



HAL
open science

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

Diane Rekow, Arnaud Leleu, Fanny Poncet, Fabrice Damon, Bruno Rossion, Karine Durand, Benoist Schaal, Jean Yves Baudouin

► To cite this version:

Diane Rekow, Arnaud Leleu, Fanny Poncet, Fabrice Damon, Bruno Rossion, et al.. 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*, 2020, 55, pp.100930. 10.1016/j.cogdev.2020.100930 . hal-02969609

HAL Id: hal-02969609

<https://hal.inrae.fr/hal-02969609>

Submitted on 22 Aug 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution-NonCommercial 4.0 International License

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

Diane Rekow^a, Arnaud Leleu^a, Fanny Poncet^a, Fabrice Damon^a, Bruno Rossion^{b,c}, Karine
Durand^a, Benoist Schaal^a & Jean-Yves Baudouin^d

Corresponding authors: DR (diane.rekow@u-bourgogne.fr) and JYB (j.baudouin@univ-lyon2.fr)

Corresponding address:

Centre des Sciences du Goût et de l'Alimentation
Laboratoire d'Éthologie Développementale et Psychologie Cognitive
9E Boulevard Jeanne d'Arc, 21000 Dijon, France

Authors affiliations

^a Laboratoire « Developmental Ethology and Cognitive Psychology », Centre des Sciences du Goût et de l'Alimentation, AgroSup Dijon, CNRS, Inrae, Université Bourgogne Franche-Comté, F-21000 Dijon, France [DR (diane.rekow@u-bourgogne.fr); AL (arnaud.leleu@u-bourgogne.fr); FP (fanny.poncet@u-bourgogne.fr); FD (fabrice.damon@u-bourgogne.fr); KD (karine.durand@u-bourgogne.fr); BS (benoist.schaal@u-bourgogne.fr)]

^b Université de Lorraine, CNRS, CRAN - UMR 7039, F-54000 Nancy, France

^c Université de Lorraine, CHRU-Nancy, Service de Neurologie, F-54000 Nancy, France [BR (bruno.rossion@univ-lorraine.fr)]

^d 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), 5, avenue Pierre-Mendès-France, 69676 Bron cedex, France [JYB (j.baudouin@univ-lyon2.fr)]

Declaration of interest: The authors declare no competing interest.

CRedit roles

Diane Rekow: Data curation, Investigation, Formal analysis, Methodology, Visualization, Writing - original draft, Writing - review & editing. **Arnaud Leleu:** Methodology, Formal analysis, Supervision, Writing - review & editing. **Fanny Poncet:** Investigation. **Fabrice Damon:** Investigation, Writing - review & editing. **Bruno Rossion:** Resources, Writing - review & editing. **Karine Durand:** Conceptualization, Writing - review & editing. **Benoist Schaal:** Conceptualization, Writing - review & editing. **Jean-Yves Baudouin:** Conceptualization, Funding acquisition, Project administration, Writing - review & editing

1 Introduction

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

17 Categorization [ability of infants has](#) also been investigated [with](#) event-related
18 potentials (ERPs) and tasks derived from familiarization/novelty preference paradigms. In 4-
19 to 7-month-olds, a larger negative component over central [brain](#) regions is observed for
20 novel exemplar(s) when contrasting living object categories (Marinović et al., 2014; Quinn et
21 al., 2006) or living vs. non-living object categories (Elsner et al., 2013; Grossmann et al.,
22 2009), suggesting sustained attention to novelty (Reynolds & Richards, 2005). When
23 comparing ERPs between familiarization and test phases, the brain response to the first
24 learned exemplars is equivalent in amplitude to the response to the novel category
25 exemplars at test, while the response to the last learned exemplars is not different from the
26 response to the familiar category at test, providing a neural signature of online category
27 learning (Quinn et al., 2006). The N290 and P400 medial occipital ERP components in
28 response to faces have also been largely investigated in 3- to 12-month-old infants (Halit et
29 al., 2003; Hoehl, 2016, for reviews; [Conte et al., 2020, for more recent evidence](#)) and related
30 to the early visual expertise developed for same- over other-species faces (de Haan et al.,

1 2002; Halit et al., 2003), female over male faces (Peykarjou et al., 2016), or more generally
2 for faces over nonface objects (e.g., toys or houses; Conte et al., 2020).

3 Recently, a fast periodic visual stimulation approach in scalp electroencephalography
4 (FPVS-EEG) was introduced to measure rapid categorization in infants (de Heering & Rossion,
5 2015; Leleu et al., 2020; Peykarjou et al., 2017; see also Barry-Anwar et al., 2018). By
6 presenting visual stimuli from various categories at a rapid base rate (e.g., 6 Hz) and
7 inserting stimuli from a target category at a lower rate (e.g., 1 Hz; i.e., every 6 stimuli), a
8 direct *differential* response (i.e., without post-hoc subtraction) to the target category is
9 objectively measured at the predicted frequency (e.g., 1 Hz) in the EEG spectrum if the infant
10 brain discriminates this category from the other(s) for the different category exemplars (i.e.,
11 generalizes). Most significantly, contrasting faces with several living and non-living
12 categories using a large set of natural images unsegmented from their background, a neural
13 face categorization response can be isolated over the right occipito-temporal cortex of 4- to
14 6-month-old infants (de Heering & Rossion, 2015). Importantly, this response is not
15 accounted for by the low-level visual properties contained in the amplitude spectrum of the
16 images (de Heering & Rossion, 2015).

17 To clarify the developmental origin of this neural face categorization response, Leleu
18 et al., 2020 recently showed that it is substantially enhanced in 4-month-olds by the
19 concomitant presentation of the mother's body odor compared with a control stimulus.
20 These results are in line with previous evidence that odor exposure leads to increased
21 orientation toward congruent visual information at 3 and 4 months (Durand et al., 2013;
22 Godard et al., 2016), suggesting that initial categorization of visual stimuli as faces is shaped
23 by multisensory inputs. More generally, although visual categorization has been mainly
24 investigated from a unisensory perspective, such observations support the view that
25 multisensory inputs promote the development of visual categories (Bremner et al., 2012;
26 Lewkowicz, 2010). After birth, the visual system must apprehend a myriad of rapidly
27 changing novel inputs across variable exposure conditions (e.g. movement, lighting,
28 viewpoint). In this context, olfaction has a specific status from the earliest steps of
29 development which confers the ability to mediate visual perception. The olfactory system is
30 already able to process and encode mother-induced variations of the amniotic environment,
31 shaping long-term memories which can function as familiarity references for the newborn
32 (e.g., Schaal et al., 2000). This transnatal conservation of familiar odor cues do then co-occur

1 with the reception of the first visual events and eventually engage early multisensory
2 integration (Schaal & Durand, 2012, for review). In addition, odor perception is less sensitive
3 to spatial and temporal variations than visual perception (Sela & Sobel, 2010). This property
4 places olfaction in an ideal position to promote the acquisition of visual categories by
5 reducing the sensory noise induced by physical variability and thus adding reliability across
6 visual inputs from a single category. Prior experience of the association between a
7 (maternal) body odor and a face could thus trigger a consistent discrimination response
8 between faces and other categories (i.e., face categorization), leading to greater attention to
9 [the former](#) (Durand et al., 2013).

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

26

27 **Materials and methods**

28 **Participants**

29 Twenty-one full-term and healthy 4-month-olds participated in the study. Parents were
30 recruited through the local birth registry. They were fully [informed about](#) the purpose and
31 methods of the study before agreeing to participate. [They were then](#) sent the material for
32 maternal body odor collecting at home (see details below). Written and informed consent

1 was obtained for all infants, and no parents reported their infant having any visual, olfactory
2 or neurological disorder. The study was conducted in accordance with the Declaration of
3 Helsinki for human experimentation and approved by the French ethics committee (CPP Sud-
4 Est III - 2016-A02056-45). Three infants were discarded from the final sample due to less
5 than two sequences per condition (n=2) retained after preprocessing the data (see *EEG*
6 *recording and preprocessing* section for more details) and atypical data compared to the
7 group (n=1; mean corrected amplitude across odor conditions over O2 (8.95 μ V) above 2 SDs
8 of the group's mean amplitude (1.38 μ V, SD = 2.62 μ V)). The final sample was thus
9 composed of 18 infants (9 females, mean age \pm SD: 131 \pm 5 days, range: 124–140 days).
10 Since no previous study explored whether maternal odor has a modulatory effect on the
11 neural categorization of a nonface object, we estimated sample size by considering that (1)
12 maternal odor elicits a strong effect on neural face categorization (Cohen's d = +1.20 over
13 channel O2) with N = 18 infants, leading to maximal power $1-\beta = 1$ (Leleu et al., 2020); (2)
14 even if the odor effect on car categorization would be twice lower (i.e., Cohen's d = +0.60),
15 estimated sample size would remain close (N = 17) by considering a significance level $\alpha = .05$
16 (one-tailed, maternal > control) and the usual power $1-\beta = .80$. We therefore made sample
17 sizes equal in the two studies.

18 **Visual stimuli**

19 Natural images (i.e., unsegmented from the original background) of various objects (man-
20 made objects including non-car vehicles, plants and animals; N=170, same stimulus set as in
21 Leleu et al., 2020) and cars (variable models; N=66) were used (Figure 1A). Pictures of cars
22 were used as the single object category, for several reasons: cars have a canonical
23 orientation, they form a visually homogenous category, and they have multiple parts, just
24 like faces (“internal”: lights, radiator grill, window, bumper; “external”: mirrors, wheels,
25 etc.). Also, pictures of cars have been used as control stimuli to faces in numerous
26 neuroimaging (e.g., Gauthier et al., 2000; Grill-Spector et al., 2004; Rossion et al., 2012) or
27 electrophysiological studies (e.g., Rossion & Caharel, 2011; Rossion & Curran, 2010) with
28 adults. Finally, pictures of cars were contrasted with those of faces in the first behavioral
29 study showing that infants look longer at a face in the presence of maternal odor (Durand et
30 al., 2013). Here, all the images varied substantially in terms of color, viewpoint and lighting
31 condition, and each depicted only one object. Each image was cropped to a square then

1 resized to 400×400 pixels. In addition to their variable shapes, the objects were off-
2 centered to increase their eccentricity so that no object can be identified from the mean
3 image (Figure S1). Stimuli were presented at the center of a computer screen placed 57 cm
4 in front of the infant's face. They subtended roughly a $24 \times 24^\circ$ of visual angle, representing
5 a large part of the infant's visual field.

6 **Odor stimuli**

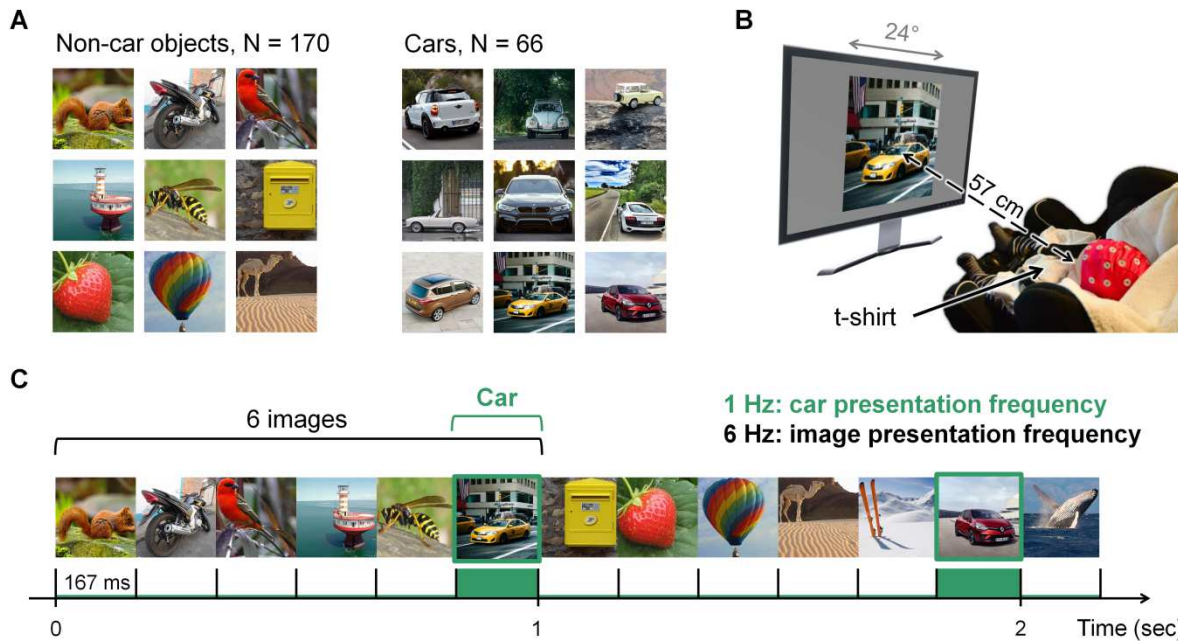
7 Following previous studies (Durand et al., 2013; Leleu et al., 2020), the maternal and control
8 odors were delivered from worn and unworn white t-shirts (100% cotton), respectively. Both
9 t-shirts were first laundered using a scentless hypoallergenic powder detergent (Persavon,
10 France). For the collection of the maternal odor, a prewashed t-shirt enclosed in a hermetic
11 zip-lock plastic bag was sent to the mothers one week before the testing day. The t-shirt was
12 worn the three consecutive nights before testing. A written procedure detailing the
13 standardized night-wear instructions (to minimize activity-related individual differences, see
14 Durand et al., 2013) was provided to the mothers. Notably, they were asked to refrain from
15 using odorous soap or perfume before wearing the t-shirt. During the days of the collection
16 period, the t-shirt was stored in the hermetic bag at room temperature but carefully left
17 away from any heating device. The control odor condition consisted of an identical t-shirt,
18 unworn and following equivalent storage procedure.

19 **Procedure**

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

29 Each stimulation sequence was composed of 5 non-car images alternating with an image of a
30 car placed as 6th stimulus, i.e., introduced at the rate of $6/6 = 1$ Hz. All images were randomly

1 picked from their respective sets (objects vs. cars) without repetition within a sequence. This
 2 frequency-tagging approach is used to directly quantify and isolate the general visual
 3 response (6 Hz and harmonics; i.e., integer multiples) and a car categorization response (1 Hz
 4 and harmonics). Moreover, thanks to periodicity, the brain response recorded at 1 Hz is a
 5 direct marker of the categorization of car exemplars, reflecting their discrimination from the
 6 other objects and their generalization into a single category despite their variability.



7
 8 **Figure 1. An EEG frequency-tagging approach to measure car categorization in odor contexts.** **A.**
 9 Example of the stimuli used in the experiment and depicting various non-car objects and cars. **B.**
 10 During the experiment, infants were installed in a seat placed at 57 cm from a computer screen and
 11 odorous t-shirts (control vs. maternal) were placed on their chest while stimuli appeared rapidly on
 12 the screen covering roughly $24 \times 24^\circ$ of visual angle. **C.** Excerpt of 2 sec of fast periodic stimulation
 13 (from 32-sec-long sequences) showing 6 images/sec (i.e., 6-Hz base rate) and interspersing images of
 14 cars every 6th stimulus (i.e., 1-Hz car-selective rate). Each stimulus lasts 167 ms on screen (i.e., one
 15 fixation). This design implies that two dissociable responses are tagged in the EEG frequency
 16 spectrum: a general visual response (6 Hz and harmonics) reflecting the common processing of all
 17 stimuli and a car categorization response (1 Hz and harmonics) triggered by the discrimination of cars
 18 from other objects and the generalization of this selective response across variable exemplars.

19 [The procedure was identical to Leleu et al. \(2020\).](#) After a size-adjusted electrode cap was
 20 placed on the infant's head, infants were seated in a car seat positioned at a 57 cm distance
 21 from the computer screen, in a light- and sound-attenuated room. The room was aired
 22 between testing sessions and equipped with an air-extractor placed approximately 2 m
 23 above the seat which continuously renewed the air with a silent and undetectable air flow.

1 To reduce the olfactory noise, the experimenters did not ingest, inhale or use any odorous
2 product before testing. Experimenters were not blind to the odor context presented to the
3 infant. During stimulation sequences, the infant was tested alone, behind occluding
4 (scentless) blinds in order to minimize distraction. A camera placed on top of the screen
5 monitored the infant continuously. In addition, parents were asked to stay at a relative
6 distance (at least 2.5 m) of their infant and not to interact with them during testing, except
7 in case of manifest distress.

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

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

1 ± 3.4 sequences), for an overall testing duration ranging from 2 min 18 sec to 9 min 12 sec
2 per infant.

3 **EEG recording and preprocessing**

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

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

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

1 two extreme (i.e., minimum and maximum) bins) divided by the standard deviation of the
2 noise. Sequences were **included** if at least two Z-scores were greater than 1.64 ($p < .05$, one
3 tailed, signal > noise) or at least one Z-score greater than 2.32 ($p < .01$, one-tailed) over the
4 usually responding middle occipital electrodes (Oz, POz, O1, O2; de Heering & Rossion, 2015;
5 Leleu et al., 2020; Peykarjou et al., 2017). **One-tailed testing was used to determine the**
6 **significance of the neural response because the frequency spectrum is expressed in absolute**
7 **amplitudes, leading to the *a priori* hypothesis of signal > noise (Rossion et al., in press). Thus,**
8 **a significant neural response means a larger response than surrounding noise, and a**
9 **negative Z-score is considered non-significant.** Nine epochs were excluded in a total of 5
10 infants. The second criterion was used to further removed epochs with atypical scalp-wide
11 power calculated on the 1-Hz response. Channels were pooled together based on FFT
12 amplitude spectra and amplitude at the 1 Hz frequency was corrected by subtracting the
13 mean noise (baseline-corrected amplitude, BCA), estimated here from the 6 surrounding
14 bins (due to high EEG power in the low-frequency range and non-linear decrease as
15 frequency increases (Fransson et al., 2013), noise is steeper for lower than for higher
16 frequency bins around 1 Hz; considering too many bins would overestimate noise level).
17 Atypical sequences were defined by noise-corrected amplitude at 1 Hz greater or lower than
18 2 SDs of the mean of all sequences (calculated individually) remaining after application of
19 the first criterion, rejecting 5 epochs in a total of 5 infants. Once these two criteria were
20 applied, the final number of sequences was 4 to 15 per infant (mean \pm SD: 9.2 ± 3.2), with an
21 overall rejection of 14 epochs out of 180. The resulting number of sequences was 84
22 sequences for the control odor condition (mean \pm SD: 4.7 ± 1.7) vs. 82 for the maternal odor
23 condition (4.6 ± 1.8).

24 **Frequency-domain analysis**

25 For each infant, remaining 32-sec segments were sorted per condition and averaged in the
26 time domain to reduce cerebral activity non phase-locked to the stimuli. FFT was applied and
27 amplitude spectra were extracted for all electrodes. In a first step, we estimated the
28 significance of the brain responses and defined the range of significant harmonics (i.e.,
29 integer multiples) to consider for further analysis regardless of the condition. FFT data were
30 averaged across conditions and for each frequency bin and each channel, and amplitude was
31 normalized (i.e., by dividing by the square root of the sum of squared amplitudes of all

1 channels; McCarthy & Wood, 1985). Normalization was used to scale differences between
2 electrodes on the global magnitude of the response across the scalp to identify the
3 electrodes over which the response is the largest and reduce the high amplitude variance in
4 the low-frequency band that may mask significant responses. Individual datasets were then
5 grand-averaged and Z-scores calculated for each electrode. As the first study investigating
6 the categorization brain response to a nonface category in infants, posterior channels (N =
7 13, Figure S2) were explored for both the general (6 Hz and harmonics) and the
8 categorization (1 Hz and harmonics) responses, using a threshold of $Z > 2.32$ ($p < .01$, one-
9 tailed, signal > noise). Harmonics were included until Z-scores over one channel were no
10 longer significant. Then, individual normalized amplitudes for each response were summed
11 across harmonics. Final Z-scores were calculated on these summed amplitudes for individual
12 and grand-averaged datasets, estimating the significance of the overall responses for
13 individual infants and the group. Baseline-corrected amplitudes (BCA) were also calculated
14 on non-normalized dataset for each individual infant and each condition, and then summed
15 across significant harmonics to quantify each response in a single value expressed in
16 microvolts. Individual BCAs were averaged across odor conditions and then grand-averaged
17 to illustrate group-level brain responses.

18 In a second step, the difference between the two odor conditions was analyzed. We first
19 determined significant electrodes for each condition separately to identify any electrode
20 that would be significant in only one odor condition. For each brain response, individual
21 datasets were normalized on the global power previously calculated, harmonics were
22 summed, and Z-scores were computed on grand-averaged data. A standard threshold ($Z >$
23 1.64 , $p < .05$, one-tailed, signal > noise) was applied to channels identified at the previous
24 step whereas the significance of other posterior channels was assessed with the more
25 conservative threshold ($Z > 2.32$, $p < .01$, one-tailed). The direct comparison between the
26 two odor conditions was then performed on individual BCA for each significant channel using
27 T-tests (two-tailed) and individual data were grand averaged for illustration purpose. To
28 quantify evidence in support of the null hypothesis for non-significant effects, Bayes factors
29 (BF_{10}) were calculated using JASP (<https://jasp-stats.org/>) and a standard zero-centered
30 Cauchy prior with effect size scaled at $1/\sqrt{2}$ (Gronau et al., 2020).

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

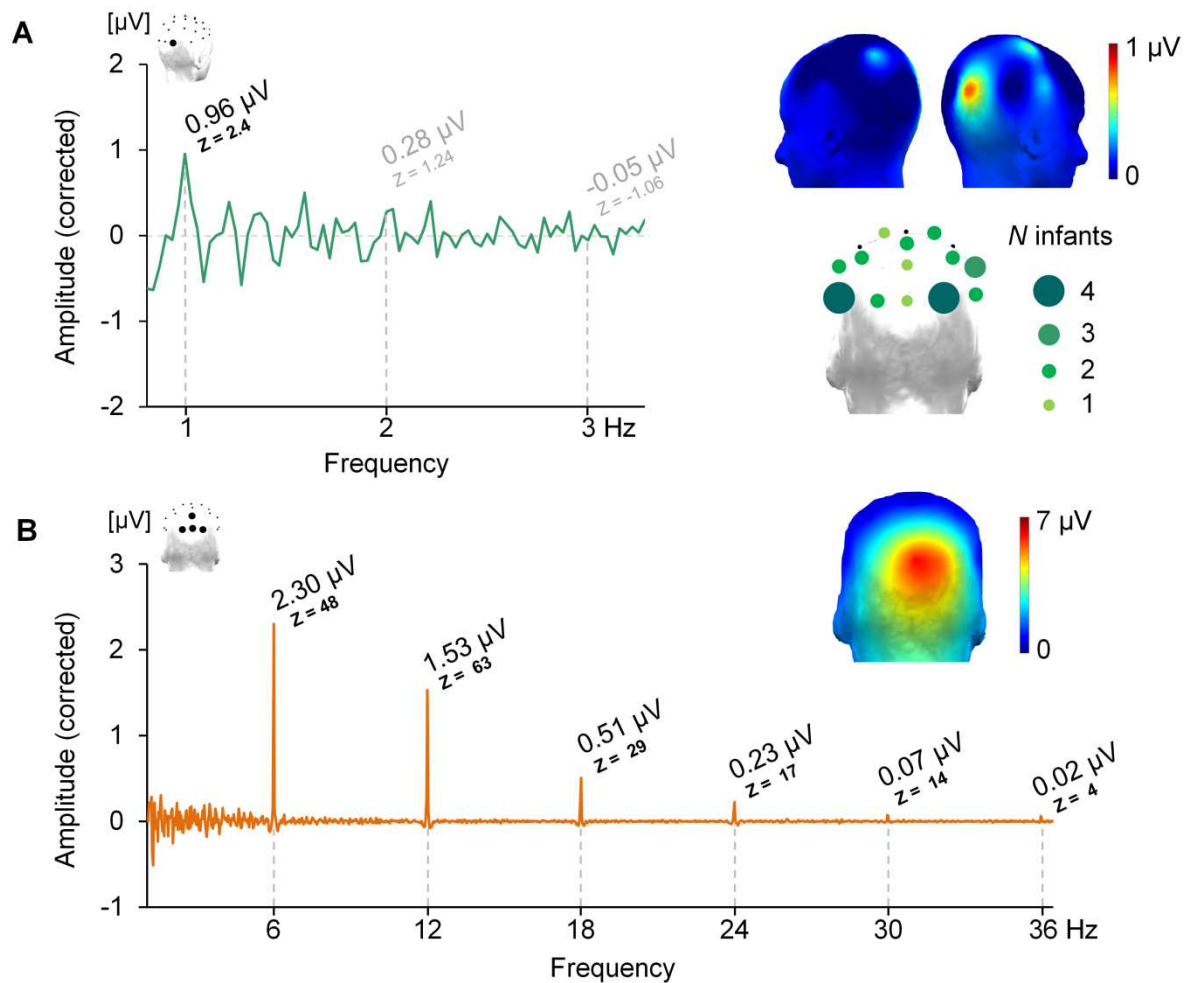
19 Results

20 Car categorization and general visual responses in the 4-month-old infant brain

21 For both odor conditions combined, a brain response was found at the predefined 1-Hz rate
22 of car pictures presentation (Figure 2A). Exploring posterior channels (see Methods), we
23 found only one significant electrode reaching the threshold of $Z > 2.32$ ($p < .01$, one-tailed,
24 signal > noise): O2 ($Z = 2.44$, $p = .007$). No other electrode reached significance. Over O2, the
25 car categorization response was found only on the 1st harmonic ($Z = 1.24$ and $Z = -1.06$ for
26 the second (i.e., 2 Hz) and third (i.e., 3 Hz) harmonics, respectively), with a magnitude of 0.96
27 ± 0.46 (SEM) μ V (Figure 2A). This categorization response is robust, since it is not induced by
28 a small subset of infants (T-test against 0: $T(17) = 2.45$; $p = .025$, one-tailed, signal > noise).
29 Four infants presented a significant response over O2 ($Z > 1.64$, $p < .05$, one tailed), five
30 others over one immediate neighboring electrode (Oz, POz, P4 or P8), six more over at least

1 one other posterior electrode, and the last 3 infants showed a significant 1-Hz response
2 elsewhere over the scalp (Figure 2A and Table S1).

3 A general brain response to the rapid stream of visual stimuli was recorded at 6 Hz and
4 harmonics (i.e., 12 Hz, 18 Hz, etc.) over the middle occipital cortex (Figure 2B). This response
5 represents a mixture of low- (e.g. color) and higher-level (e.g. object identification)
6 processes elicited by all visual stimuli. Across odor conditions, Z-scores highlighted a
7 significant response ($Z > 2.32$, $p < .01$, one-tailed, signal $>$ noise) over POz ($Z = 4.95$, $p < .001$),
8 O1 ($Z = 6.15$, $p < .001$), Oz ($Z = 13.09$, $p < .001$) and O2 ($Z = 10.96$, $p < .001$) at 6 Hz. Following
9 harmonics were significant until the 5th harmonic (i.e., 30 Hz) over POz ($Z = 3.85$, $p < .001$)
10 and O1 ($Z = 4.99$, $p < .001$) and until the 6th harmonic (i.e., 36 Hz) over Oz ($Z = 4.52$, $p < .001$)
11 and O2 ($Z = 4.41$, $p < .001$). The general visual response was thus collapsed across 6
12 harmonics. Z-scores for this overall response were significant for all four electrodes (from $Z =$
13 6.95 , $p < .001$ for POz to $Z = 12.09$, $p < .001$ for Oz) with amplitudes ranging from 2.80 ± 0.72
14 μV over POz, to $6.23 \pm 0.83 \mu\text{V}$ over Oz ($4.66 \pm 0.65 \mu\text{V}$ pooled across the four channels). No
15 other posterior electrodes reached significance. The general visual response is significant in
16 every infant for Oz and O2, in 13 infants for O1, and in 10 infants for POz ($Z > 1.64$, $p < .05$,
17 signal $>$ noise; Table S2 and Figure S3).



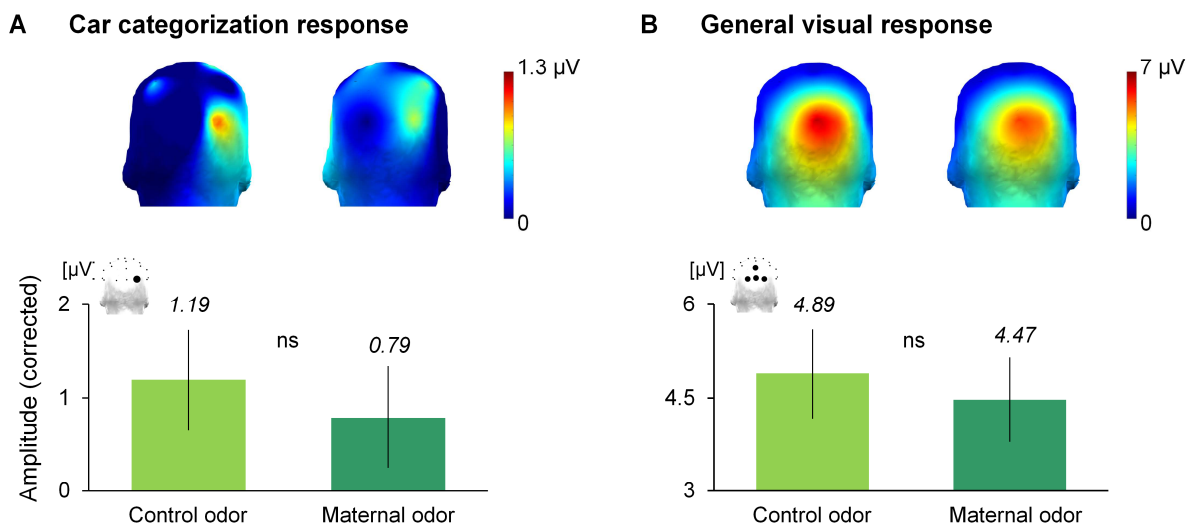
1
2 **Figure 2. (A) Car categorization response and (B) general visual response (N=18).** **A. (left)** Amplitude
3 (noise corrected) of the EEG spectrum recorded over the right occipital channel O2 across odor
4 conditions. Numerical values indicate the amplitude of the response with corresponding Z-scores.
5 Only the 1st harmonic is significant (black, $Z > 2.32$, $p < .01$ one tailed, non-significant peaks are
6 indicated in grey). **(top-right)** 3-D topographical head maps of the car categorization response at 1 Hz
7 over left and right hemispheres. The response is clearly visible over channel O2. **(bottom-right)** Head
8 map (back view) showing the density of significant individual Z-scores ($Z > 1.64$, $p < .05$, signal >
9 noise) over all 13 posterior channels. Circle size and color illustrate the number of infants with a
10 significant response on the corresponding channel. **B.** Amplitude (noise corrected) of the EEG
11 spectrum recorded over the middle occipital region (O1, Oz, O2 and POz) across odor conditions
12 along with 3-D topographical head maps (back view) of the general visual response summed across
13 significant ($Z > 2.32$, $p < .01$, one tailed) harmonics (i.e., 6 Hz and integer multiples). Numerical values
14 indicate the amplitude of the response with corresponding Z-scores.

15 **No effect of maternal odor on both car categorization and general visual responses**

16 When comparing between the two odor conditions, the car categorization response
17 remained clearly visible over the right posterior occipital channel O2 (Figure 3A), with a
18 significant response in both odor contexts (control odor: $Z = 2.02$, $p = .022$; maternal odor: Z

1 = 1.70, $p = .045$). Again, no other posterior channels showed a significant Z-score in any odor
 2 condition. On this particular site, the maternal odor had no effect [maternal – control] on
 3 the categorization response to cars. The amplitude of the response recorded over O2 in the
 4 control odor condition ($1.19 \pm 0.54 \mu\text{V}$) is barely diminished in the maternal odor context
 5 ($0.79 \pm 0.54 \mu\text{V}$), corresponding to a non-significant decrease of $-0.40 \pm 0.63 \mu\text{V}$ ($T(17) = -$
 6 0.63 , $p = .54$) in support of a null result ($\text{BF}_{10} = 0.28$).

7 As for the car categorization response, the general visual response is observed in
 8 both odor conditions (Z-scores ranging from 4.18 to 11.60, $p_s < .001$). A faint but non-
 9 significant decrease in amplitude was found in the maternal odor context (maternal –
 10 control: $-0.41 \pm 0.47 \mu\text{V}$; $T(17) = -0.88$, $p = .40$), probing evidence in favor of the null
 11 hypothesis ($\text{BF}_{10} = 0.29$). In sum, the 4-month-old brain is sensitive to the rapid stream of
 12 stimulation but this robust general visual response appears to be immune to the
 13 concomitant presentation of a maternal odor context (Figure 3B).



14 **Figure 3. Both brain responses are immune to maternal odor.** A. Amplitude (noise corrected) of the
 15 car categorization response over O2 in the control (left) and maternal (right) odor conditions,
 16 showing a slight non-significant decrease of amplitude in the maternal odor condition ($-0.40 \mu\text{V} \pm$
 17 $0.63 \mu\text{V}$, ns: $p = .54$). B. Amplitude (noise corrected) of the general visual response across 4 middle
 18 occipital channels (POz, O1, Oz, O2) in the control (left) and maternal (right) odor conditions,
 19 showing a small non-significant decrease of amplitude in the maternal odor condition (-0.41 ± 0.47
 20 μV , ns: $p = .40$). 3-D topographical head maps (back views) show the spatial distribution of each
 21 response. Error bars represent standard errors of the mean.

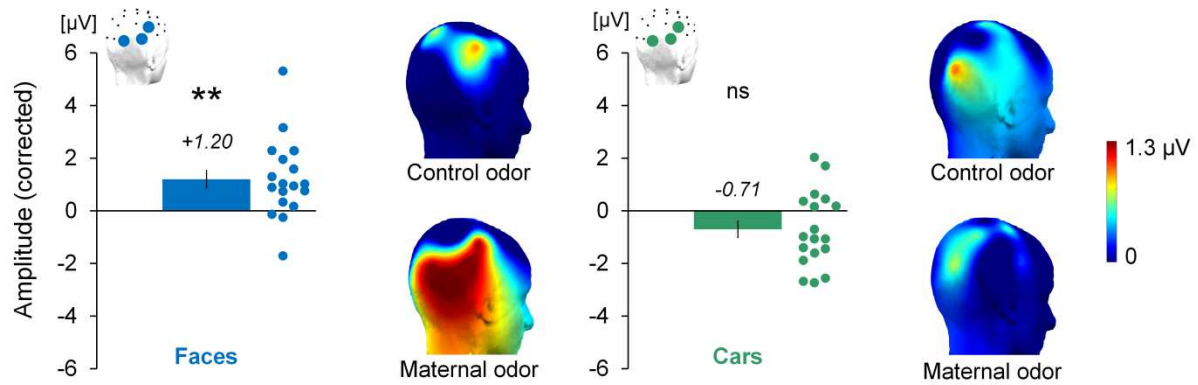
23

1 **Maternal odor effect on the visual categorization of cars and faces**

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

9 For the categorization response at 1 Hz, we considered two lateral regions-of-interest (ROIs)
10 as defined in Leleu and collaborators' (2020) study: right (rOT, pooling channels CP6, P8 and
11 O2) and left (lOT, pooling CP5, P7 and O1) occipito-temporal ROIs, and observed a main
12 effect of *Hemisphere* ($F(1, 34) = 12.54, p = .001, \eta_p^2 = .27$) with a greater amplitude over rOT
13 ($0.65 \pm 0.17 \mu\text{V}$) than lOT ($-0.0043 \pm 0.20 \mu\text{V}$). More importantly, the *Odor* \times *Hemisphere* \times
14 *Category* interaction reached significance ($F(1, 34) = 7.06, p = .012, \eta_p^2 = .17$). A significant
15 *Odor* \times *Category* interaction was found over rOT ($F(1, 34) = 15.27, p = .0004, \eta_p^2 = .31$) but
16 not over lOT ($F < 1$). While the face categorization response is increased by $+1.20 \pm 0.36 \mu\text{V}$
17 ($p = .007$) in the maternal ($1.52 \pm 0.31 \mu\text{V}$) vs. control ($0.32 \pm 0.29 \mu\text{V}$) odor context, the car
18 categorization response is not significantly changed ($p = .19$) despite a decrease of $-0.71 \pm$
19 $0.33 \mu\text{V}$ (control odor: $0.74 \pm 0.32 \mu\text{V}$; maternal odor: $0.03 \pm 0.23 \mu\text{V}$) over the infant right
20 occipito-temporal cortex (Figure 4). **When considering O2, the only channel with a significant**
21 **categorization response to cars, the conclusion remains similar with a significant *Odor* \times**
22 ***Category* interaction ($F(1, 34) = 11.7, p = .002, \eta_p^2 = 0.26$) explained by an odor effect for**
23 **faces ($+2.25 \pm 0.45 \mu\text{V}, p = .001$) but not for cars ($-0.40 \pm 0.63 \mu\text{V}, p = .89$). In contrast, no**
24 **significant main effects or interactions were found for the general visual response (all $F_s <$**
25 **1.76, all $p_s > 0.19$).**

26



1
 2 **Figure 4. Maternal odor effect [maternal – control] for the categorization responses to faces (blue)**
 3 **and cars (green).** Maternal odor significantly enhances the response to faces (left, **: $p = .007$, $N =$
 4 18) and does not significantly diminish the response to cars (right, ns: $p = .19$, $N = 18$) over the right
 5 occipito-temporal region (channels CP6, P8 and O2). Individual amplitudes are plotted. 3-D
 6 topographical head maps show the spatial distribution of the responses (right lateral view). Error
 7 bars represent standard errors of the mean.

8 Discussion

9 By isolating a response over the right occipital cortex at the 1-Hz frequency of car
 10 pictures presentation, the present study demonstrates the 4-month-old infant brain's ability
 11 to rapidly assign a series of highly variable exemplars of cars to a single category, as
 12 previously observed for faces with the same FPVS-EEG approach (de Heering & Rossion,
 13 2015; Leleu et al., 2020). However, contrary to the face categorization response identified in
 14 Leleu and collaborators' study (2020), which was strongly enhanced in the maternal odor
 15 context, no modulation of the neural categorization response to cars was found in the
 16 context of maternal odor. The general visual response to the fast train of visual stimuli is also
 17 immune to the presence of maternal odor, reflecting a similar level of visual attention or
 18 arousal in both odor contexts (Leleu et al., 2020).

19 The first major result of the present study is the recording of a neural categorization
 20 response to variable car images over the right occipital cortex. This extends the visual
 21 categorization response with natural images and fast periodic visual stimulation in EEG to a
 22 novel category, following studies in adults with faces but also houses and body parts
 23 (Jacques et al., 2016). In infants, this finding indicates that rapid categorization of numerous
 24 exemplars is not limited to faces (de Heering & Rossion, 2015; Leleu et al., 2020) but extends
 25 to a non-social object that is less familiar than faces in the infant everyday visual
 26 environment at 4 months. Infant behavioral studies have already shown categorization

1 abilities for more or less familiar objects using familiarization/novelty preference paradigms
2 in which two simultaneously presented segmented stimuli must be discriminated (see Oakes
3 et al., 2009; Quinn, 2011, for reviews). Here, our data reveal an ability to discriminate
4 natural views of cars from many other living and non-living categories and to generalize this
5 discrimination across numerous car exemplars. This is not a trivial achievement for the infant
6 visual system since the car exemplars must be categorized at a glance (i.e., 167 ms per
7 stimulus) from forward- and backward-masked natural images implying figure-ground
8 segregation. Despite these high constraints, the car categorization response is **reliable**, as it
9 is found over posterior scalp regions for a majority of infants. **In addition, a complementary
10 analysis revealed that the response tends to increase during the course of the experiment
11 (Supplementary Information and Figure S4), suggesting that despite a large set of stimuli and
12 a fast presentation mode, 4-month-olds rapidly acquire an unfamiliar category from
13 relatively short exposure (i.e., online category learning; e.g., Eimas & Quinn, 1994; Quinn et
14 al., 2006). Overall, by providing a valid measure of visual categorization including both
15 discrimination and generalization processes thanks to a fair amount of naturalistic stimuli
16 presented in a few minutes, FPVS-EEG brings interesting perspectives for the study of
17 category formation in infancy (see Rakison & Yermolayeva, 2010, for a discussion), where
18 the constraint of short infants' attentional span usually restricts the use of numerous stimuli
19 in a single group of infants.**

20 Interestingly, this response is, overall, **not different in amplitude** than the response to
21 faces presented in the same context, **but is however** restricted to a single lateral occipital
22 channel (compared to a face response extending more anteriorly to the temporal cortex).
23 This suggests that car categorization is less robust than face categorization at this age and, as
24 in adults for categorization responses to houses and body parts, is generated by different
25 brain regions (Jacques et al., 2016). Note that it could be argued that cars are relatively
26 homogeneous visual exemplars that could be categorized solely from systematic differences
27 in basic structural properties (e.g., elongated shapes) or low-level cues (e.g., uniformity of
28 color). For instance, the car and its typical background (frequently showing a road) could
29 lead to a higher proportion of obvious convergence lines than other objects. Nonetheless,
30 the high variability of models, viewpoints and relative positions of the car in each image, as
31 well as the use of control objects that share some basic properties with cars (e.g., bikes,

1 trolley and motorcycles also have wheels and a distinctive metallic texture) reduces the
2 potential contribution of these physical cues, especially with such a fast presentation mode
3 that only allows one fixation per stimulus.

4 The second main observation is that contrary to the face categorization response
5 isolated in Leleu and collaborators' study (2020), the car categorization response is not at all
6 enhanced by the maternal body odor, **neither when considering the single responding**
7 **electrode O2, nor the broader right occipito-temporal region where the face categorization**
8 **response is measured**. This reveals that maternal odor does not merely facilitate the
9 detection of any regular (i.e., periodic) visual category, but selectively improves the
10 categorization of faces, according to the view that early perceptual development takes
11 advantage of intersensory congruency across simultaneous inputs from different sensory
12 modalities (Bahrick & Lickliter, 2000). Hence, we suggest that maternal odor acts as a prime
13 to socially relevant inputs by pre-selecting dedicated neural substrates in the ventral visual
14 pathway. This would lead to a larger or broader activation of face-selective cortical regions
15 when a face appears in the visual environment. This interpretation is supported by findings
16 from adult studies. Even in the absence of faces, body odors activate face-selective neural
17 responses in the human lateral fusiform gyrus (Prehn-Kristensen et al., 2009; Zheng et al.,
18 2018; Zhou & Chen, 2008). Since multisensory integration is considered as a key aspect of
19 (social-)cognitive development (e.g., Bremner et al., 2012; Schaal & Durand, 2012 for
20 review), and that mounting evidence orients toward multimodal building of knowledge in
21 the brain (von Kriegstein et al., 2005; Lewkowicz & Ghazanfar, 2009; Mattioni et al., 2020;
22 see Ghazanfar & Schroeder, 2006), the categorization of social information could develop
23 from multisensory experience with conspecifics. In this perspective, repeated exposure to
24 co-occurring social inputs from the different senses could progressively strengthen the
25 connectivity between underlying cortical areas through reentrant signaling (Edelman, 1993),
26 so that a body odor would become rapidly able to mediate face-selective activity in the
27 developing visual system.

28 **One may wonder whether the selective effect of maternal odor on face**
29 **categorization relies on a general matching mechanism between congruent multisensory**
30 **information, or whether it is specific to social information. In our view, both interpretations**
31 **are not mutually exclusive. In adults, a large body of research indeed indicates that**

1 olfactory-visual congruency applies to nonsocial categories (Lundström et al., 2019;
2 Seigneuric et al., 2010; Zhou et al., 2010). However, social objects are arguably the most
3 familiar objects for young infants, with prominent exposure to faces in the first year of life,
4 followed by gradual experience with other body parts, especially hands, in the second year
5 (Fausey et al., 2016). This may lead to progressive changes in congruency effects between
6 social odors and visual categories that could be further addressed throughout development.
7 Besides, although future studies could also evaluate to which extent the observed effect of
8 odors applies to more familiar nonsocial objects (e.g., toys) to exclude any mere contribution
9 of familiarity, it can be argued that familiar objects are necessarily associated with social
10 situations in infancy and can thus acquire a “social meaning”. Given that these familiar
11 objects are also a nest of socially-relevant familiar odors (Ferdenzi et al., 2008), it would be
12 interesting to investigate maternal odor’s influence on their categorization to evaluate such
13 a socially-/familiarity-related account of olfactory-visual integration in young infants.
14 Admittedly, since the comparison of data obtained for the neural categorization of cars was
15 conducted with previously published data for the categorization of faces, it is noteworthy
16 that these observations should be reinforced and replicated in a novel, and certainly larger,
17 sample to provide more stringent evidence for the selective influence of maternal odor on
18 face categorization. This could be done, for instance, by comparing faces with another social
19 category, in order to test the social origin of the odor effect on visual categorization.

20 Regardless of the inherent neural mechanisms subtending this specific modulatory effect,
21 our results are in line with studies showing that maternal odor mediates infants’ visual
22 behavior toward faces (Durand et al., 2013, 2020), and neural responses to facial expressions
23 (Jessen, 2019). It is interesting to note that these studies did not all use the body odor of the
24 own mother but also of a stranger mother (Durand et al., 2020; Jessen, 2019). A maternal
25 odor, as a body odor, represents a mixture of several cues conveying a wealth of information
26 about the person (e.g., identity, sex, age) and her internal states (e.g., physiology, emotion,
27 health; de Groot et al., 2017, for review) and constitutes the most effective olfactory signal
28 for human neonates and infants (Schaal et al., 2002). Hence, the own mother’s body odor
29 was used in the present study because it is arguably the most powerful chemosignal that is
30 reliably associated with an infant’s social context. However, future studies should determine
31 whether any mother’s (and even human) body odor is able to enhance the visual

1 categorization of human faces, and how long this association is maintained across
2 development. In particular, for that latter point, the facilitating effect of maternal odor may
3 progressively fade as the sole visual system becomes able to readily categorize faces (see
4 e.g., Lochy et al., 2019 for a discussion of the development of the face categorization
5 response through childhood and adulthood). In that case, it would be relevant to evaluate
6 whether the odor effect re-emerges in children or adults when the visual input is less
7 identifiable (e.g., blurry, or presented for very brief durations), leading to reduced face
8 categorization responses (e.g., Quek et al., 2018; Retter et al., 2020).

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

22 **Acknowledgments**

23 This work was supported by the French “Investissements d’Avenir” program, project ISITE-
24 BFC (contract ANR-15-IDEX-0003), the “Conseil Régional Bourgogne Franche-Comté”, the
25 FEDER (European Funding for Regional Economic Development), and a PhD scholarship from
26 the French MESR to F.P. The authors are grateful to the participating parents and infants,
27 and thank Sylviane Martin for her help in recruiting them.

1 **References**

2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

Bahrick, L. E., & Lickliter, R. (2000). Intersensory redundancy guides attentional selectivity and perceptual learning in infancy. *Developmental Psychology*, *36*(2), 190.
<https://doi.org/10.1037/0012-1649.36.2.190>

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>

Bremner, A. J., Lewkowicz, D. J., & Spence, C. (2012). The multisensory approach to development. In *Multisensory development* (pp. 1–26). Oxford University Press.

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>

de Groot, J. H., Semin, G. R., & Smeets, M. A. (2017). On the communicative function of body odors: a theoretical integration and review. *Perspectives on Psychological Science*, *12*(2), 306–324. <https://doi.org/10.1177/1745691616676599>

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>

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*(8), 1–8. <https://doi.org/10.1371/journal.pone.0070677>

- 1 Durand, K., Schaal, B., Goubet, N., Lewkowicz, D. J., & Baudouin, J.-Y. (2020). Does any
2 mother's body odor stimulate interest in mother's face in 4-month-old infants?
3 *Infancy*, 25(1). <https://doi.org/10.1111/infa.12322>
- 4 Edelman, G. M. (1993). Neural darwinism: selection and reentrant signaling in higher brain
5 function. *Neuron*, 10(2), 115–125. [https://doi.org/10.1016/0896-6273\(93\)90304-A](https://doi.org/10.1016/0896-6273(93)90304-A)
- 6 Eimas, P. D., & Quinn, P. C. (1994). Studies on the formation of perceptually based basic-
7 level categories in young infants. *Child Development*, 65(3), 903–917.
8 <https://doi.org/10.1111/j.1467-8624.1994.tb00792.x>
- 9 Elsner, B., Jeschonek, S., & Pauen, S. (2013). Event-related potentials for 7-month-olds'
10 processing of animals and furniture items. *Developmental Cognitive Neuroscience*, 3,
11 53–60. <https://doi.org/10.1016/j.dcn.2012.09.002>
- 12 Fausey, C. M., Jayaraman, S., & Smith, L. B. (2016). From faces to hands: Changing visual
13 input in the first two years. *Cognition*, 152, 101–107.
14 <https://doi.org/10.1016/j.cognition.2016.03.005>
- 15 Ferdenzi, C., Coureaud, G., Camos, V., & Schaal, B. (2008). Human awareness and uses of
16 odor cues in everyday life: Results from a questionnaire study in children.
17 *International Journal of Behavioral Development*, 32(5), 422–431.
18 <https://doi.org/10.1177/0165025408093661>
- 19 Fransson, P., Metsäranta, M., Blennow, M., Åden, U., Lagercrantz, H., & Vanhatalo, S.
20 (2013). Early development of spatial patterns of power-law frequency scaling in fMRI
21 resting-state and EEG data in the newborn brain. *Cerebral Cortex*, 23(3), 638–646.
22 <https://doi.org/10.1093/cercor/bhs047>
- 23 Fujioka, T., Mourad, N., He, C., & Trainor, L. J. (2011). Clinical neurophysiology
24 comparison of artifact correction methods for infant EEG applied to extraction of

1 event-related potential signals. *Clinical Neurophysiology*, 122(1), 43–51.
2 <https://doi.org/10.1016/j.clinph.2010.04.036>

3 Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and
4 birds recruits brain areas involved in face recognition. *Nature Neuroscience*, 3(2),
5 191–197.

6 Ghazanfar, A., & Schroeder, C. (2006). Is neocortex essentially multisensory? *Trends in*
7 *Cognitive Sciences*, 10(6), 278–285. <https://doi.org/10.1016/j.tics.2006.04.008>

8 Godard, O., Baudouin, J.-Y., Schaal, B., & Durand, K. (2016). Affective matching of odors
9 and facial expressions in infants: shifting patterns between 3 and 7 months.
10 *Developmental Science*, 19(1), 155–163. <https://doi.org/10.1111/desc.12292>

11 Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The fusiform face area subserves face
12 perception, not generic within-category identification. *Nature Neuroscience*, 7(5),
13 555–562. <https://doi.org/10.1038/nn1224>

14 Gronau, Q. F., Ly, A., & Wagenmakers, E.-J. (2020). Informed Bayesian t-Tests. *The*
15 *American Statistician*, 74(2), 137–143.
16 <https://doi.org/10.1080/00031305.2018.1562983>

17 Grossmann, T., Gliga, T., Johnson, M. H., & Mareschal, D. (2009). The neural basis of
18 perceptual category learning in human infants. *Journal of Cognitive Neuroscience*,
19 21(12), 2276–2286. <https://doi.org/10.1162/jocn.2009.21188>

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

23 Heron-Delaney, M., Damon, F., Quinn, P. C., Méary, D., Xiao, N. G., Lee, K., & Pascalis, O.
24 (2017). An adult face bias in infants that is modulated by face race. *International*

1 *Journal of Behavioral Development*, 41(5), 581–587.
2 <https://doi.org/10.1177/0165025416651735>

3 Hoehl, S. (2016). The development of category specificity in infancy--What can we learn
4 from electrophysiology? *Neuropsychologia*, 83.
5 <https://doi.org/10.1016/j.neuropsychologia.2015.08.021>

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

10 Jessen, S. (2019). Maternal odor reduces the neural threat response in human infants. *BioRxiv*.
11 <https://doi.org/10.1101/827626>

12 Kelly, D. J., Quinn, P. C., Slater, A. M., Lee, K., Gibson, A., Smith, M., Ge, L., & Pascalis,
13 O. (2005). Three-month-olds, but not newborns, prefer own-race faces. *Developmental*
14 *Science*, 8(6), 31–36. <https://doi.org/10.1111/j.1467-7687.2005.0434a.x>.

15 Leleu, A., Rekow, D., Poncet, F., Schaal, B., Durand, K., Rossion, B., & Baudouin, J.-Y.
16 (2020). Maternal odor shapes rapid face categorization in the infant brain.
17 *Developmental Science*, 23(2), e12877. <https://doi.org/10.1111/desc.12877>

18 Lewkowicz, D. J. (2010). The ontogeny of human multisensory object perception: a
19 constructivist account. In J. Kaiser & M. J. Naumer (Eds.), *Multisensory Object*
20 *Perception in the Primate Brain* (pp. 303–327). Springer.

21 Lewkowicz, D. J., & Ghazanfar, A. A. (2009). The emergence of multisensory systems
22 through perceptual narrowing. *Trends in Cognitive Sciences*, 13(11), 470–478.
23 <https://doi.org/10.1016/j.tics.2009.08.004>

- 1 Lochy, A., de Heering, A., & Rossion, B. (2019). The non-linear development of the right
2 hemispheric specialization for human face perception. *Neuropsychologia*, *126*, 10–19.
3 <https://doi.org/10.1016/j.neuropsychologia.2017.06.029>
- 4 Lundström, J. N., Regenbogen, C., Ohla, K., & Seubert, J. (2019). Prefrontal Control Over
5 Occipital Responses to Crossmodal Overlap Varies Across the Congruency Spectrum.
6 *Cerebral Cortex*, *29*(7), 3023–3033. <https://doi.org/10.1093/cercor/bhy168>
- 7 Mareschal, D., & Quinn, P. C. (2001). Categorization in infancy. *Trends in Cognitive*
8 *Sciences*, *5*(10), 443–450. [https://doi.org/10.1016/S1364-6613\(00\)01752-6](https://doi.org/10.1016/S1364-6613(00)01752-6)
- 9 Marinović, V., Hoehl, S., & Pauen, S. (2014). Neural correlates of human–animal distinction:
10 An ERP-study on early categorical differentiation with 4- and 7-month-old infants and
11 adults. *Neuropsychologia*, *60*, 60–76.
12 <https://doi.org/10.1016/j.neuropsychologia.2014.05.013>
- 13 Mattioni, S., Rezk, M., Battal, C., Bottini, R., Cuculiza Mendoza, K. E., Oosterhof, N. N., &
14 Collignon, O. (2020). Categorical representation from sound and sight in the ventral
15 occipito-temporal cortex of sighted and blind. *ELife*, *9*, e50732.
16 <https://doi.org/10.7554/eLife.50732>
- 17 McCarthy, G., & Wood, C. C. (1985). Scalp distributions of event-related potentials: an
18 ambiguity associated with analysis of variance models. *Electroencephalography and*
19 *Clinical Neurophysiology*, *62*, 203–208. [https://doi.org/10.1016/0168-5597\(85\)90015-](https://doi.org/10.1016/0168-5597(85)90015-2)
20 2
- 21 Mourad, N., Reilly, J. P., de Bruin, H., Hasey, G., & MacCrimmon, D. (2007). A simple and
22 fast algorithm for automatic suppression of high-amplitude artifacts in EEG data. *2007*
23 *IEEE International Conference on Acoustics, Speech and Signal Processing-*
24 *ICASSP'07, 1*, I–393. <https://doi.org/10.1109/ICASSP.2007.366699>

- 1 Oakes, L. M., Horst, J. S., Kovack-Lesh, K. A., & Perone, S. (2009). How infants learn
2 categories. In *Learning and the infant mind* (pp. 144–171). Oxford University Press.
- 3 Peykarjou, S., Hoehl, S., Pauen, S., & Rossion, B. (2017). Rapid categorization of human and
4 ape faces in 9-month-old infants revealed by fast periodic visual stimulation. *Scientific*
5 *Reports*, 7(1), 1–12. <https://doi.org/10.1038/s41598-017-12760-2>
- 6 Peykarjou, S., Pauen, S., & Hoehl, S. (2016). 9-month-old infants recognize individual
7 unfamiliar faces in a rapid repetition ERP paradigm. *Infancy*, 21(3), 288–311.
8 <https://doi.org/10.1111/infa.12118>
- 9 Prehn-Kristensen, A., Wiesner, C., Bergmann, T. O., Wolff, S., Jansen, O., Mehdorn, H. M.,
10 Ferstl, R., & Pause, B. M. (2009). Induction of empathy by the smell of anxiety. *PLoS*
11 *One*, 4(6), e5987. <https://doi.org/10.1371/journal.pone.0005987>
- 12 Quek, G. L., Liu-Shuang, J., Goffaux, V., & Rossion, B. (2018). Ultra-coarse, single-glance
13 human face detection in a dynamic visual stream. *NeuroImage*, 176, 465–476.
14 <https://doi.org/10.1016/j.neuroimage.2018.04.034>
- 15 Quinn, P. C. (2011). Born to categorize. In U. Goswami (Ed.), *The Wiley-Blackwell handbook*
16 *of childhood cognitive development* (2nd ed., Vol. 2, pp. 129–152). Wiley-Blackwell.
- 17 Quinn, P. C., Eimas, P. D., & Rosenkrantz, S. L. (1993). Evidence for representations of
18 perceptually similar natural categories by 3-month-old and 4-month-old infants.
19 *Perception*, 22(4), 463–475. <https://doi.org/10.1068/p220463>
- 20 Quinn, P. C., Westerlund, A., & Nelson, C. A. (2006). Neural markers of categorization in 6-
21 month-old infants. *Psychological Science*, 17(1), 59–66.
22 <https://doi.org/10.1111/j.1467-9280.2005.01665.x>
- 23 Quinn, P. C., Yahr, J., Kuhn, A., Slater, A. M., & Pascalis, O. (2002). Representation of the
24 gender of human faces by infants: A preference for female. *Perception*, 31(9), 1109–
25 1121. <https://doi.org/10.1068/p3331>

- 1 Rakison, D. H., & Yermolayeva, Y. (2010). Infant categorization. *WIREs Cognitive Science*,
2 1(6), 894–905. <https://doi.org/10.1002/wcs.81>
- 3 Retter, T. L., Jiang, F., Webster, M. A., & Rossion, B. (2020). All-or-none face categorization
4 in the human brain. *NeuroImage*, 213, 116685.
5 <https://doi.org/10.1016/j.neuroimage.2020.116685>
- 6 Reynolds, G. D., & Richards, J. E. (2005). Familiarization, attention, and recognition memory
7 in infancy: an event-related potential and cortical source localization study.
8 *Developmental Psychology*, 41(4), 598–615. [https://doi.org/10.1037/0012-](https://doi.org/10.1037/0012-1649.41.4.598)
9 1649.41.4.598
- 10 Rossion, B., & Caharel, S. (2011). ERP evidence for the speed of face categorization in the
11 human brain: Disentangling the contribution of low-level visual cues from face
12 perception. *Vision Research*, 51(12), 1297–1311.
13 <https://doi.org/10.1016/j.visres.2011.04.003>
- 14 Rossion, B., & Curran, T. (2010). Visual expertise with pictures of cars correlates with RT
15 magnitude of the car inversion effect. *Perception*, 39(2), 173–183.
- 16 Rossion, B., Hanseeuw, B., & Dricot, L. (2012). Defining face perception areas in the human
17 brain: A large-scale factorial fMRI face localizer analysis. *Brain and Cognition*, 79(2),
18 138–157. <https://doi.org/10.1016/j.bandc.2012.01.001>
- 19 Rossion, B., Jacques, C., & Jonas, J. (2018). Mapping face categorization in the human
20 ventral occipitotemporal cortex with direct neural intracranial recordings: Intracranial
21 mapping of face categorization. *Annals of the New York Academy of Sciences*,
22 1426(1), 5–24. <https://doi.org/10.1111/nyas.13596>
- 23 Rossion, B., Retter, T. L., & Liu-Shuang, J. (in press). Understanding human individuation of
24 unfamiliar faces with oddball fast periodic visual stimulation and
25 electroencephalography. *European Journal of Neuroscience*.

1 Schaal, B., & Durand, K. (2012). The role of olfaction in human multisensory development.
2 In A. J. Bremner, D. J. Lewkowicz, & C. Spence (Eds.), *Multisensory Development*
3 (pp. 29–62). Oxford University Press.

4 Schaal, B., Marlier, L., & Soussignan, R. (2000). Human fetuses learn odours from their
5 pregnant mother's diet. *Chemical Senses*, 25(6), 729–737.
6 <https://doi.org/10.1093/chemse/25.6.729>

7 Schaal, B., Soussignan, R., & Marlier, L. (2002). Olfactory cognition at the start of life: the
8 perinatal shaping of selective odor responsiveness. In C. Rouby, B. Schaal, D. Dubois,
9 R. Gervais, & A. Holley (Eds.), *Olfaction, taste, and cognition* (pp. 421–440).
10 Cambridge University Press.

11 Seigneuric, A., Durand, K., Jiang, T., Baudouin, J. Y., & Schaal, B. (2010). The nose tells it
12 to the eyes: Crossmodal associations between olfaction and vision. *Perception*, 39(11),
13 1541–1554. <https://doi.org/10.1068/p6740>

14 Sela, L., & Sobel, N. (2010). Human olfaction: A constant state of change-blindness.
15 *Experimental Brain Research*, 205(1), 13–29. [https://doi.org/10.1007/s00221-010-](https://doi.org/10.1007/s00221-010-2348-6)
16 [2348-6](https://doi.org/10.1007/s00221-010-2348-6)

17 von Kriegstein, K., Kleinschmidt, A., Sterzer, P., & Giraud, A.-L. (2005). Interaction of Face
18 and Voice Areas during Speaker Recognition. *Journal of Cognitive Neuroscience*,
19 17(3), 367–376. <https://doi.org/10.1162/0898929053279577>

20 Zheng, Y., You, Y., Farias, A. R., Simon, J., Semin, G. R., Smeets, M. A., & Li, W. (2018).
21 Human chemosignals of disgust facilitate food judgment. *Scientific Reports*, 8(1), 1–
22 10. <https://doi.org/10.1038/s41598-018-35132-w>

23 Zhou, W., & Chen, D. (2008). Encoding human sexual chemosensory cues in the orbitofrontal
24 and fusiform cortices. *Journal of Neuroscience*, 28(53), 14416–14421.
25 <https://doi.org/10.1523/JNEUROSCI.3148-08.2008>

1 Zhou, W., Jiang, Y., He, S., & Chen, D. (2010). Olfaction Modulates Visual Perception in

2 Binocular Rivalry. *Current Biology*, 20(15), 1356–1358.

3 <https://doi.org/10.1016/j.cub.2010.05.059>

4