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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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## **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  $\mu$ V) above 2 SDs  
8 of the group's mean amplitude (1.38  $\mu$ V, SD = 2.62  $\mu$ 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  $400 \times 400$  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.

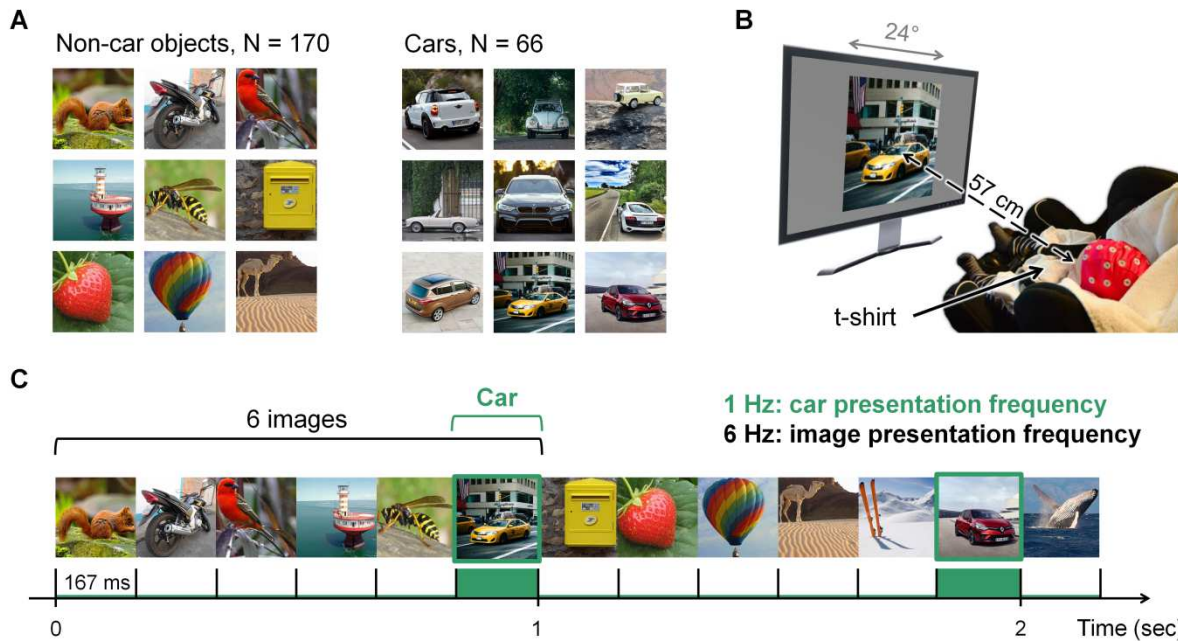
## 19 **Procedure**

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  $1920 \times 1080$  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 6<sup>th</sup> 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 × 24° 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 6<sup>th</sup> 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  $\pm 3.4$  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 $\Omega$ . 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 4<sup>th</sup>-  
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  $\pm 500$   $\mu$ 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:  $9.2 \pm 3.2$ ), 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:  $4.7 \pm 1.7$ ) vs. 82 for the maternal odor  
23 condition ( $4.6 \pm 1.8$ ).

#### 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 ( $\eta_p^2$ ).

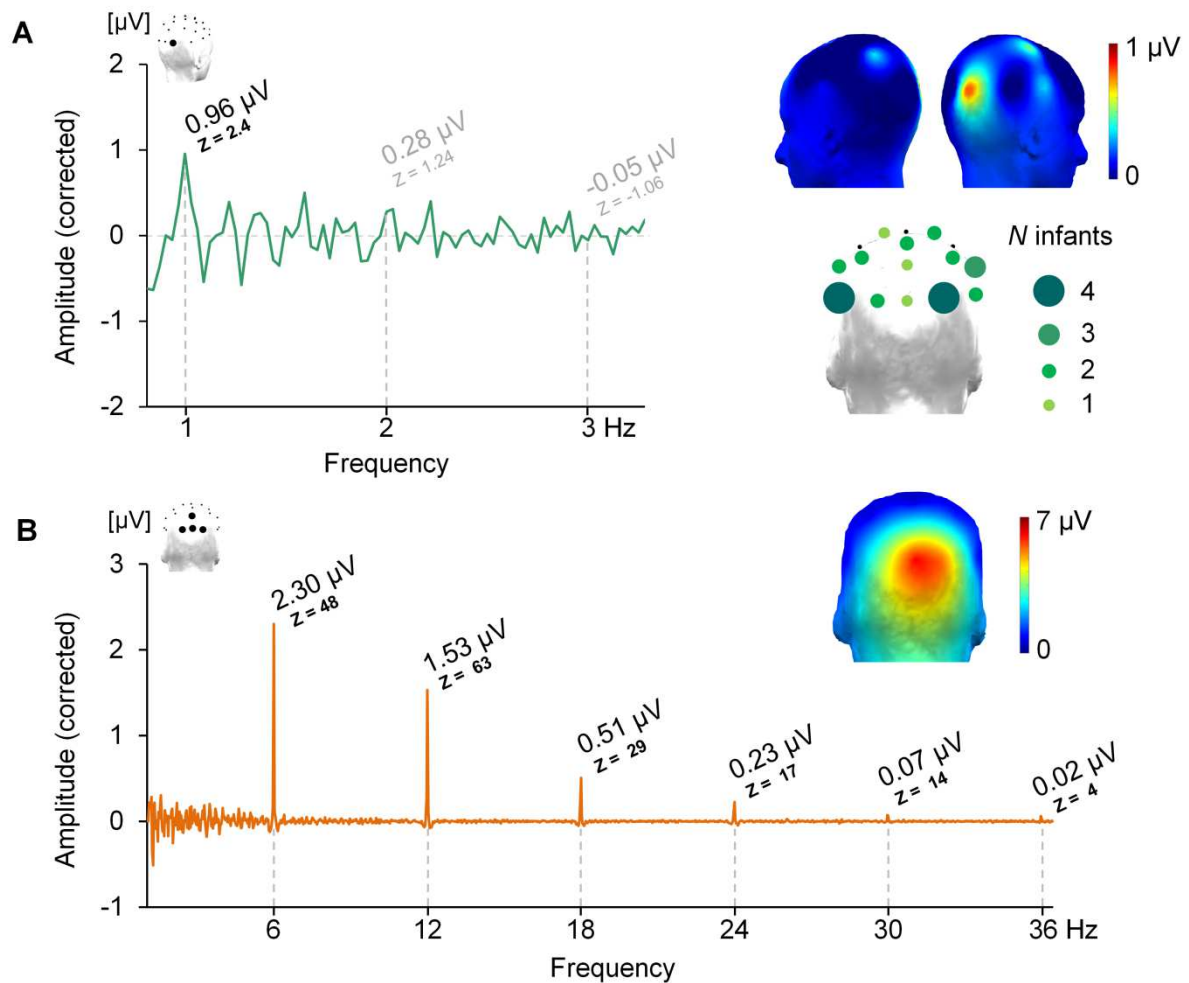
## 19 Results

### 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 1<sup>st</sup> 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  $\pm 0.46$  (SEM)  $\mu$ 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 5<sup>th</sup> harmonic (i.e., 30 Hz) over POz ( $Z = 3.85$ ,  $p < .001$ )  
10 and O1 ( $Z = 4.99$ ,  $p < .001$ ) and until the 6<sup>th</sup> 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  $2.80 \pm 0.72$   
14  $\mu\text{V}$  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.

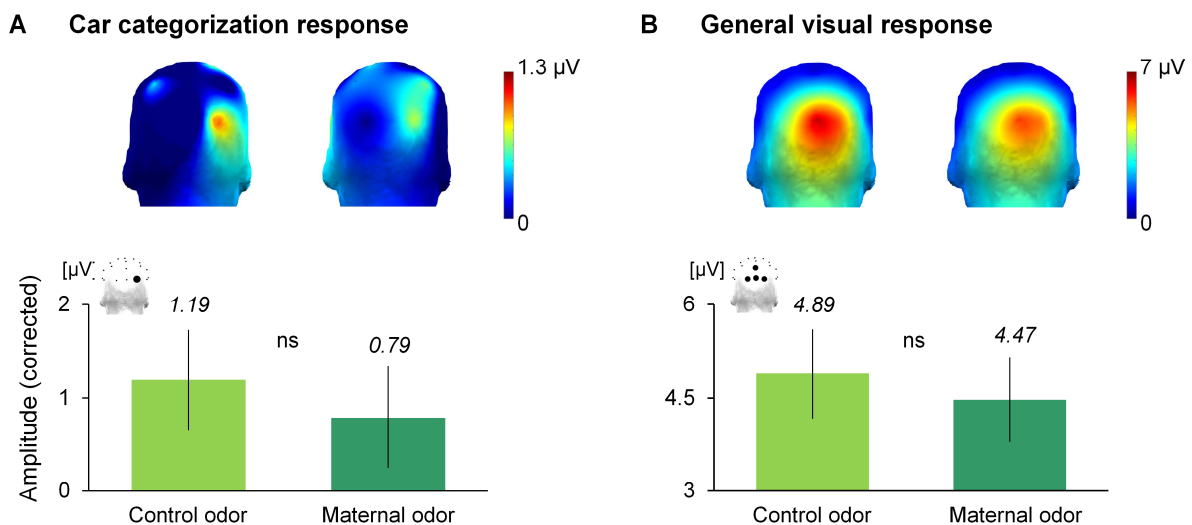
### 15 **No effect of maternal odor on both car categorization and general visual responses**

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 ( $BF_{10} = 0.28$ )**.

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,  $ps < .001$ ). 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 ( $BF_{10} = 0.29$ )**. 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 ( $-0.41 \pm 0.47$   
 20  $\mu\text{V}$ , 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.

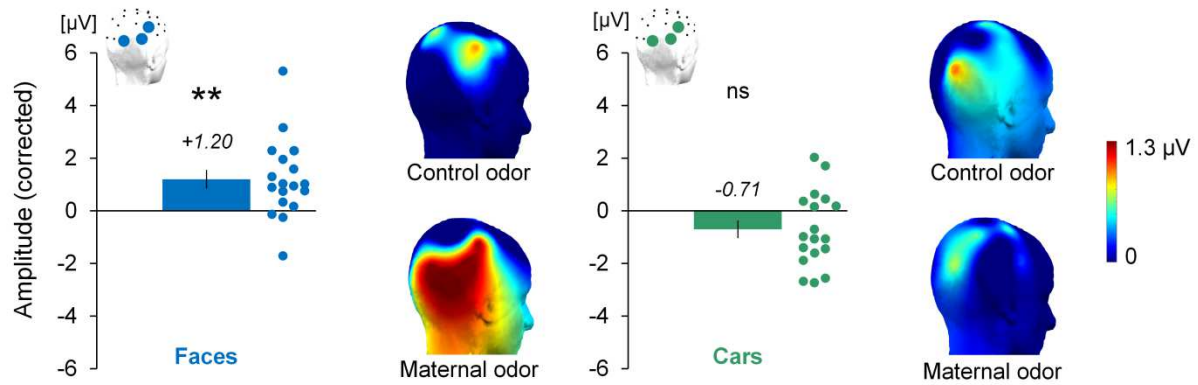
23

## 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.

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