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Maternal odor shapes rapid face categorization in the infant brain

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Data availability statement

The data that support the findings of this study are available from Arnaud Leleu (arnaud.leleu@u-bourgogne.fr) upon reasonable request.

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Conflict of interest statement

The authors declare no competing interest.

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Maternal odor shapes rapid face categorization in the infant brain

Research highlights

- We provide neural evidence that visual categorization of faces is shaped by concomitant maternal odor inputs at 4 months of age
- The odor effect is observed in individual infant brains
- Common visual processes elicited by both face and non-face images are not affected by the odor context, excluding a general increase in arousal/visual attention
- These results support a multisensory account of category acquisition in the human brain

Abstract

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

observations show that face-selective neural activity in infancy is mediated by the presence of a (maternal) body odor, providing strong support for multisensory inputs driving category acquisition in the developing human brain and having important implications for our understanding of human perceptual development.

Keywords

Maternal body odor, face categorization, infant brain, multisensory, EEG, frequency-tagging

Introduction

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

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

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

To investigate odor-driven early development of visual categorization in the human brain, we examine here whether a neural correlate of the earliest and most salient form of visual categorization for young infants, human face categorization, is shaped by the concurrent presentation of a relevant odor for infants, maternal body odor. We take advantage of relatively recent evidence for rapid face categorization of natural images over the right occipito-temporal cortex of 4- to 6-month-old infants with frequency-tagging in electroencephalography (EEG) (de Heering & Rossion, 2015). We extend this observation in a younger age group of eighteen 4-month-old infants with a new set of highly variable face images (Fig.S1) subtending a large area (28°) of the infants' visual field (Fig.1). Infants are

exposed to two odor conditions: a control odor using an unworn t-shirt and the maternal odor using a t-shirt worn by each mother during three nights preceding testing (Durand et al., 2013). We therefore explore whether the high-level face categorization response in the infant brain is modulated by concurrent odor cues from the maternal body odor.

Materials and Methods

Participants

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

Visual stimuli

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

Odor stimuli

Infants were exposed to maternal odor cues in contrast with a control odor condition (Durand et al., 2013). Maternal body odor was collected on a white t-shirt (100% cotton) sent to the mother enclosed in a zip-locked hermetic plastic bag one week preceding the experiment. The t-shirt was worn by the mother for the three consecutive nights preceding testing. Night wear improves standardization across participants by attenuating activity-related individual differences. In addition, mothers were asked to refrain from using perfume and odorous soap during the collection period. During the days, they were instructed to store the t-shirt in the hermetic bag that could be left at ambient temperature but far from any heating device. The control condition consisted of an unworn identical t-shirt with equivalent storage procedure. Before sending the t-shirt to the mother, both t-shirts were laundered using hypoallergenic powder detergent (Persavon, France).

Procedure

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

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

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

EEG recording and analysis

EEG was continuously recorded from 32 Ag/AgCl electrodes mounted in a cap (Waveguard, ANT Neuro, The Netherlands) according to the 10-10 classification system (acquisition reference: AFz, electrode impedance < 15 k Ω , sampling rate: 1024 Hz). EEG data were then

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

Results

Rapid face categorization in the infant brain

For combined odor conditions, visual inspection revealed a face-selective brain response at the predefined 1-Hz rate of face pictures presentation mainly over right posterior regions (Fig.2.A). The face categorization response reached significance over the right occipito-temporal channel P8 ($Z = 4.79, p < .001$, one-tailed, signal > noise) and its contiguous electrode CP6 ($Z = 4.26, p < .001$) with a noise-corrected amplitude across conditions of 1.14 ± 0.49 (SEM) μV and $1.18 \pm 0.37 \mu\text{V}$, respectively. This response was lower ($0.34 \pm 0.49 \mu\text{V}$) but significant over the left occipito-temporal channel P7 ($Z = 1.91, p = .028$). The response was only recorded on the first harmonic (Table S1) and was not driven by a small subset of infants (Fig.2.B. and Table S2) since 10 infants presented a significant response over CP6 and/or P8 and another 3 infants over at least one other electrode (i.e., O2, P4) within the right-hemispheric ROI. Given that a face-selective response was previously isolated in the

infant brain with some infants installed in a car seat and others seated on their mother's lap (de Heering & Rossion, 2015), these observations across odor conditions replicate and extend this finding in a younger age group with a novel, even more challenging, stimulus set. They indicate that, at 4 months of age, the infant brain is already able to categorize at a glance multiple variable faces embedded in their natural background and presented in a fast train of various non-face images.

Maternal odor shapes the neural signature of face categorization

Visually, the face-selective response evolves from a parieto-temporal response slightly larger in the right hemisphere in the control odor context to a stronger right-hemispheric response in the maternal odor context (Fig.2C). Accordingly, a significant categorization response to face pictures was found over the right channel CP6 ($Z = 2.15, p = .016$) and the left channel P7 ($Z = 2.64, p = .004$) in the control odor context, while the right-hemispheric electrodes CP6 ($Z = 2.19, p = .014$), P8 ($Z = 3.36, p < .001$) and O2 ($Z = 2.71, p = .003$) reached significance in the maternal odor context. Pooling the three latter channels (CP6, P8, O2), the neural signature of face categorization was larger in the maternal than the control odor context, with a highly significant odor effect (maternal – control) of $+1.20 \pm 0.36 \mu\text{V}$, $T(17) = 3.37, p = .004$. In contrast, no significant difference was found over the homologous electrodes (CP5, P7, O1) in the left hemisphere ($+0.32 \pm 0.55 \mu\text{V}$, $T(17) = 0.57, p = .57$). The odor effect was strong over O2 ($+2.25 \pm 0.45 \mu\text{V}$, $T(17) = 5.03, p < .001$), while smaller and non-significant over P8 ($+0.95 \pm 0.75 \mu\text{V}$, $T(17) = 1.27, p = .22$) and CP6 ($+0.40 \pm 0.93 \mu\text{V}$; $T(17) = 0.42, p = .68$). It was not significant over P7 ($-0.47 \pm 1.12 \mu\text{V}$; $T(17) = -0.42, p = .68$).

To further highlight the strength of the odor effect over the right posterior region, Fig.3.A and 3.B depict its magnitude over channel O2 and its topographical pattern for the group and for individual infants. Individual data for electrode O2 revealed that 17 out of 18 infants presented descriptively larger amplitude of the face categorization response in the maternal vs. control odor context. When considering the three right channels CP6, P8 and O2, 17 infants showed at least one electrode with a minimum increase of $1.48 \mu\text{V}$ in the maternal odor context. Individual odor effects estimated from Z-scores (Table S3; $Z > 1.96$ or $< -1.96, p < .05$, two-tailed, maternal \neq control) indicated that 9 infants presented a significantly larger response in the maternal odor context over at least one electrode within the ROIs. According to one-tailed significance testing of a larger face-selective response for

the maternal vs. control odor ($Z > 1.64$, $p < .05$), a significant effect was found for 7 infants over O2 and/or P8 and/or CP6, and over at least one other channel within the ROIs for another 5 infants (spatial distribution illustrated in Fig.3.C).

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

As expected (de Heering & Rossion, 2015), the 6-Hz base rate of fast periodic stimulation elicits a large brain response at exactly the same frequency and its harmonics (e.g., 12 Hz, 18 Hz.) over the medial occipital cortex (Fig.4.A). This response reflects the brain synchronization to visual cues rapidly changing 6 times per second. It was significant at 6 Hz over the four medial occipital channels (Oz, POz, O1, O2) with Z-scores ranging from 2.48 ($p = .007$) for POz to 17.79 ($p < .001$) for Oz (Table S4). The same four electrodes reached significance until the fifth harmonic (30 Hz) and Oz and O2 until the sixth harmonic (36 Hz). The common visual response was thus quantified from the sum of the six first harmonics (Retter & Rossion, 2016). This combined response was significant for the four channels (from $Z = 4.42$ for POz to $Z = 17.39$ for Oz, $ps < .001$). Its noise-corrected amplitude ranged from $2.62 \pm 0.74 \mu\text{V}$ over POz to $7.17 \pm 0.88 \mu\text{V}$ over Oz, for a global magnitude of $4.65 \pm 0.60 \mu\text{V}$ pooled across the four channels. The high reliability of this response is attested by individual data (Table S5), with a significant response in every infant over channel Oz.

The common visual response was clearly visible in both odor conditions (Fig.4.B) with a significant response over Oz, O1 and O2 in both conditions (Z-scores ranging from 7.56 to 18.03, $ps < .001$), and over POz only in the maternal odor context ($Z = 6.30$, $p < .001$). A slight non-significant increase was observed for maternal odor vs. the control odor (separate four channels: $Ts < 1.68$, $ps > .11$, pooled channels: $T(17) = 1.12$, $p = .28$, maternal – control = $+0.35 \pm 0.33 \mu\text{V}$). Fig.4.B. shows that infants' individual odor effects are homogeneously distributed around zero. In brief, the 4-month-old infant brain clearly responds to the rapid 6-Hz stream of widely variable natural images, but this common response to all stimuli is not influenced by concomitant maternal odor cues.

Discussion

Taken together, these observations demonstrate that concurrent body odor inputs from the mother actively shape face categorization at 4 months of age by enhancing a face-selective response in individual infant brains, especially over the right occipito-temporal cortex. This

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result builds upon behavioral observations of specific association between a face and a voice (Guellai et al., 2011), and is consistent with odor-driven enhancement of 4-month-olds' preference for a face over another object category (Durand et al., 2013). It goes well beyond the latter observation however by providing evidence that the neural basis of a rich and rapid face categorization response (i.e., against many types of biological and non-biological objects, and across widely variable unsegmented pictures of faces) is directly constrained by a concomitant socially relevant odor. In contrast, the medial occipital common response to the rapid 6-Hz stream of face and non-face images is not affected by the presence of the maternal body odor, excluding a general increase in arousal or visual attention that typically leads to larger brain activity in response to periodic visual stimulation (Morgan, Hansen, & Hillyard, 1996; Müller et al., 2006; see Norcia, Appelbaum, Ales, Cottureau, & Rossion, 2015 for review).

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

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

well suited to improve the generalization of variable visual inputs by providing constant related information from another sensory system.

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

Admittedly, the present study is limited in that it cannot fully determine whether the odor effect is specific to maternal odor or generalizable to any human body odor. Here we used own mothers' body odor since it conveys many relevant cues for human infants compared with the odor of an unworn t-shirt, as a proof of concept. Maternal odor is experienced before birth, enabling transnatal stability and familiarity in the postnatal world replete with sensory novelty (Schaal, Soussignan, & Marlier, 2002). Mother's odor is a complex mixture of compounds conveying nested informative cues about conspecifics (e.g.,

human-, female-, mother-, identity-related) sometimes pertaining to biological status (e.g., lactation-related odor). In that respect, building on the present demonstration, future studies should precisely delineate which odor cues in the familiar maternal body odor support infants in categorizing faces (e.g., does an unfamiliar mother's body odor boost face categorization? Do some cues have a supra-additive effect when combined?). As an indication, we did not find a different odor effect between breast-fed and bottle-fed infants (Fig.S3) suggesting a weak contribution of lactating status, but further investigation is needed to reach a definitive conclusion.

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

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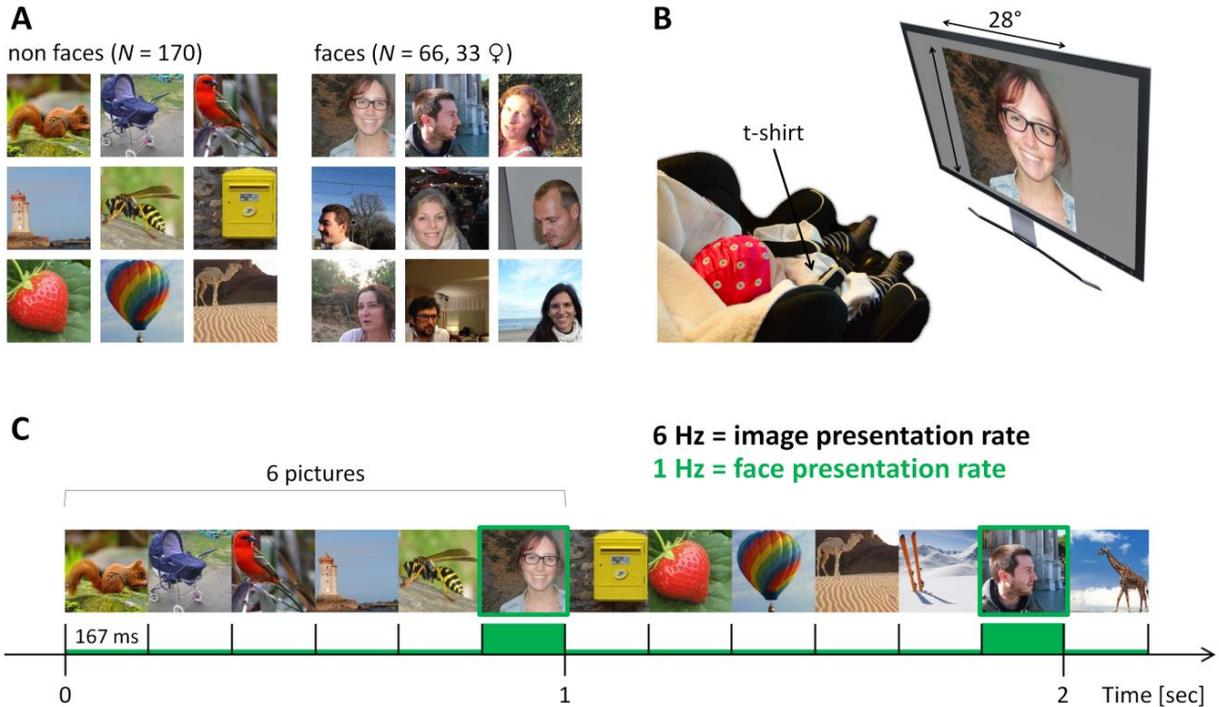


Fig. 1. A frequency-tagging approach in electroencephalography (EEG) isolating a neural marker of face categorization in an odor context. (A) Examples of the unsegmented images of objects and faces used as stimuli. (B) After EEG-cap placement, infants were installed in a seat facing a computer screen.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

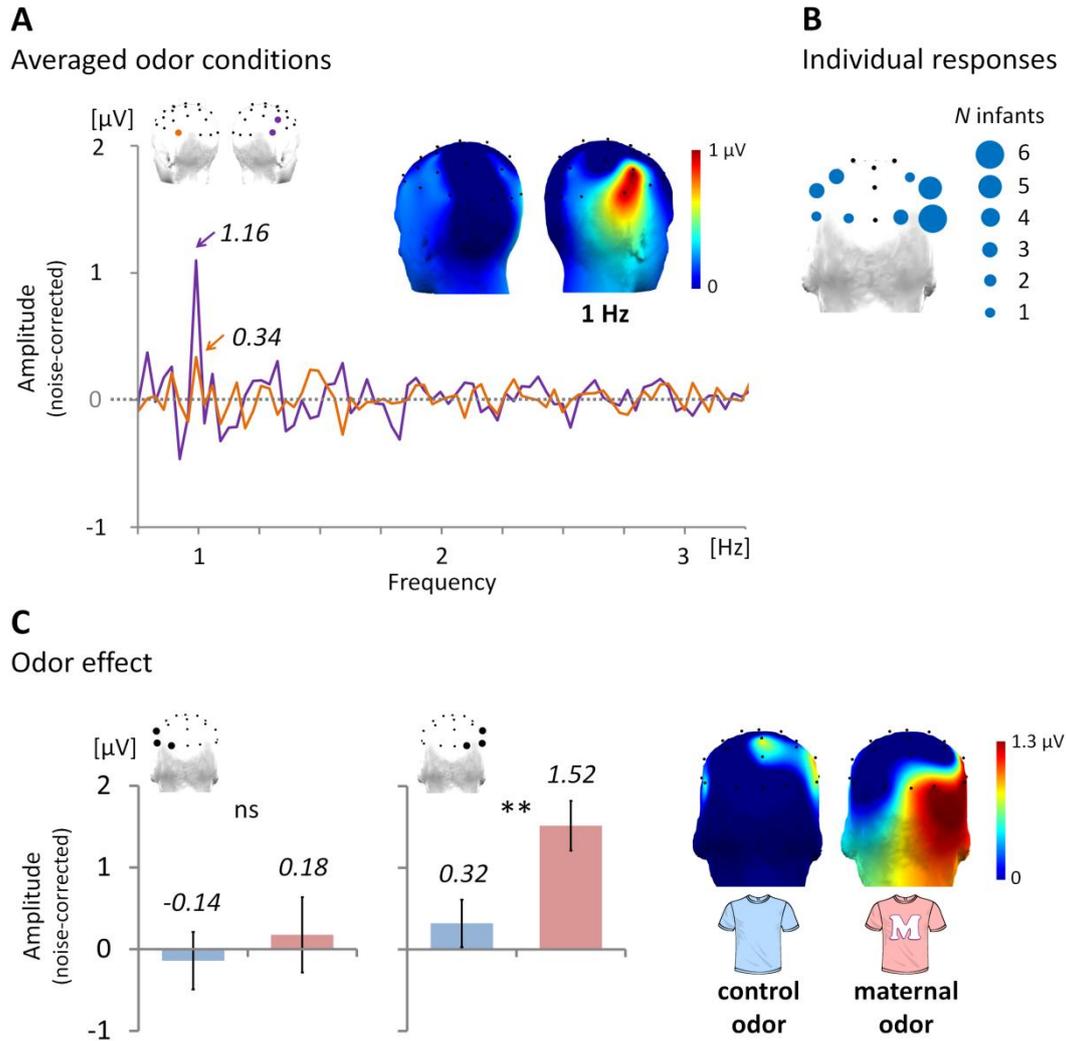


Fig. 2. Face categorization response over lateral posterior brain regions. (A) Noise-corrected amplitude of the EEG frequency spectrum averaged across the two odor conditions over left (orange: P7) and right (purple: averaged across CP6 and P8) posterior channels showing a neural response at the predefined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

Odor effect (mother – control)

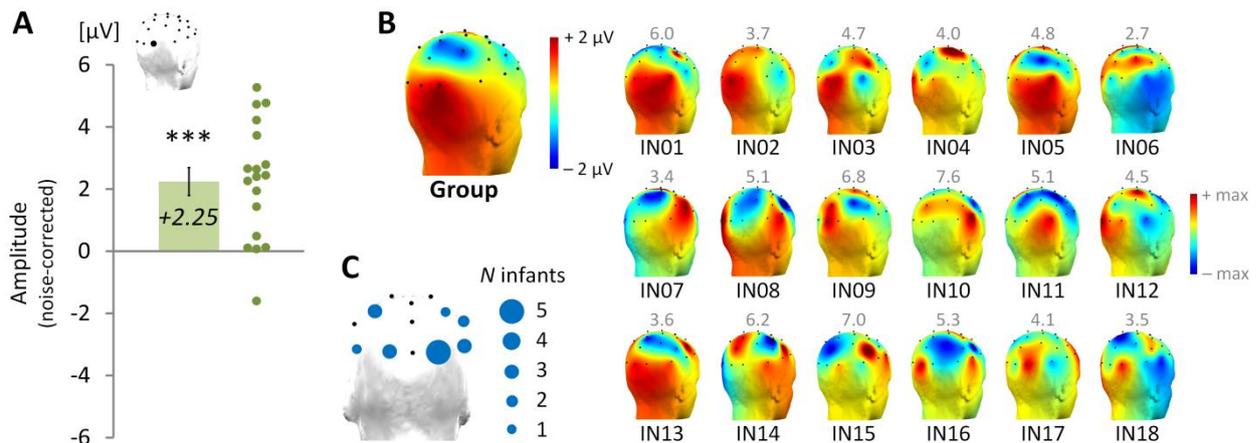


Fig. 3. Effect of maternal odor cues on the face categorization response recorded in each individual infant brain. (A) Odor effect (i.e., maternal odor minus control odor) on the face-selective response plotted over channel O2 for grand-averaged noise-corrected amplitude (***) $p = .0001$, error bar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

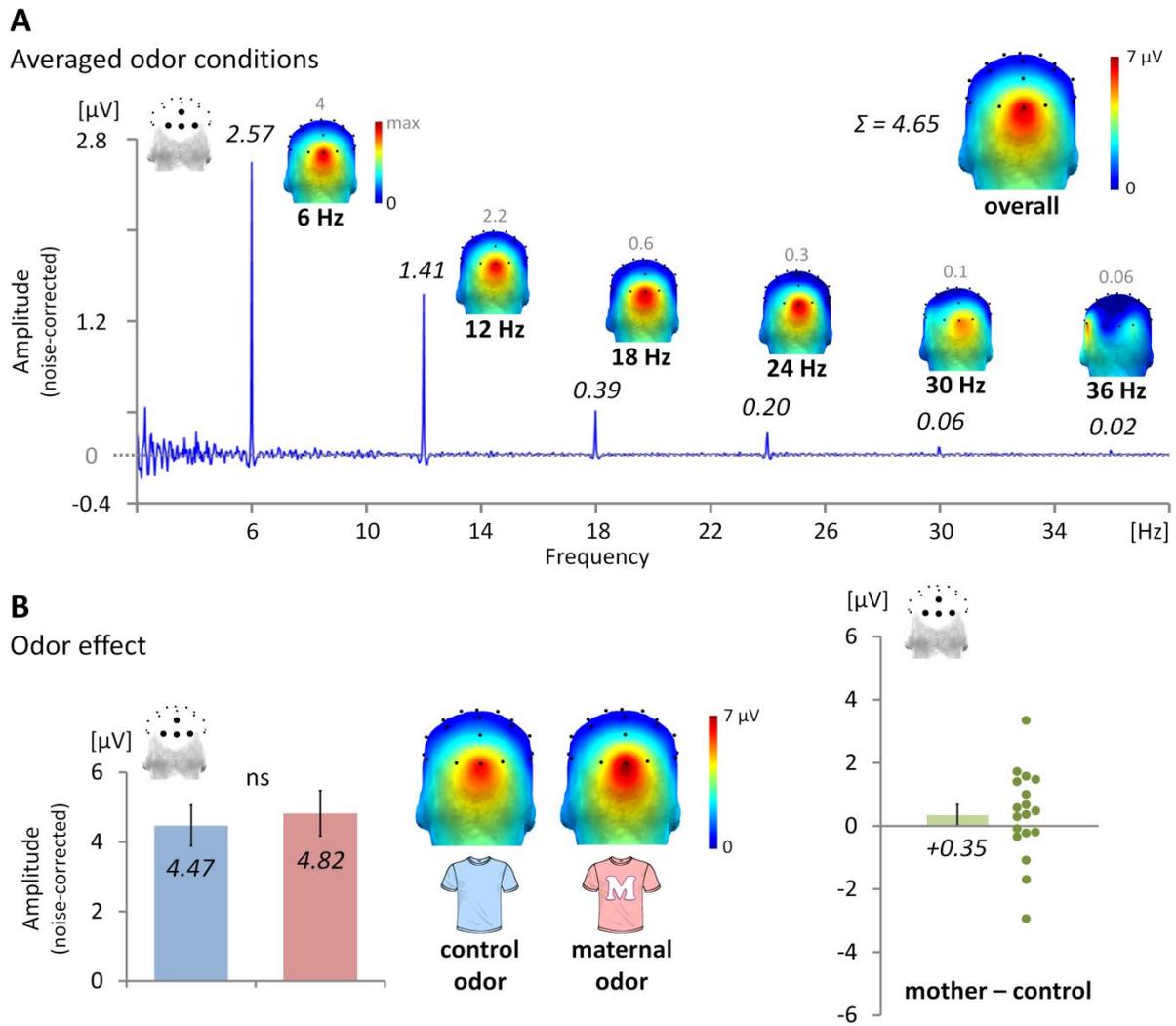


Fig. 4. Common visual response to the rapid stream of natural images over medial occipital regions. (A) Noise-corrected amplitude of the EEG frequency spectrum averaged across the two odor conditions and across four medial occipital channels (Oz, O1, O2, POz) revealing highly identifiable responses at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

Appendix A

EEG preprocessing and frequency-domain analysis

All EEG analyses were carried out using Letswave 6 (<http://nocions.github.io/letswave6>) running on Matlab 2012 (MathWorks, USA). Left and right mastoid electrodes (M1 and M2) were removed from the montage (Fig. S2) before processing since they were noisy or artifact-ridden for most infants. EEG data were first bandpass filtered at 0.1 – 100 Hz (butterworth filter, 4th order) and then resampled to 200 Hz to reduce file size and processing time. Data were cropped according to each sequence in 36-sec segments starting from the fade-in. To reduce very high-amplitude artefacts, each segment was processed using the Artifact Blocking algorithm (Fujioka, Mourad, He, & Trainor, 2011; Mourad, Reilly, de Bruin, Hasey, & MacCrimmon, 2007) windowed on the overall segment with a large threshold of $\pm 500 \mu\text{V}$. For one infant, a remaining noisy channel (Fpz) was then rebuilt using linear interpolation from the two nearest electrodes (Fp1 and Fp2). Data were then re-referenced according to a common average reference. EEG segments were further cropped in shorter epochs starting from the first full contrast face image in the stimulation sequence (i.e., just after the fade-in) and lasting 32 secs (i.e., exactly thirty-two 1 Hz cycles).

To increase signal-to-noise ratio (SNR), two data-driven criteria were used for each infant to remove sequences with no general response of the visual system to the rapid stream of stimulation (Barry-Anwar, Hadley, Conte, Keil, & Scott, 2018; de Heering & Rossion, 2015; Peykarjou, Hoehl, Pauen, & Rossion, 2017), or with atypical scalp-wide power at the 1-Hz face-selective rate compared with the other sequences. A fast Fourier transform (FFT) was first applied to every epoch and amplitude spectra were extracted for all electrodes with a frequency resolution of $1/32 = 0.03125$ Hz. For the first criterion, Z-scores were calculated for each channel and each frequency bin as the difference between the signal amplitude and the mean noise amplitude (estimated from the 20 surrounding bins, 10 on each side, excluding the two immediately adjacent and the two most extreme (minimum and maximum) bins) divided by the standard deviation (*SD*) of the noise. Since a general response of the infant visual system has been previously observed over medial occipital sites to both meaningful or meaningless (i.e., phase-scrambled) fast trains of images (de Heering & Rossion, 2015), sequences were kept for further analysis when at least two Z-scores were greater than 1.64 ($p < .05$, one-tailed, signal > noise) or at least one Z-score was

larger than 2.32 ($p < .01$, one-tailed) over medial occipital electrodes (Oz, POz, O1, O2) for the 6-Hz base frequency or its first harmonic (i.e., integer multiple = 12 Hz) as a general marker of adequate looking at the stimulation screen. For the second criterion, FFT amplitude spectra were pooled across all channels and amplitude at the 1-Hz face-selective frequency was corrected by subtracting the mean noise amplitude. Here, mean noise was estimated using 6 instead of 20 frequency bins since EEG power is high in the low-frequency range and non-linearly decreases as frequency increases (Fransson et al., 2013). Accordingly, considering too many frequency bins would overestimates the background noise (and therefore underestimates the face-selective response) because the power spectrum is steeper for lower than for higher frequency bins around the 1-Hz target frequency. A sequence was considered atypical when its noise-corrected amplitude was above or below 2 SDs of the mean of all sequences retained after application of the first criterion. Once these two criteria were applied, between 4 and 15 sequences were kept per infant for an overall rejection of 10 out of 145 sequences. On average, 3.72 ± 0.35 (SEM) and 4 ± 0.41 sequences were respectively retained for the control and the body odor conditions with no significant difference between them, $T(17) = 1.05$, $p = .31$. Finally, to reduce EEG activity non phase-locked to the stimuli, sequences were separated according to the odor conditions and averaged in the time-domain to obtain one single 32-sec epoch per condition for each infant. FFT was applied and amplitude spectra were extracted for each electrode.

Statistical analysis

Statistical analysis was conducted on both brain responses to the 6-Hz base rate of image presentation and the 1-Hz selective rate of face presentation in two consecutive steps: 1/ channels with significant responses were identified in grand-averaged data using Z-scores (i.e., using amplitude variance across frequency bins; e.g., de Heering & Rossion, 2015; Rossion et al., 2015); 2/ odor conditions were compared over identified channels using *T*-tests calculated on noise-corrected amplitudes (i.e., using amplitude variance across individual infants).

For 1/, the aim was to determine whether each brain response was significantly larger than surrounding noise level ($Z > 1.64$, $p < .05$, one-tailed, signal > noise). Given that such responses were isolated in the infant brain using a similar paradigm with some infants

installed in a car seat and others seated on their mother's lap (de Heering & Rossion, 2015), we first estimated significant responses for the frequencies of interest and their harmonics (i.e., integer multiples) regardless of the odor condition in an attempt to replicate de Heering & Rossion's findings. FFT data were averaged across conditions for each infant and amplitude over each channel was normalized by dividing by the square root of the sum of squared amplitudes of all channels (McCarthy & Wood, 1985) at each frequency bin. Normalization was intended to identify the main electrodes over which a response is recorded by scaling differences between electrodes on the global magnitude of the response across the scalp. After normalization, data were grand-averaged across infants and Z-scores were calculated for each electrode. We expected significant common (6 Hz and harmonics) and face-selective (1 Hz and harmonics) visual responses mainly over channels Oz and P7/8 respectively (de Heering & Rossion, 2015). We thus considered a medial occipital region-of-interest (ROI) centered on Oz and including contiguous channels (POz, O1, O2) for the common visual response, and two lateral posterior ROIs centered on P7 and P8 and including contiguous channels (O1/2, P3/4, C5/6) for the face categorization response (Fig. S2). Harmonics were considered for further analysis until Z-scores over one channel were no longer significant (Tables S1 and S4). For each response, individual normalized amplitudes were then summed for significant harmonics and Z-scores were calculated on these summed amplitudes for each infant (Tables S2 and S5) as well as for the grand-averaged data (Table S4 for the common visual response) to estimate the significance of the overall responses distributed on several harmonics. For visualization purpose, each response was also quantified in a single value expressed in microvolts by summing noise-corrected amplitudes (before normalization) across significant harmonics (Retter & Rossion, 2016). Thereafter, we determined which electrodes presented significant responses separately for each odor condition. Individual datasets for each condition were first normalized on the global power of both conditions combined as previously calculated. Normalized amplitudes were then summed across significant harmonics and Z-scores were finally computed on grand-averaged data.

For 2/, the aim was to analyze the difference in amplitude between the two odor conditions for each brain response. Individual summed responses expressed in non-normalized noise-corrected amplitudes were extracted for the relevant channels identified in step 1/. Analysis was performed using *T*-tests comparing the two conditions (significance

threshold: $p < .05$, two-tailed, maternal odor \neq control odor) and individual data were grand-averaged for visualization. To explore the significance of the odor effect (maternal odor minus control odor) on the face-selective response in every infant brain, uncorrected normalized amplitudes obtained in the control odor condition were subtracted from those recorded in the maternal odor condition for each individual dataset. Z-scores were calculated at each electrode within the ROIs for significance testing of the difference between odor conditions ($Z > 1.96$ or < -1.96 , $p < .05$, two-tailed, maternal odor \neq control odor; Table S3). According to the results of the group-level analysis showing a significantly larger face categorization response over right posterior regions in the presence of maternal odor cues (see Results), the significance of each individual odor effect was also estimated using one-tailed Z-scores ($Z > 1.64$, $p < .05$, maternal odor $>$ control odor; Table S3).