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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

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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 & 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 & 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 (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 (see 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 & 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 & 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 & 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 & 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 & Durand, 2012, for review). In addition, odor perception is less sensitive to spatial and temporal variations than visual perception (Sela & 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.

Materials and methods

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 SDs 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.

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 1A). 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 & Caharel, 2011; Rossion & 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). 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.

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. 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.

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 x 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.

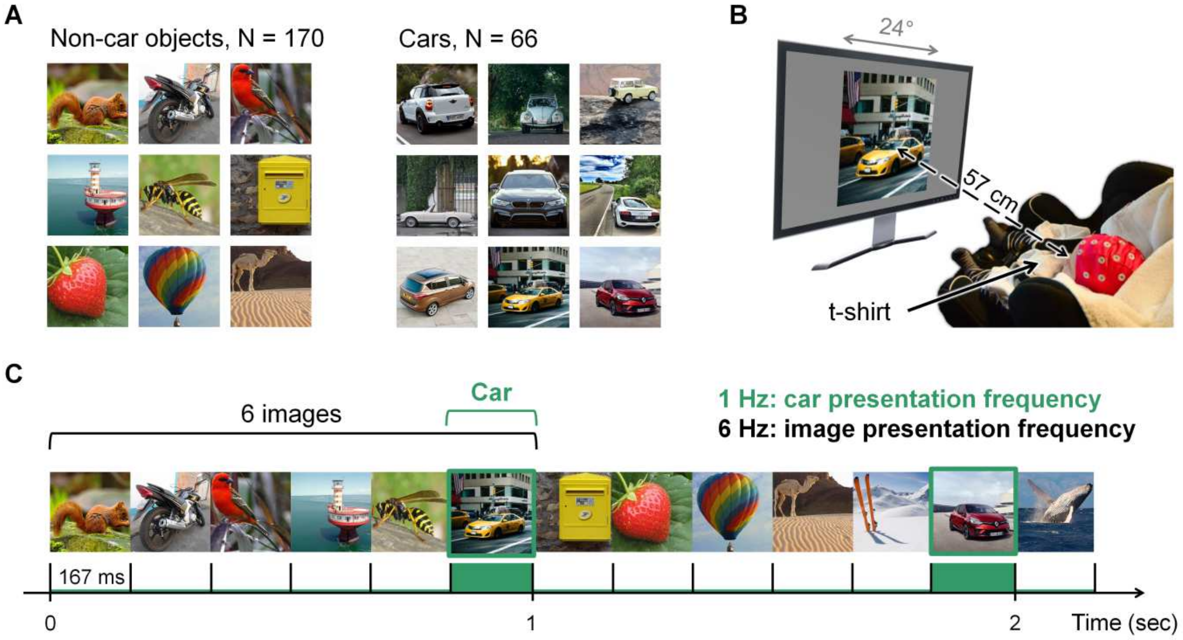

Figure 1. An EEG frequency-tagging approach to measure car categorization in odor contexts. A. Example of the stimuli used in the experiment and depicting various non-car objects and cars. **B.** During the experiment, infants were installed in a seat placed at 57 cm from a computer screen and odorous 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.

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.

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 & 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 & 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., in press). 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 SDs 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).

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 & 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) 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 ps > .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' (2020) study: 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).

Results

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 2A). 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 2A). 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 2A and Table S1).

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 2B). 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).

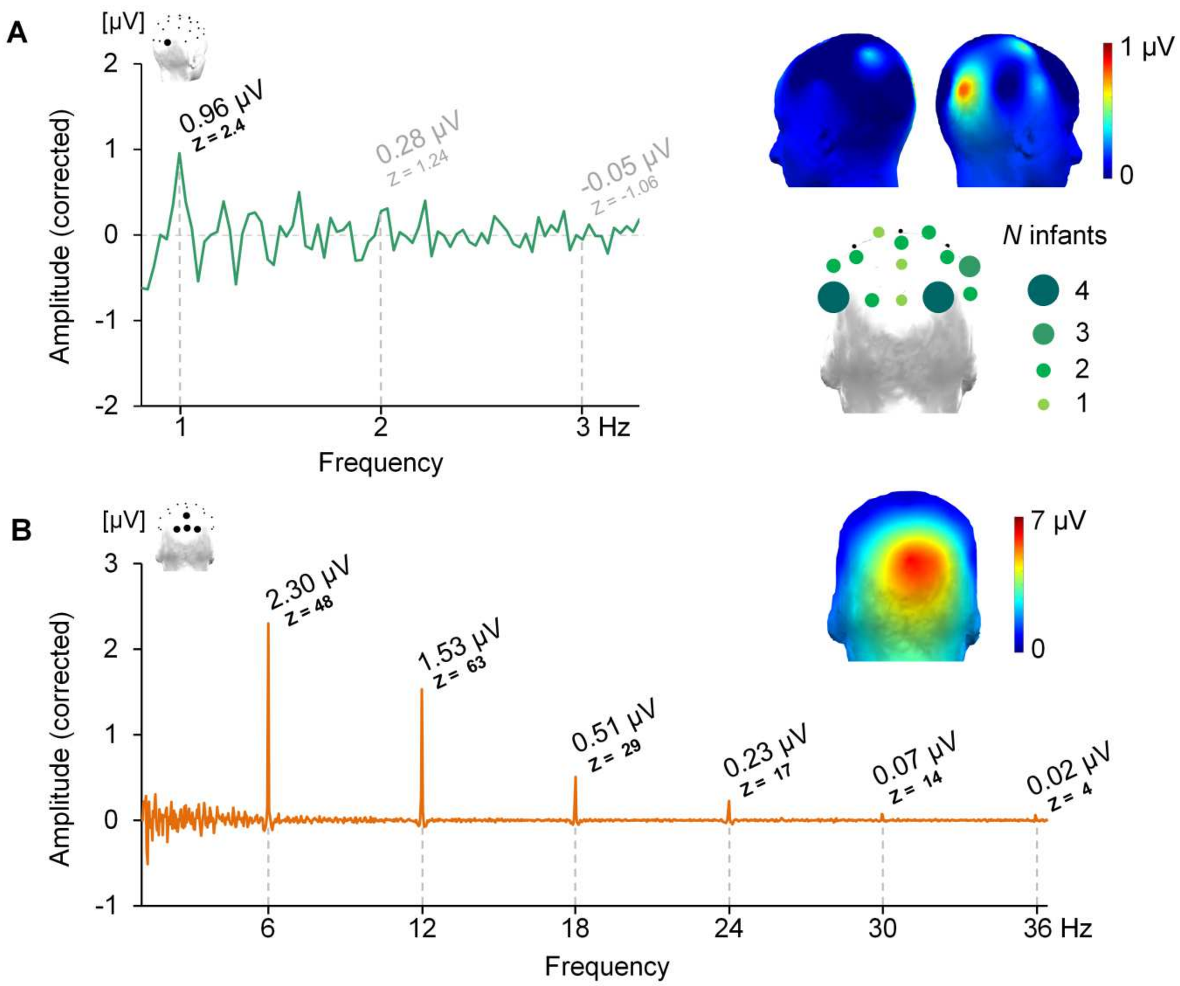

Figure 2. (A) Car categorization response and (B) general visual response (N=18). A. (left) Amplitude (noise corrected) of the EEG spectrum recorded over the right occipital channel O2 across odor conditions. Numerical values indicate the amplitude of the response with corresponding Z-scores. Only the 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.

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 3A), 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, ps < .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 3B).

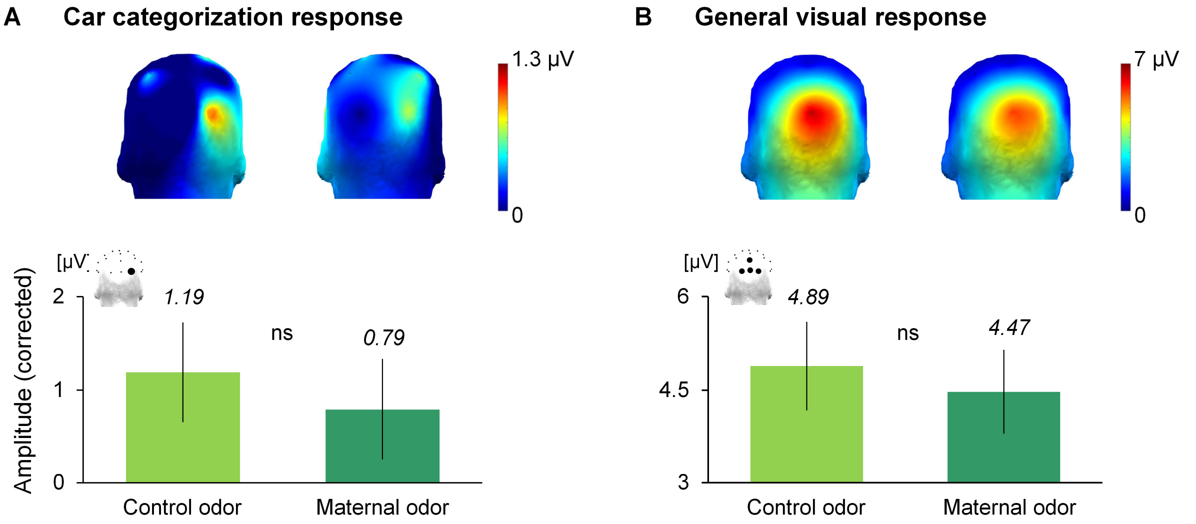

Figure 3. Both brain responses are immune to maternal odor. A. Amplitude (noise corrected) of the car categorization response over O2 in the control (left) and maternal (right) odor conditions, showing a slight non-significant decrease of amplitude in the maternal odor condition (-0.40 µV ± 0.63 µV, 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.

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' (2020) study: 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 4). When considering O2, the only channel with a significant categorization response to cars, the conclusion remains similar with a significant *Odor* × *Category* interaction ($F(1, 34) = 11.7$, $p = .002$, $\eta p^2 = 0.26$) explained by an odor effect for faces (+2.25 ± 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 $ps > 0.19$).

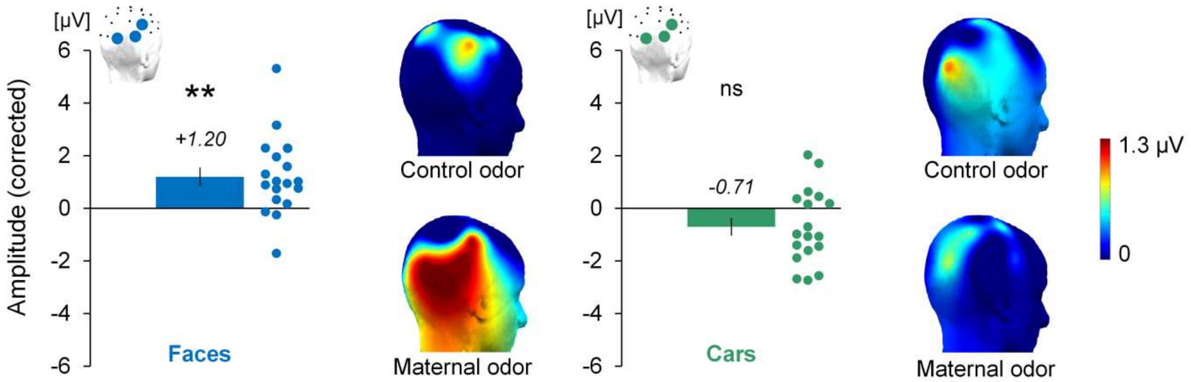

Figure 4. Maternal odor effect [maternal – control] for the categorization responses to faces (blue) and cars (green). Maternal odor significantly enhances the response to faces (left, **: p = .007, N = 18) and does not significantly diminish the response to cars (right, ns: p = .19, N = 18) over the 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.

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 & 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., 2016). In infants, this finding indicates that rapid categorization of numerous exemplars is not limited to faces (de Heering & 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; 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), 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 & 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 & 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., 2016). 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 & 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 & Chen, 2008). Since multisensory integration is considered as a key aspect of (social-)cognitive development (e.g., Bremner et al., 2012; Schaal & Durand, 2012 for review), and that mounting evidence orients toward multimodal building of knowledge in the brain (von Kriegstein et al., 2005; Lewkowicz & Ghazanfar, 2009; Mattioni et al., 2020; see Ghazanfar & 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 these familiar objects are also a nest of socially-relevant familiar odors (Ferdenzi et al., 2008), it would be interesting to investigate maternal odor's influence on their categorization to evaluate such a socially-/familiarity-related account of olfactory-visual integration in young infants. 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., 2013, 2020), and neural responses to facial expressions (Jessen, 2019). 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, 2019). 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 (see e.g., Lochy et al., 2019 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., 2018; 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.

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References

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

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*(1). https://doi.org/10.1111/infa.12322

Edelman, G. M. (1993). Neural darwinism: selection and reentrant signaling in higher brain function. *Neuron*, *10*(2), 115–125. https://doi.org/10.1016/0896-6273(93)90304-A

Eimas, P. D., & Quinn, P. C. (1994). Studies on the formation of perceptually based basic-level categories in young infants. *Child Development*, *65*(3), 903–917. https://doi.org/10.1111/j.1467-8624.1994.tb00792.x

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

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., Coureaud, G., Camos, V., & Schaal, B. (2008). Human awareness and uses of odor cues in everyday life: Results from a questionnaire study in children. *International Journal of Behavioral Development*, *32*(5), 422–431. https://doi.org/10.1177/0165025408093661

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. *Cerebral Cortex*, *23*(3), 638–646. https://doi.org/10.1093/cercor/bhs047

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*(1), 43–51. https://doi.org/10.1016/j.clinph.2010.04.036

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*(2), 191–197.

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

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*(1), 155–163. https://doi.org/10.1111/desc.12292

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

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

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*(12), 2276–2286. https://doi.org/10.1162/jocn.2009.21188

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

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*(5), 581–587. https://doi.org/10.1177/0165025416651735

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

Jacques, C., Retter, T. L., & Rossion, B. (2016). 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

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

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*(6), 31–36. https://doi.org/10.1111/j.1467-7687.2005.0434a.x.

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. https://doi.org/10.1111/desc.12877

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

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

Lochy, A., de Heering, A., & Rossion, B. (2019). 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

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*(7), 3023–3033. https://doi.org/10.1093/cercor/bhy168

Mareschal, D., & Quinn, P. C. (2001). Categorization in infancy. *Trends in Cognitive Sciences*, *5*(10), 443–450. https://doi.org/10.1016/S1364-6613(00)01752-6

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

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

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

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. *2007 IEEE International Conference on Acoustics, Speech and Signal Processing-ICASSP'07*, *1*, I–393. https://doi.org/10.1109/ICASSP.2007.366699

Oakes, L. M., Horst, J. S., Kovack-Lesh, K. A., & Perone, S. (2009). How infants learn categories. In *Learning and the infant mind* (pp. 144–171). Oxford University Press.

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), 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*(3), 288–311. https://doi.org/10.1111/infa.12118

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*(6), e5987. https://doi.org/10.1371/journal.pone.0005987

Quek, G. L., Liu-Shuang, J., Goffaux, V., & Rossion, B. (2018). 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

Quinn, P. C. (2011). Born to categorize. In U. Goswami (Ed.), *The Wiley-Blackwell handbook of childhood cognitive development* (2nd ed., Vol. 2, pp. 129–152). Wiley-Blackwell.

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*(4), 463–475. https://doi.org/10.1068/p220463

Quinn, P. C., Westerlund, A., & Nelson, C. A. (2006). Neural markers of categorization in 6-month-old infants. *Psychological Science*, *17*(1), 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*(9), 1109–1121. https://doi.org/10.1068/p3331

Rakison, D. H., & Yermolayeva, Y. (2010). Infant categorization. *WIREs Cognitive Science*, *1*(6), 894–905. https://doi.org/10.1002/wcs.81

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

Reynolds, G. D., & Richards, J. E. (2005). Familiarization, attention, and recognition memory in infancy: an event-related potential and cortical source localization study. *Developmental Psychology*, *41*(4), 598–615. https://doi.org/10.1037/0012-1649.41.4.598

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*(12), 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*(2), 173–183.

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*(2), 138–157. https://doi.org/10.1016/j.bandc.2012.01.001

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*(1), 5–24. https://doi.org/10.1111/nyas.13596

Rossion, B., Retter, T. L., & Liu-Shuang, J. (in press). Understanding human individuation of unfamiliar faces with oddball fast periodic visual stimulation and electroencephalography. *European Journal of Neuroscience*.

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

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

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

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*(11), 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*(1), 13–29. https://doi.org/10.1007/s00221-010-2348-6

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*(3), 367–376. https://doi.org/10.1162/0898929053279577

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

Zhou, W., & Chen, D. (2008). Encoding human sexual chemosensory cues in the orbitofrontal and fusiform cortices. *Journal of Neuroscience*, *28*(53), 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*(15), 1356–1358. https://doi.org/10.1016/j.cub.2010.05.059