faces: Evidence from masked priming. Conscious. Cogn. 20, 1272–1281 (2011).
2. Fisch, L. et al. Neural "Ignition": Enhanced Activation Linked to Perceptual Awareness in Human Ventral Stream Visual Cortex. Neuron 64, 562–574 (2009).
3. Quian Quiroga, R., Mukamel, R., Isham, E. A., Malach, R. & Fried, I. Human single-neuron re-sponses at the threshold of conscious recognition. Proc. Natl. Acad. Sci. 105, 3599–3604 (2008).
4. Retter, T. L., Jiang, F., Webster, M. A. & Rossion, B. All-or-none face categorization in the human brain. NeuroImage 213, 116685 (2020).
5. Edelman, G. M. Naturalizing consciousness: A theoretical framework. Proc. Natl. Acad. Sci. 100, 5520–5524 (2003).
6. Aru, J. et al. Local Category-Specific Gamma Band Responses in the Visual Cortex Do Not Reflect Conscious Perception. J. Neurosci. 32, 14909–14914 (2012).
7. Moutoussis, K. & Zeki, S. The relationship between cortical activation and perception investigated with invisible stimuli. Proc. Natl. Acad. Sci. 99, 9527–9532 (2002).
8. Perry, G. The visual gamma response to faces reflects the presence of sensory evidence and not awareness of the stimulus. R. Soc. Open Sci. 3, 150593 (2016).
9. Gregory, R. L. Knowledge in perception and illusion. Philos. Trans. R. Soc. Lond. B Biol. Sci. 352, 1121–1127 (1997).
10. Brouwer, G. J., Ee, R. van & Schwarzbach, J. Activation in Visual Cortex Correlates with the Awareness of Stereoscopic Depth. J. Neurosci. 25, 10403–10413 (2005).
11. Srinivasan, R., Russell, D. P., Edelman, G. M. & Tononi, G. Increased Synchronization of Neuro-magnetic Responses during Conscious Perception. J. Neurosci. 19, 5435–5448 (1999).
12. Sterzer, P., Kleinschmidt, A. & Rees, G. The neural bases of multistable perception. Trends Cogn. Sci. 13, 310–318 (2009).
13. Dolan, R. J. et al. How the brain learns to see objects and faces in an impoverished context. Nature 389, 596–599 (1997).
14. Hadjikhani, N., Kveraga, K., Naik, P. & Ahlfors, S. P. Early (M170) activation of face-specific cortex by face-like objects: NeuroReport 20, 403–407 (2009).
15. McKeeff, T. J. & Tong, F. The Timing of Perceptual Decisions for Ambiguous Face Stimuli in the Human Ventral Visual Cortex. Cereb. Cortex 17, 669–678 (2007).
16. Rossion, B., Dricot, L., Goebel, R. & Busigny, T. Holistic Face Categorization in Higher Order Visual Areas of the Normal and Prosopagnosic Brain: Toward a Non-Hierarchical View of Face Perception. Front. Hum. Neurosci. 4, (2011).
17. Caharel, S. et al. Early holistic face-like processing of Arcimboldo paintings in the right occipito-temporal cortex: Evidence from the N170 ERP component. Int. J. Psychophysiol. 90, 157–164 (2013).
18. Churches, O., Baron-Cohen, S. & Ring, H. Seeing face-like objects: an event-related potential study: NeuroReport 20, 1290–1294 (2009).
19. Sagiv, N. & Bentin, S. Structural Encoding of Human and Schematic Faces: Holistic and Part-Based Processes. J. Cogn. Neurosci. 13, 937–951 (2001).
20. Andrews, T. J. & Schluppeck, D. Neural responses to Mooney images reveal a modular representation of faces in human visual cortex. NeuroImage 21, 91–98 (2004).
21. Bentin, S., Sagiv, N., Mecklinger, A., Friederici, A. & von Cramon, Y. D. Priming Visual Face-Processing Mechanisms: Electrophysiological Evidence. Psychol. Sci. 13, 190–193 (2002).
22. George, N., Jemel, B., Fiori, N., Chaby, L. & Renault, B. Electrophysiological correlates of facial decision: Insights from upright and upside-down Mooney-face perception. Cogn. Brain Res. 24, 663–673 (2005).
23. Shafto, J. P. & Pitts, M. A. Neural Signatures of Conscious Face Perception in an Inattentional Blindness Paradigm. J. Neurosci. 35, 10940–10948 (2015).
24. Davidenko, N., Remus, D. A. & Grill-Spector, K. Face-likeness and image variability drive responses in human face-selective ventral regions. Hum. Brain Mapp. 33, 2334–2349 (2012).
25. Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottereau, B. R. & Rossion, B. The steady-state visual evoked potential in vision research: A review. J. Vis. 15, 4–4 (2015).
26. Jacques, C., Retter, T. L. & Rossion, B. A single glance at natural face images generate larger and qualitatively different category-selective spatio-temporal signatures than other ecologically-relevant categories in the human brain. NeuroImage 137, 21–33 (2016).
27. Retter, T. L. & Rossion, B. Uncovering the neural magnitude and spatio-temporal dynamics of natural image categorization in a fast visual stream. Neuropsychologia 91, 9–28 (2016).
28. Rossion, B., Torfs, K., Jacques, C. & Liu-Shuang, J. Fast periodic presentation of natural images reveals a robust face-selective electrophysiological response in the human brain. J. Vis. 15, 18 (2015).
29. Gao, X., Gentile, F. & Rossion, B. Fast periodic stimulation (FPS): a highly effective approach in fMRI brain mapping. Brain Struct. Funct. 223, 2433–2454 (2018).
30. Robert, F. & Robert, J. Face to face. (Lars Müller Publishers, 1996).
31. Wagemans, J. et al. A century of Gestalt psychology in visual perception: I. Perceptual grouping and figure–ground organization. Psychol. Bull. 138, 1172–1217 (2012).
32. Rubin, E. Synsoplevede Figurer. (1915).
33. Jonas, J. et al. A face-selective ventral occipito-temporal map of the human brain with intracerebral potentials. Proc. Natl. Acad. Sci. 113, E4088–E4097 (2016).
34. Sergent, J., Ohta, S. & Macdonald, B. Functional neuroanatomy of face and object processing: a positron emission tomography study. Brain 115, 15–36 (1992).
35. Zhen, Z. et al. Quantifying interindividual variability and asymmetry of face-selective regions: A probabilistic functional atlas. NeuroImage 113, 13–25 (2015).
36. Gegenfurtner, K. R. & Rieger, J. Sensory and cognitive contributions of color to the recognition of natural scenes. Curr. Biol. 10, 805–808 (2000).

37. Tanaka, J., Weiskopf, D. & Williams, P. The role of color in high-level vision. Trends Cogn. Sci. 5, 211–215 (2001).
38. Andrews, T. J., Davies-Thompson, J., Kingstone, A. & Young, A. W. Internal and External Features of the Face Are Represented Holistically in Face-Selective Regions of Visual Cortex. J. Neurosci. 30, 3544–3552 (2010).
39. Goffaux, V., Schiltz, C., Mur, M. & Goebel, R. Local Discriminability Determines the Strength of Holistic Processing for Faces in the Fusiform Face Area. Front. Psychol. 3, (2013).
40. Quek, G., Nemrodov, D., Rossion, B. & Liu-Shuang, J. Selective Attention to Faces in a Rapid Visual Stream: Hemispheric Differences in Enhancement and Suppression of Category-selective Neural Activity. J. Cogn. Neurosci. 30, 393–410 (2018).
41. Omer, Y., Sapir, R., Hatuka, Y. & Yovel, G. What Is a Face? Critical Features for Face Detection. Perception 48, 437–446 (2019).
42. Johnson, M. H., Dziurawiec, S., Ellis, H. & Morton, J. Newborns' preferential tracking of face-like stimuli and its subsequent decline. Cognition 40, 1–19 (1991).
43. Simion, F. & Di Giorgio, E. Face perception and processing in early infancy: inborn predispositions and developmental changes. Front. Psychol. 6, (2015).
44. Keysers, C., Xiao, D.-K., Földiák, P. & Perrett, D. I. The Speed of Sight. J. Cogn. Neurosci. 13, 90–101 (2001).
45. Bacon-Macé, N., Macé, M. J.-M., Fabre-Thorpe, M. & Thorpe, S. J. The time course of visual processing: Backward masking and natural scene categorisation. Vision Res. 45, 1459–1469 (2005).
46. Mohsenzadeh, Y., Qin, S., Cichy, R. M. & Pantazis, D. Ultra-Rapid serial visual presentation reveals dynamics of feedforward and feedback processes in the ventral visual pathway. eLife 7, e36329 (2018).
47. Potter, M. C., Wyble, B., Hagmann, C. E. & McCourt, E. S. Detecting meaning in RSVP at 13 ms per picture. Atten. Percept. Psychophys. 76, 270–279 (2014).
48. Hagen, S. et al. Spatially Dissociated Intracerebral Maps for Face- and House-Selective Activity in the Human Ventral Occipito-Temporal Cortex. Cereb. Cortex 30, 4026–4043 (2020).
49. Boly, M. et al. Are the Neural Correlates of Consciousness in the Front or in the Back of the Cerebral Cortex? Clinical and Neuroimaging Evidence. J. Neurosci. 37, 9603–9613 (2017).
50. Dehaene, S., Lau, H. & Kouider, S. What is consciousness, and could machines have it? Science 358, 486–492 (2017).
51. Koch, C., Massimini, M., Boly, M. & Tononi, G. Neural correlates of consciousness: progress and problems. Nat. Rev. Neurosci. 17, 307–321 (2016).
52. Odegaard, B., Knight, R. T. & Lau, H. Should a Few Null Findings Falsify Prefrontal Theories of Conscious Perception? J. Neurosci. 37, 9593–9602 (2017).
53. Makeig, S., Bell, A. J., Jung, T.-P. & Sejnowski, T. J. Independent component analysis of electroencephalographic data. in Advances in neural information processing systems (eds. D. Touretzky, M. Mozer & M. Hasselmo) vol. 8 145–151 (MIT Press, 1996).
54. Quek, G. L. & Rossion, B. Category-selective human brain processes elicited in fast periodic visual stimulation streams are immune to temporal predictability. Neuropsychologia 104, 182–200 (2017).
55. Benjamini, Y. & Hochberg, Y. Controlling the false discovery rate: a practical and powerful ap-proach to multiple testing. J. R. Stat. Soc. Ser. B Methodol. 289–300 (1995).
56. McCarthy, G. & Wood, C. C. Scalp distributions of event-related potentials: An ambiguity associ-ated with analysis of variance models. Electroencephalogr. Clin. Neurophysiol. Potentials Sect. 62, 203–208 (1985).

VI. Appendix 6: Supporting information of Study 4

Supporting information

Supplementary Materials and Methods

Collection and selection of odor stimuli

Body odor collection

Volunteer donors complied to follow a strict 24-hour hygiene procedure forbidding the use of odorous products (soap, perfume) on the chest and armpits as well as the consumption of specific food and substances (marinated or spicy food, garlic and onion, tobacco and alcohol) before collection. On the day of collection, they washed their armpit with clear water and a cotton glove (pre-washed with scentless powder detergent (Persavon, France)) at the lab. A trained experimenter then disposed cotton pads under each armpit using dedicated and disposable scentless nitrile gloves and fixing the pads with adhesive strip on the original paper sack of the sterile cotton pads. Collection lasted between 45 and 150 minutes while donors participated in a non-related study. Cotton pads were then removed with gloves, and cut in 16 equivalent units, before being immediately stored in tinfoil and an individual zip-locked plastic bag in a -20°C freezer. They were used within 6 months to preserve odor characteristics (Lenochova et al., 2008). All donors and participants of the EEG experiment were of Caucasian origin.

Independent characterization of body odor pools

In a first pilot experiment, body odors of 8 individuals (4 females, mean age: 27 ± 5 years-old; mean sampling duration: 60 ± 10 min) were gathered as a single pool (not used in the main EEG experiment). Twelve independent participants (7 females, mean age ± SD: 30 ± 8 years olds) rated twice this body odor pool *vs.* two unworn cotton pads soaked with distilled water in same-looking flasks presented under a counterbalanced order across participants. Participants rated the cotton pads on 1–9 Likert scales for their pleasantness (1: not pleasant at all, 9: very pleasant), their intensity (1: barely perceptible, 9: very intense) and familiarity (1: not familiar at all, 9: very familiar). The mean hedonic valence of the body odor pool was 3.75 ± 1.08 (vs. 4.63 ± 0.8 for water: $t_{11} = 2.22$, $p = .05$) for a perceived intensity of 4.25 ± 1.85 (vs. 2.83 ± 1.86 for water: $t_{11} = 2.20$, $p = .05$). Odor conditions were judged of similar familiarity (body: 3.29 ± 2.18, water: 3.54 ± 1.75; $t_{11} = 0.74$, $p = .34$).

Body odor pools for the EEG experiment

The axillary sweat of 16 novel independent non-smoker donors (8 females, mean age ± *SD*: 25 ± 4 years old) were collected after they followed the 24-hour hygiene procedure (see above). Two pools comprising the samples of 8 individuals each (4 females) were created by matching sampling duration and age across pools (Table S1; all *t*s < 1.95, all *p*s > .07). Each participant of the EEG experiment was exposed to only one pool (N = 13 for each pool). Importantly, each group of participants (depending on their overt report of facelike objects, i.e., aware *vs.* unaware participants) was equally presented with both odor pools (aware: 5 and 4 participants for pool 1 and 2, respectively; unaware: 8 and 9 participants for pool 1 and 2, respectively).

Table S1. Details of the body odor pools used in the EEG experiment. From the 16 body odor samples, two pools of 8 individual odors were composed in adjusting for sex ratio (1:1), sampling duration and age of donor.

		Sampling duration (min)	Age of donor (year)
All	Range	45-150	20-35
	Mean ± SD	92 ± 34	25 ± 4
Pool 1	Range	45-150	22-35
	Mean ± SD	98 ± 41	27 ± 5
Pool 2	Range	45-120	20-27
	Mean ± SD	87 ± 28	23 ± 3

Selecting and adjusting the gasoline odor

Based on a previous study in which 38 independent participants (22 females, mean age ± *SD*: 25 ± 4 years old) rated 50 odors from flasks (Vieillard et al., 2020), we identified that the odor of gasoline matches body odor pools in terms of hedonic valence (mean ± *SD*: 3.76 ± 1.7 on a 1–9 Likert scale, when using a 10^{-3} dilution in mineral oil). We thus decided to retain a gasoline odor with 10^{-2} and 10^{-3} dilutions in mineral oil for a direct comparison with the body odor pools used in the main EEG experiment. In this second pilot experiment, fourteen independent participants (10 females, mean age ± *SD*: 21 ± 2 years old) evaluated 4 odorants delivered with the diffusing system of the EEG cabin (see Materials and Methods for details). The odorants consisted in the two body odor pools and the two concentrations of gasoline. Each odorant was diffused 4 times in a randomized order (i.e., corresponding to a total of 16 trials) avoiding immediate repetition, during 5 seconds each and with a minimum inter-stimulus interval of 15 seconds. Participants had to rate odorants on 1–9 Likert scales for their pleasantness (1: not pleasant at all, 9: very pleasant), their familiarity (1: not familiar at all, 9: very familiar) and their intensity (1: barely perceptible, 2: very intense) immediately after the 5 seconds of diffusion. Messages on the screen indicated whether participants had to smell or rate what they previously smelled. The 10^{-3} diluted gasoline evoked similar intensity (2.63 ± 1.88), pleasantness (5.09 ± 0.81) and familiarity (3.84 ± 2.06) than both body odor pools (means: 2.54 ± 1.30, 4.95 ± 0.69 and 3.87 ± 1.60, respectively; all *t*s < 0.9, all *p*s > .05), unlike the 10^{-2} dilution judged more intense and more familiar (means: 4.16 ± 2.11, 5.80 ± 1.99 and 5.95 ± 2.37, respectively; all *t*s > 2.82, all *p*s < .01). The 10^{-3} gasoline odor was thus chosen for the main experiment.

Post-EEG odor ratings

After the experimenter disclosed the implicit diffusion of odors, participants were blindly presented with the flasks of the 3 samples used during their own EEG session. They were asked to rate the odorants in the same order they have been exposed to, on 1–9 Likert scales for their pleasantness (1: not pleasant at all, 9: very pleasant), their familiarity (1: not familiar at all, 9: very familiar) and their intensity (1: barely perceptible, 9: very intense). For the whole sample of participants, gasoline and body odors did not differ in perceived pleasantness (t_{25} = 1.95, *p* = .06), intensity (t_{25} = 0.41, *p* = .68) or familiarity (t_{25} = 1.05, *p* = .30). Furthermore, dissociating aware and unaware participants revealed no difference in ratings (all *t*s < 1.6, all *p*s > .12). The full post-test rating scores are available in Table S2.

Additionally, participants were invited to write down any *evocation* the odor induced, considering that *identification* is hardly achieved in humans and that we used barely detectable odors. Thus, providing an answer was strongly encouraged but not mandatory. The complete set of given answers is compiled in Table S3. Even if some participants found the accurate identification, responses are varied and seem unrelated to the odor effect observed at the brain level. Indeed, while participants aware of facelike objects have the strongest body odor effect, their personal odor evocations are not different from the other group: among the 4 hits for body odor identifications (i.e., correct designation as "sweat"), 2 of them correspond to aware participants (i.e., 50%). Participants were equally prone to give a tentative answer (i.e., at least 1 tentative answer for the 3 odors), with 8/9 aware vs. 13/17 unaware participants (mean number of answers: 1.77 ± 1 vs. 1.83 ± 0.8, respectively; $t_{19} = 0.18$, $p = .86$). In addition, no difference in the accurate identification arises from descriptive group analysis (12% vs. 15% correct answers for aware and unaware, respectively; $t_{19} = 0.31$, $p = .76$).

Table S2. Post-EEG odor ratings. Participants were presented with the flasks used during their EEG session after being informed that odors have been diffused during the EEG experiment. They were asked to smell each flask (see text for details) and rate its content on 1–9 Likert scales regarding pleasantness (1: not at all to 9: very pleasant), intensity (1: barely perceptible to 9: very strong), and familiarity (1: not familiar at all to 9: highly familiar). Mean ratings ± *SD*s are presented below.

		Pleasantness			**Intensity**			**Familiarity**		
	N	**Baseline**	**Body**	**Gasoline**	**Baseline**	**Body**	**Gasoline**	**Baseline**	**Body**	**Gasoline**
All	***26***	**4.9 ± 1.8**	**3.7 ± 2**	**4.7 ± 1.7**	**3 ± 1.9**	**4.2 ± 2.6**	**4.5 ± 2**	**3.5 ± 2.5**	**4.2 ± 2.8**	**5 ± 2.3**
aware	*9*	4.8 ± 0.7	3.4 ± 0.6	4.1 ± 0.4	2.8 ± 0.7	3.1 ± 0.6	4.1 ± 0.6	3.7 ± 0.8	4 ± 1	4.3 ± 0.7
unaware	*17*	4.9 ± 0.4	3.7 ± 0.5	4.9 ± 0.5	3 ± 0.5	4.8 ± 0.7	4.7 ± 0.5	3.5 ± 0.6	4.2 ± 0.7	5.3 ± 0.6

Table S3. Post-EEG odor descriptions. Along with the odor ratings, participants were invited to note down whatever the odor evoked. Answers were translated from French (all participants were native speakers). Participants reporting awareness of facelike stimuli are identified by a star.

	Baseline	Body	Gasoline
#01*			gasoline or permanent marker
#02			gasoline
#03*	food (hazelnut)	sweat	paint
#04	food (chocolate)	sweat	gasoline
#05*	food (banana)		
#06		food (tortilla)	gasoline
#07*		food (garlic)	plastic or playdough
#08			food (citruses)
#09	sweat		citrus
#10		sweat	bleach
#11*			
#12			
#13			gasoline
#14*		pencil	plastic
#15			
#16			
#17*	food (vanilla) or medicine	cloth	cleaning product (detergent) or paint
#18	cleaning product		
#19*	acid	acid	
#20	musty smell	fat	wood
#21	cleaning product (solvent)	plant	interior of a new car
#22		cat litter	cleaning product
#23			
#24*		sweat	cleaning product
#25	cleaning product (detergent)		soda
#26			dried grass

Table S4. Regions of interest (ROIs) for the category-selective response. After summing baseline-corrected amplitudes across significant harmonics of the 1.33-Hz category-selective frequency (i.e., up to 18.67 Hz; i.e., 14th harmonic), the category-selective response was considered averaged across odor contexts to estimate the regions of interest for further analysis according to the channels with the largest amplitude among the 64 channels. For all categories, the six highest channels were located over the right and left occipito-temporal cortices, such that two ROIs were defined (rOT and lOT, respectively in blue and red). See Figure S1 A for electrode location.

Faces			Cars			Facelikes		
Channel	**Rank**	**Amplitude**	**Channel**	**Rank**	**Amplitude**	**Channel**	**Rank**	**Amplitude**
P10	1	3.70	P10	1	1.86	P10	1	0.51
P9	2	2.94	PO8	2	1.59	P9	2	0.34
P8	3	2.48	P9	3	1.42	P8	3	0.30
PO8	4	2.46	P8	4	1.37	PO8	4	0.27
P7	5	1.92	PO7	5	1.09	PO7	9	0.19
PO7	6	1.88	P7	6	0.96	P7	13	0.16

Table S5. Regions of interest (ROIs) for the general visual response. After summing baseline-corrected amplitudes across significant harmonics of the 12-Hz image presentation frequency (i.e., up to 48 Hz; i.e., 4th harmonic), the general visual response was considered averaged across odor contexts to estimate the region of interest for further analysis according to the channels with the largest amplitude among the 64 channels. For all categories, the exact same four highest channels were located over the middle occipital (mO) cortex, constituting a single ROI. See Figure S1 B for electrode location.

Faces			Cars			Facelikes		
Channel	**Rank**	**Amplitude**	**Channel**	**Rank**	**Amplitude**	**Channel**	**Rank**	**Amplitude**
Iz	1	1.93	Iz	1	2.00	Iz	1	1.90
Oz	2	1.83	Oz	2	1.90	Oz	2	1.81
O1	3	1.82	O1	3	1.87	O1	3	1.79
O2	4	1.71	O2	4	1.75	O2	4	1.67

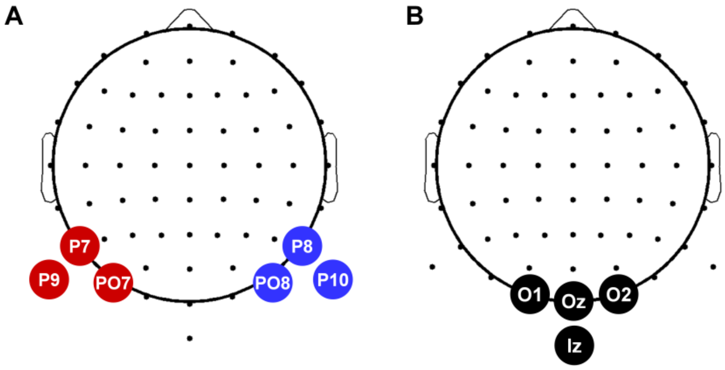


Figure S1. 2D head-maps showing the regions of interest (ROIs) for the category-selective response (A) and the general visual response (B). Each set of colored electrodes corresponds to one ROI. See Tables S4 and S5 for more details on (A) and (B), respectively.

Additional behavioral experiment

In a previous FPVS-EEG study (without any odor context) presenting 6-Hz stimulation sequences of nonface and facelike objects (every 6 stimuli; i.e., at 1 Hz), 48% (i.e., 13 out of 27) of the participants reported having noticed the presence of facelike objects after testing (Rekow et al., in prep.). In the present study, the proportion of aware participants dropped to 35% (i.e., 9 out of 26), but the stimulation rate was twice as fast (i.e., 12 Hz) with facelike objects at 1.33 Hz. Hence, we conducted a side behavioral experiment to estimate the expected proportion of aware participants when using 12-Hz sequences with facelike objects at 1.33 Hz and without any odor context. Twenty-six novel participants performed a cross-detection task while presented with 12-Hz sequences of nonface objects with facelike objects interspersed at 1.33 Hz (exact same stimuli as in the main EEG experiment). Twelve 27-second-long sequences were presented before the experimenter asked participants whether they had perceived facelike objects in the sequence. Only 15% (i.e., 4 out of 26) of the participants reported facelike objects (aware participants). Hence, compared to this theoretical proportion in the absence of contextual odors, the proportion of aware and unaware participants in the main EEG experiment is significantly higher ($\chi^2_1 = 7.39$, $p = .007$).

References

Lenochova, P., Roberts, S.C., Havlícek, J., 2008. Methods of Human Body Odor Sampling: The Effect of Freezing. *Chemical Senses* **34**, 127–138. doi: 10.1093/chemse/bjn067

Rekow, D., Baudouin, J., Brochard, R., Rossion, B., Leleu, A. Did you spot the face in the clouds? Conscious categorization of illusory faces (face pareidolia) in the human brain. *In preparation.*

Vieillard, S., Ronat, L., Baccarani, A., Schaal, B., Baudouin, J.-Y., Brochard, R., 2020. Age differences in olfactory affective responses: Evidence for a positivity effect and an emotional dedifferentiation. *Aging, Neuropsychology, Cognition*. doi: 10.1080/13825585.2020.1799926