Odor-driven face-like categorization in the human infant brain

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Understanding how the young infant brain starts to categorize the flurry of ambiguous sensory inputs coming in from its complex environment is of primary scientific interest. Here, we test the hypothesis that senses other than vision play a key role in initiating complex visual categorizations in 20 4-mo-old infants exposed either to a baseline odor or to their mother's odor while their electroencephalogram (EEG) is recorded. Various natural images of objects are presented at a 6-Hz rate (six images/second), with face-like object configurations of the same object categories (i.e., eliciting face pareidolia in adults) interleaved every sixth stimulus (i.e., 1 Hz). In the baseline odor context, a weak neural categorization response to face-like stimuli appears at 1 Hz in the EEG frequency spectrum over bilateral occipitotemporal regions. Critically, this face-like–selective response is magnified and becomes right lateralized in the presence of maternal body odor. This reveals that nonvisual cues systematically associated with human faces in the infant's experience shape the interpretation of face-like configurations as faces in the right hemisphere, dominant for face categorization. At the individual level, this intersensory influence is particularly effective when there is no trace of face-like categorization in the baseline odor context. These observations provide evidence for the early tuning of face-(like)–selective activity from multisensory inputs in the developing brain, suggesting that perceptual development integrates information across the senses for efficient category acquisition, with early maturing systems such as olfaction driving the acquisition of categories in later-developing systems such as vision.

infancy | maternal body odor | face pareidolia | fast periodic visual stimulation | EEG frequency tagging

From the first moments of life, the human infant brain has to deal with a complex multisensory environment. To avoid being overwhelmed by responding to each object, person, or event as unique, sensory inputs are grouped into categories. Although this key function, categorization, has been the topic of much interest in cognitive science (1), its emergence and development remain largely unknown and debated (2, 3). In general, the development of categorization is studied separately for each sensory modality, the rationale being that unisensory categories are formed before being combined into more abstract conceptual categories (4). However, experience is replete with cues coming concurrently from all sensory modalities, each maturing at a specific rate during early development (5). An outstanding issue is whether categories in early maturing senses, such as smell, play a decisive role in initiating categories in more slowly developing senses, such as vision. Here, we address this hypothesis by testing whether maternal body odor, a nonvisual cue repeatedly associated with a human face in the infant's experience, can initiate a category-selective neural response to visual stimuli hardly categorized as faces by the young infant brain: face-like objects that elicit face pareidolia in adults (i.e., the illusory perception of a face in nonface stimuli; Fig. 1*A* and *SI Appendix*, Fig. S1).

As complex and highly familiar stimuli categorized at multiple levels (e.g., emotional expression, sex, identity), faces are ideal to study categorization in vision. The most basic and yet challenging categorization of a visual stimulus as a face has been of interest to researchers in cognitive (neuro)science and artificial intelligence for decades (see ref. 6 for review). The adult human brain is particularly impressive at automatically categorizing faces in a single fixation (7, 8), this rapid categorization being subtended by a distributed network of face-selective regions in the occipito-temporal cortex with a right hemispheric advantage (e.g., ref. 9).

By contrast, the development of face categorization is more contentious. At birth, human infants already prefer looking at schematic face-like stimuli [(10, 11) e.g., ref. 12 for a neural signature in electroencephalography (EEG)], although the origin of this neonatal ability has been debated (refer to ref. 13 for review). The ability to rapidly gaze at human faces embedded in naturalistic displays improves during the first year, markedly after 6 mo of age (e.g., ref. 14; refer to ref. 15 for review). However, infants do not preferentially look at complex face-like stimuli (e.g., Arcimboldo paintings) over nonface stimuli before 7 mo (16). At the neural level, distinct activity for faces versus other meaningful or meaningless stimuli has been recorded after at least 3 to 4 mo with EEG (e.g., refs. 17–20).

Significance

The adult human brain is organized in unimodal regions responding selectively to categories of environmental sensory stimuli. Here, we document the origin of category-selective visual brain responses in infancy, demonstrating the key contribution of other senses. Visual categorization is recorded neurally in 4-mo-old infants presented with rapid trains of natural images of nonface objects. A concurrent maternal odor initiates the neural response to periodically presented face-like objects categorized as faces in the specialized right hemisphere. This observation provides invaluable clues to understand how the developing visual system builds upon multisensory experience to start categorizing ambiguous and complex unimodal sensory inputs.

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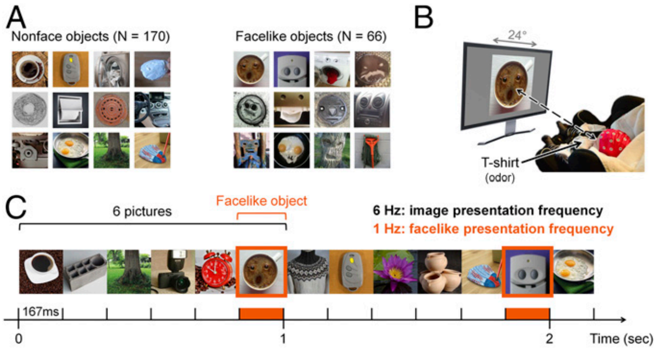

Fig. 1. An EEG frequency-tagging approach to measure face-like categorization in odor contexts. (*A*) Natural images embedded in their original background were used as stimuli. The set comprised many visual object categories, common to nonface- and face-like objects (full set in *SI Appendix*, Fig. S1). (*B*) After EEG cap placement, infants were installed in a car seat in front of a monitor where stimuli sustained 24° of visual angle. Odors were delivered using T-shirts (unworn or worn by the mother) disposed on the infant's chest during visual stimulation. (*C*) Excerpt of a 2-s clip of fast periodic visual stimulation where images are presented at a 6-Hz rate (six images/s, i.e., each lasting 167 ms) and face-like images interspersed every sixth stimulus (i.e., at a 1-Hz rate). This frequency-tagging approach allows the identification of two distinct responses in the EEG spectrum: a general visual response results from the 6-Hz image presentation frequency, and a face-like categorization response emerges at 1 Hz if the face-like objects are reliably discriminated from the nonface objects.

Yet, these neural responses are recorded over more medial occipital and central scalp regions than adult responses (refer to ref. 21 for review), likely reflecting the contribution of low-level visual cues.

In recent years, a neural categorization response to natural face images has been found as early as 4 mo of age using EEG frequency tagging (22, 23). This direct *differential* response to faces versus other objects generalizes across numerous variable individual faces, is not accounted for by low-level image statistics, and is mainly recorded over right occipitotemporal sites as in adults (8). Importantly, this face-selective response increases when infants are presented with their mother's body odor compared to a baseline odor (23). This is in line with behavioral (24–28) and neural evidence (29, 30) that intersensory associations mediate how infants process facial information and supports the view that the weaving of inputs from different modalities favors knowledge acquisition (for review, refer to ref. 31).

However, whether nonvisual inputs systematically associated with a face in the infant's experience can initiate face-selective activity in the infant brain when face categorization is challenging for the sole visual system has yet to be demonstrated. We address this issue in the present study by using a variety of nonface objects categorized as faces by neurotypical adults (i.e., eliciting face pareidolia, Fig. 1*A* and *SI Appendix*, Fig. S1) but which, to our knowledge, have never been associated with face-selective neural activity in infants. In line with our most recent investigation (23), we rely on concurrent maternal odors to trigger face-selective neural responses. Olfaction is indeed ideal for this purpose since it functions earlier than vision, enabling an olfaction to vision transfer of knowledge (32). Moreover, odors are perceived as more stable in space and time than visual information (33), a functional property that can increase generalization across variable visual inputs of the same category. Finally, since body odors co-occur with faces in the infant's experience, their categorizations could be closely tied in the infant brain through reentrant connections between the olfactory and visual systems (34), allowing efficient face categorization when the response to the sole visual input is weak [following the *inverse effectiveness* principle of multisensory integration (35)]. On this basis, we hypothesize that concurrent maternal odor could directly activate face-selective regions of the infant visual cortex to foster their responsiveness to face-like stimuli.

To test this hypothesis, we record scalp EEG in 4-mo-olds within two odor contexts (maternal versus baseline). By contrasting natural images of objects resembling faces from other nonface objects every six images in fast streams of six images per second (i.e., 6-Hz base rate), we tag a face-like categorization response at 1 Hz in the EEG frequency spectrum (Fig. 1*C*). Importantly, face-like and nonface stimulus sets depict the same object categories

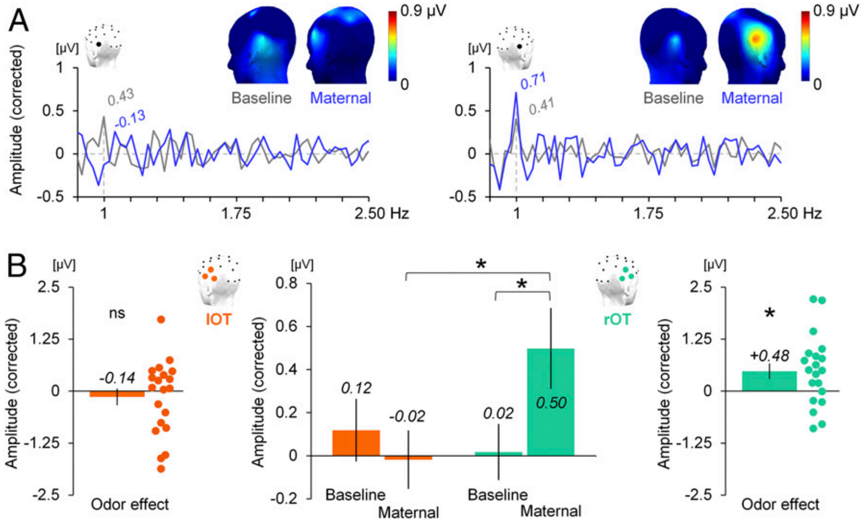

Fig. 2. Maternal odor shapes the face-like categorization response. (*A*) Amplitude spectra (noise corrected) showing the face-like categorization response at 1 Hz over the left channel P7 and the right channel P8 (significant in the baseline odor context) with corresponding three-dimensional head maps (lateral back view) for the baseline (gray) and maternal (blue) odor contexts. (*B*) Amplitude of the face-like–selective response over the right (rOT, green) region of interest encompassing P8, CP6, and T8 (significant in the maternal odor context) and over the left (lOT, orange) homologous region (encompassing P7, CP5, and T7) for each odor condition (*Middle*). Maternal odor enhances the response only over the right hemisphere, leading to a difference between hemispheres in the maternal odor condition but not in the baseline odor condition. On the *Left* and *Right*, the odor effect [maternal minus baseline] in each hemisphere is depicted together with individual data (dots). Error bars represent the SEMs. (*$P < 0.05$, *ns:* $P > 0.05$.)

(Fig. 1*A* and *SI Appendix*, Fig. S1), making the categorization of face-like stimuli challenging for the young infant brain. Indeed, a face-like–selective neural response would emerge only if exemplars from different categories elicit similar neural responses according to their face-likeness, and exemplars from the same categories (i.e., face-like and nonface stimuli) elicit dissimilar neural responses.

Results

Face-Like Categorization in the Infant Brain: A Matter of Smell? To determine whether the 4-mo-old infant brain can categorize a large set of naturalistic face-like stimuli, we first explored occipital, parietal, and temporal channels (*SI Appendix*, Fig. S2) at the group level and identified whether they present a significant categorization response ($Z > 1.64$, $P < 0.05$, one-tailed, signal > noise) following cluster-based permutation testing to control for multiple comparisons (36). Across odor conditions, the mean face-like categorization response measured at 1 Hz is significantly above noise level only over the right hemispheric channel P8 ($Z = 3.13$). When differentiating odor contexts, the response is significant over both the left (P7, $Z = 1.76$) and right hemisphere (P8, $Z = 2.75$) in the baseline odor context but significant only over the right hemisphere in the maternal odor context, encompassing a cluster of three contiguous electrodes (P8, $Z = 1.88$; CP6, $Z = 2.05$; T8, $Z = 2.33$; across channels: $Z = 2.88$). No other electrodes reached significance in any odor context (*SI Appendix*, Table S1). As for the neural categorization response to human faces in infants (22, 23), the face-like–selective response is restricted to the first harmonic (i.e., integer multiple) with no identified channel being significant on the second harmonic (i.e., 2 Hz, all *Z*s < 1.10, *SI Appendix*, Table S1).

Visual inspection of the noise-corrected amplitude spectra and scalp topographies (Fig. 2*A*) confirms a weak, focal, and bilateral face-like–selective response over P7 and P8 in the baseline odor context that shifts toward a larger and spatially more extensive right hemispheric response in the maternal odor context. Therefore, we considered the three channels identified over the right occipitotemporal cortex (rOT: P8, CP6, and T8) and their homologous channels in the left hemisphere (lOT: P7, CP5, and T7) using a repeated-measures ANOVA on amplitude variation with *Odor* (baseline, maternal), *Hemisphere* (left, right), and *Electrode* (T7/8, CP5/6, P7/8) as within-subject factors. Only the *Odor* × *Hemisphere* interaction reached significance (F [1, 19] = 5.76, $P = 0.027$, $\eta_p^2 = 0.23$; all other *F*s < 2.28, all other *P*s > 0.15) because of a significantly larger face-like–selective response in the maternal than in the baseline odor context over the right (maternal minus baseline: 0.48 ± 0.19 [SEM] μV, $t_{19} = 2.56$, $P = 0.019$) but not over the left hemisphere (−0.13 ± 0.20 μV, $t_{19} = 0.67$, $P = 0.51$). Hence, the response is comparable between both hemispheres in the baseline odor condition (0.12 ± 0.15 μV versus −0.02 ± 0.14 μV for the left versus right hemisphere, respectively, $t_{19} = 0.65$, $P = 0.53$) but larger over the right (0.50 ± 0.19 μV) than the left (−0.02 ± 0.14 μV) hemisphere in the maternal odor condition ($t_{19} = 2.42$, $P = 0.026$) (Fig. 2*B*).

Maternal Odor Initiates the Right Hemispheric Advantage for Face-Like Categorization. We further investigated the lateralization of the face-like–selective response in each odor context by computing a lateralization index that estimates the size of hemispheric asymmetry reported to the overall response across both hemispheres (positive and negative values indicate a right and left lateralization, respectively). In the baseline odor context, the face-like–selective response does not differ across hemispheres (mean lateralization index: −1.6 ± 3.9%; $t_{19} = -0.41$, $P = 0.68$). In contrast, the response becomes significantly right lateralized in the maternal odor context (10.4 ± 3.7%; $t_{19} = 2.79$, $P = 0.012$), leading to a significant difference between the two odor conditions (12.0 ± 5.3%; $t_{19} = 2.28$, $P = 0.034$). The presence of maternal odor therefore elicits the right hemispheric lateralization of the face-like categorization response (Fig. 3).

Odor-Driven Face-Like Categorization Depends on the Baseline Response. Our observations suggest that maternal odor initiates the categorization of face-like objects in the right occipitotemporal cortex, except for the right hemispheric channel P8 over which the face-like–selective response is already significant without maternal odor and significant overall when odor conditions are combined. We thereby explored whether the strength of the maternal odor effect is related to the amplitude of the response in the baseline odor context (baseline response) over channel P8 by performing a Spearman's correlation between individual baseline responses and odor effects. This analysis yielded a highly significant negative relationship ($r = -0.71$, $R^2 = 0.51$, $P < 0.001$), showing that infants with low baseline responses also exhibit strong odor effects (Fig. 4*A*). In addition, we examined whether the face-like–selective response emerges with maternal odor in infants without a baseline response over P8 (Fig. 4*B*). We estimated the significance of individual responses (*SI Appendix*, Table S2) and found six out of the 20 infants with a significant baseline response over P8. After removing these infants, the mean baseline response across the 14 remaining infants decreases to −0.19 ± 0.36 μV (whole group: 0.41 ± 0.33 μV), while the face-like–selective response measured in the maternal odor context increases to 1.01 ± 0.37 μV (whole group: 0.71 ± 0.31 μV). Hence, the odor effect is strongly enhanced for these 14 infants without a baseline response (1.20 ± 0.44 μV versus 0.31 ± 0.46 μV for the whole group). These observations remain unchanged when channel P7, over which the baseline response is also significant for the whole group, is added to the analysis (*SI Appendix*, Fig. S3). Overall, this shows that maternal odor initiates the categorization of illusory faces for infants who do not respond differentially to face-like versus nonface objects in the baseline odor context.

Maternal Odor Does Not Influence the General Visual Cortical Response. By using 6-Hz streams of visual stimulation, we also measured a general visual response corresponding to the periodic brain activity elicited by the fast train of natural images and reflecting both the low- and high-level processing of the stimuli. The general visual response is centered over the middle occipital cortex (Fig. 5) with a

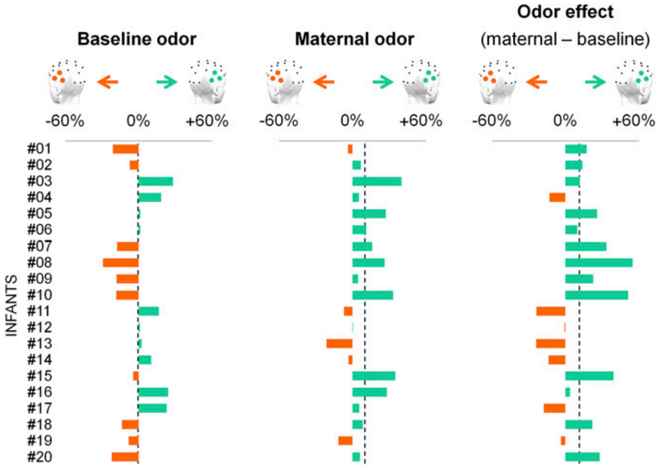

Fig. 3. The face-like–selective response becomes right lateralized in the maternal odor context. Individual lateralization indices (orange and green bars for left- and right-lateralized indices, respectively) and mean indices (dotted lines) reveal that the face-like–selective response does not differ between hemispheres in the baseline odor context (mean index = −1.6%, left), whereas it is significantly right lateralized in the maternal odor context (mean index = 10.4%, middle), leading to a significant difference between odor contexts (mean odor effect = 12.0%, right).

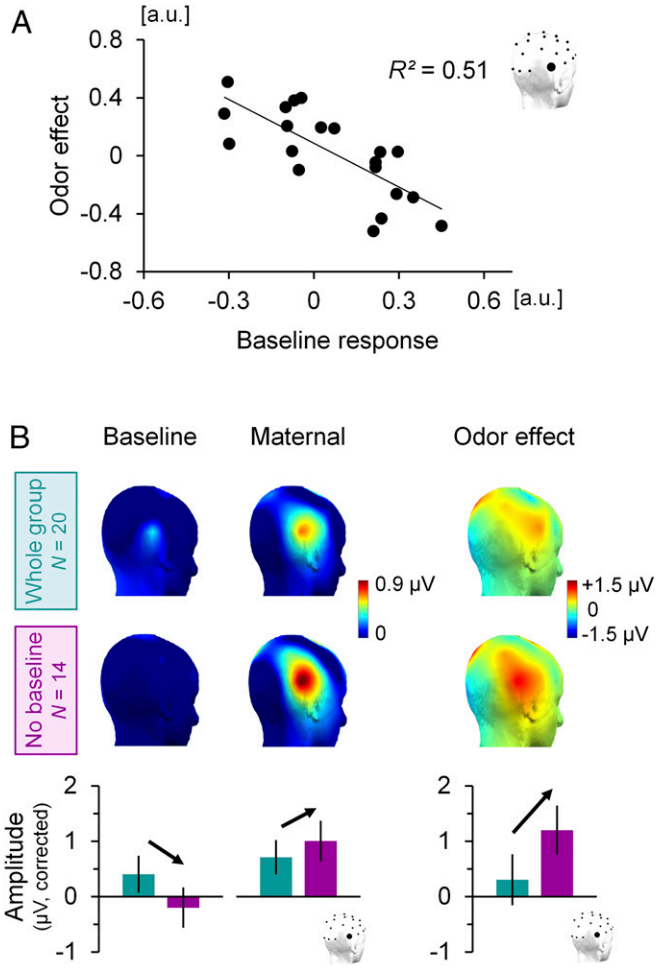

Fig. 4. Face-like categorization emerges with maternal odor. (*A*) The amplitude of the face-like–selective response recorded in the baseline odor context (baseline response) and the strength of the odor effect (maternal minus baseline, both expressed in normalized noise-corrected amplitudes, au: arbitrary unit) are negatively correlated over P8, meaning that the infants with the lowest baseline responses exhibit the strongest odor effects. (*B*) Amplitude (noise corrected) of the face-like–selective response in the baseline and maternal odor contexts and their difference (odor effect) for the whole group ($N = 20$) or after removing the six infants with a significant baseline response over P8 (“No baseline” group, $N = 14$). Right lateral three-dimensional head maps (*Top*) and histograms (*Bottom*) show the modulation of the response in the baseline and maternal odor contexts and corresponding odor effects depending on the group. Error bars represent the SEMs.

cluster of four channels (POz, Oz, O1, and O2) showing a significant response ($Z > 1.64$, $P < 0.05$, one-tailed, signal > noise) at 6 Hz as observed in previous EEG infant studies (22, 23, 37). *Z*-scores range from 3.44 for POz to 16.54 for Oz in the baseline odor condition and from 1.77 for POz to 15.02 for Oz in the maternal odor condition. The response is significant over these four channels until the seventh harmonic (i.e., 42 Hz, Fig. 5*A*). Summed across harmonics and averaged across channels, the overall general visual response corresponds to an amplitude of 3.48 ± 0.53 µV in the baseline odor context ($Z = 24.07$) and 3.47 ± 0.56 µV in the maternal odor context ($Z = 16.21$, Fig. 5*B*). The repeated-measures ANOVA run with *Odor* (maternal, baseline) and *Electrode* (POz, Oz, O1, and O2) as within-subject factors did not reveal a main effect of *Odor* nor an *Odor* × *Electrode* interaction (all Fs < 1). Only a main effect of *Electrode* reached significance (F [2.24, 42.69] $= 13.11$, $\varepsilon = 0.75$, $P < 0.001$, $\eta_p^2 = 0.41$), highlighting a lower response over POz (1.70 ± 0.35 µV) than over any other middle occipital electrode (O1: 3.42 ± 0.61 µV, Oz: 4.77 ± 0.71 µV, O2: 3.99 ± 0.69 µV, all ts > 3.04, all Ps < 0.01) along with a greater response over Oz than the other electrodes (all ts > 2.29, all Ps < 0.05).

Discussion

Using EEG frequency tagging, we hereby demonstrate the 4-mo-old infant brain’s ability to categorize face-like stimuli at a glance in the form of an occipital–temporal response recorded over “face responsive” scalp regions (22, 23). While the face-like–selective response is weak and bilateral in the baseline odor context, adding maternal body odor significantly increases and shifts the response over the right hemisphere, dominant for face categorization in the mature brain. Critically, this intersensory integration of information is particularly effective when there is no sign of face-like categorization for the sole visual system, revealing the ability of a nonvisual input to initiate a category-selective response in the infant visual cortex. In addition, no odor effect is observed on the general response to the fast train of visual stimuli, ruling out a mere influence of maternal odor on visual attention or arousal in line with previous studies (23, 37).

A Selective Response to Illusory Faces in the Infant Brain. Here, we identify a neural response selectively elicited by the periodic occurrence of face-like objects among nonface objects over brain regions typically responding to human faces (i.e., occipital–temporal locations) in previous studies using the same approach in infants (22, 23), children (38), and adults (8). This response is also in line with adult studies characterizing occipitotemporal face-like neural responses with EEG (e.g., refs. 39 and 40) and neuroimaging (e.g., refs. 41 and 42). Categorizing a variety of objects as faces may be considered a trivial achievement at 4 mo, as perceptual abilities are broad enough at that age to respond to various face formats (43–45). However, there is no previous evidence of such a complex categorization response to ambiguous face-like objects at this early age (see, for example, ref. 16) let alone in a challenging experimental situation as used here (i.e., with only a glance allowed at each stimulus in rapid streams of forward- and backward-masked natural images, with highly variable exemplars requiring a common selective response). Indeed, considering that we used a large set of well-controlled face-like and nonface objects, both depicting the same categories, the infant brain must overcome this deceptive information to produce a selective response to a subset of stimuli that only differ from the others by their face-likeness. The greater difficulty of categorizing face-like stimuli is reflected by the amplitude of the face-like–selective response being about three times lower than the categorization response obtained with natural pictures of human faces (23).

Maternal Odor Tunes the Categorization of Face-Like Objects in the Right Hemisphere. Strikingly, the face-like–selective response evolves from a weak and bilateral neural activity in the baseline odor context to a larger and strictly right hemispheric response when adding maternal odor. The implications of this finding are twofold. First, it reveals that maternal odor does not only facilitate the categorization of human faces (23) but also of a wide variety of nonhuman objects on the shared basis that they can be interpreted as faces. In that respect, one may wonder which nonhuman visual cues are perceived as face-like in the presence of maternal odor. Face-like stimuli usually have salient “eye-like features” (e.g., Fig. 1*A* and *SI Appendix*, Fig. S1), the eyes being considered the most important features to identify an illusory face in adults (46) and are the most explored face region when 4 mo olds are exposed to maternal odor (25). However, since we used the same object categories for both face-like and nonface objects, eye-like features (e.g., egg yolks) were present in both stimulus sets and had to be integrated in a configuration to be perceived as face-like. Maternal odor might therefore trigger the perception of facial attributes from the spatial

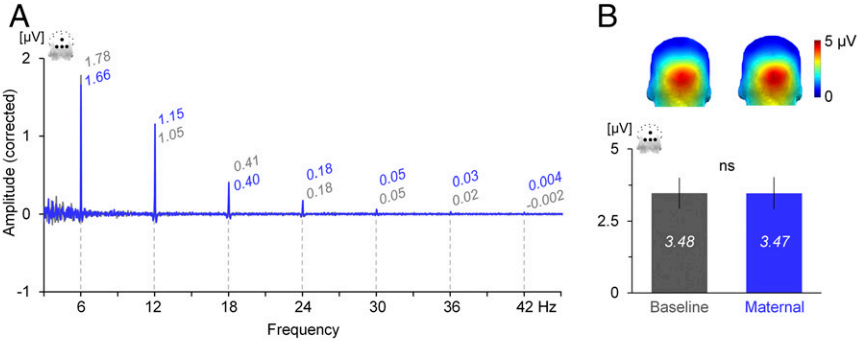

Fig. 5. The general visual response. (*A*) Amplitude spectra (noise corrected) showing the general visual response recorded over middle occipital electrodes (O1/2, POz, and Oz) at the frequency of stimulation (6 Hz) and its harmonics (i.e., integer multiples, up to 42 Hz) for the baseline (gray) and the maternal (blue) odor contexts. (*B*) Three-dimensional head maps (back view) of the overall response summed across seven harmonics (*Top*) and its mean amplitude (noise corrected) across the four middle occipital channels (*Bottom*) for each odor condition. No effect of maternal odor is noted for this response (*ns:* $P = 0.98$). Error bars represent the SEMs.

arrangement between parts rather than from isolated features. This interpretation is supported by the localization of the odor effect over the right hemisphere in line with its role in the perception of face-like configurations in adults (39, 40, 42).

Second, the right lateralization of the face-like–selective response with maternal odor is relevant to the long-standing debate about the emergence of the right hemisphere advantage for face categorization during development (for review, refer to ref. 47). While clearly established in adults (e.g., ref. 9), this right hemispheric dominance has been inconsistently observed in children and infants (17, 18, 20, 22, 38, 48, 49). This led to suggest that the right hemisphere advantage depends on the acquisition of literacy and the progressive tuning of the left occipitotemporal cortex for word recognition (50, 51). However, the present finding indicates that maternal odor elicits a strong right lateralization of face-(like)–selective responses in the infant brain. Given that infants are often tested on their parents' lap, maternal body odor and, more generally, any parental multisensory cue may constitute a potent yet neglected factor of hemispheric lateralization in infancy. While inferring localization and even hemispheric lateralization from scalp EEG must be made with caution, and while learning to read may still later contribute to strengthen hemispheric asymmetry, our observation suggests that the origin of the right hemisphere advantage for faces has to be sought in early infancy, well before the onset of literacy.

Visual Categorization Can Emerge with the Help of a Nonvisual Cue. A key finding of the present study is that the weakest individual responses in the baseline odor condition lead to the strongest odor effects: the face-like–selective response arises with maternal odor in infants who do not respond in the baseline odor context. This finding relates to the inverse effectiveness principle, whereby the efficiency of multisensory integration increases as the responsiveness to unisensory stimuli decreases (35). In other words, the more ambiguous the visual input is for a given infant, the more maternal odor cues can strengthen, and even initiate, face-(like) categorization. More generally, this supports the view that co-occurring multisensory inputs actively organize and shape infants' knowledge of the environment (31). Interestingly, while co-occurrence means that spatiotemporal relationships between events from different senses are critical, odor perception is relatively insensitive to variations in space and time (33). In addition, olfaction is an early maturing sense, ideally suited to assist the development of later-maturing senses such as vision (32). These two properties make olfaction a relevant sensory modality for the acquisition of visual categories in the developing human brain.

Along this line, one may wonder whether the odor effect would be maintained at a later age after maturation of the visual system and the progressive tuning of face categorization abilities from experience (45). The detection of human faces in naturalistic scenes strongly improves during the first year of life (refer to refs. 14 and 15 for review) following extensive exposure to faces (52, 53). Similarly, the face-selective response tagged in EEG develops quantitatively and qualitatively from infancy to adulthood (8, 22, 38). Interestingly, according to our observation, some infants do not need maternal odor to selectively respond to face-like objects. We therefore propose that the odor effect progressively declines as the sole visual system becomes able to readily categorize stimuli as faces, with a variable rate across infants. Future studies should investigate this putative decline with the development of face categorization. The potential influence of visual information on odor perception should also be delineated to precisely understand how the olfactory and visual systems support each other during development and whether this support is reciprocal and symmetrical.

Putative Neural Mechanisms for Odor-Driven Visual Categorization. In line with the role of intersensory congruency in perceptual development (54), the repeated co-occurrence of odor and visual cues in the social niche of the developing infant could prime the face category when the infant smells a (maternal) body odor. This would be reflected by strengthened connectivity between the olfactory and visual systems through reentrant signaling (34) such that maternal odor might preactivate face-selective regions in the ventral visual pathway, thereby tuning their responsiveness to a face-(like) stimulus. This interpretation is consistent with findings in adults showing that body odors alone activate the lateral fusiform gyrus (55), a well-known category-selective visual region and downstream recipient of the primary olfactory cortex (56). This is more broadly in line with large-scale connectivity between distinct "unisensory" brain regions dedicated to the same semantic domain (57). Interestingly, it has been recently shown that the functional layout of the category-selective visual cortex can be constrained by auditory inputs in people who are born blind (58). We thus speculate that this mechanism also applies in infancy because face-selective regions are too immature to readily categorize face-(like) stimuli from the sole visual input. Despite the difficulty of setting neuroimaging studies with young infants, recent advances (59, 60) offer a promising avenue for the future investigation of the neural mechanisms at stake in odor-driven category-selective visual responses.

It is worth noting that intersensory effects in the infant brain are not limited to social information (61), and evidence from adults shows that nonsocial odors actively modulate visual perception

(62–64). However, social stimuli are arguably one of the most relevant and familiar cues in early development in both visual (52, 53) and olfactory (32) domains. This makes social information the best candidate to evidence potent intersensory effects during the first months of life and, more generally, to demonstrate that the developing brain takes advantage of multisensory inputs for category acquisition. In this regard, one may question whether face-(like) categorization in the infant brain does not simply reflect the categorization of familiar as opposed to unfamiliar (visual) inputs. Indeed, the greater infants' experience with human faces (45, 52, 53) creates a unique familiarity that is intrinsically associated with the face category. Therefore, it would be impossible to compare faces to a large stimulus set of another category that would be familiar enough to infants to disentangle the effect of familiarity from the effect of face signals per se. However, by using the same unfamiliar (to infants) object categories for both face-like and nonface stimuli, our study provides the best option to measure face-(like) categorization in the infant brain while minimizing the contribution of differential familiarity between stimulus sets. Finally, one could also inquire whether body odors that do not belong to the infant's own mother would be able to shape face-(like) categorization. Body odors convey nested information about people and their internal states (65) and influence the perception of congruent facial information in adults (66, 67). However, previous infant studies investigating this question have used maternal odors for their powerful effectiveness on infant behavior and cognition (23–25, 30, 37). Whether and how different social odors interact with face perception in infancy is yet to be explored.

Materials and Methods

Participants. A total of 20 clinically normal full-term 4 mo olds participated in the study (9 females, mean age ± *SD*: 132 ± 7 d, range: 119 to 145 d). One additional infant was tested but not included in the final sample due to an insufficient number of trials. Sample size was estimated a priori by considering a moderate odor effect on face-like categorization (i.e., Cohen's $d = +0.65$), a significance level $\alpha = 0.05$ (two-tailed), and a usual power $1\text{-}\beta = 0.80$. All parents gave written informed consent, and none reported their infant suffering from any sensory (olfactory, visual), neurological, or psychiatric disorder. The full study protocol was conducted according to the Declaration of Helsinki and approved by the French ethics committee (Comité de Protection des Personnes Sud-Est III—2016-A02056-45).

Visual Stimuli. The full stimulus set consisted of 236 natural images of various objects (animals, plants, and man-made objects). They each depicted one single object unsegmented from its background, varying in color, viewpoint and lighting condition. A subset of these images ($N = 66$) depicted an illusory face (i.e., face-like objects), based on the same categories than the remaining objects (examples in Fig. 1*A*; full set in *SI Appendix*, Fig. S1, and refer to *SI Appendix, SI Materials and Methods* for more details about stimulus edition). Stimuli were displayed on a 60-Hz 24-inch light-emitting diode screen (1,920 × 1,080 pixels resolution) and subtended ~24° of visual angle (Fig. 1*B*).

Odor Stimuli. Infants were alternatively presented with the maternal odor and a baseline odor, corresponding to the two odor conditions. Odor collection followed a standardized procedure using a white T-shirt (e.g., ref. 25). One T-shirt was sent to the mother with instructions for night wear (*SI Appendix, SI Materials and Methods*). The baseline odor condition consisted in an identical, yet unworn, T-shirt.

Design and Procedure. To isolate and quantify both a face-like categorization response and a general visual response within the same stimulation sequence, we used a design similar to previous face categorization studies using fast periodic visual stimulation coupled with EEG frequency tagging (22, 23). We presented 34.5-s long sequences showing 207 images on a midlevel gray background (i.e., 128/255 in greyscale) at a base rate of 6 Hz (i.e., six images per second). At this rate, images last 167 ms. Sequences were composed of an initial blank prestimulation interval of 0.5 s followed by a fade-in of 1.833 s in which contrast modulation ramped up from 0 to 100%, and then the full-contrast stimulation of 31.167 s was followed by a fade-out of 0.833 s during which the contrast ramped down to 0%, closing on a final blank poststimulation interval of 0.167 s.

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

An adjusted EEG cap was placed on the infants' head before installing them in a baby car seat. Infants were seated at a 57 cm distance from the screen in the light- and sound-attenuated Babylab of Dijon (France). The laboratory is equipped to minimize olfactory noise (*SI Appendix, SI Materials and Methods*). Using dedicated disposable nitrile gloves, the T-shirt was folded in order to optimally expose to the most odorous areas (axillary, breast, and neck regions) and placed on the infant chest underneath the seatbelts a few seconds before a trial started. Each odor condition was therefore delivered throughout the sequence, such that odor-evoked neural activity is not periodic and does not translate at the tagged frequencies in the EEG spectrum. T-shirts were alternated every two sequences, observing a minimum 1-min interval between them. During stimulation, parents stayed distant from their infant with whom they interacted only in case of manifest distress. Sounds could be used as attention getter (*SI Appendix, SI Materials and Methods*). The experimenter stopped testing on an infant-based criterion, that is, at parental demand, when the infant showed no more interest toward the screen and/or tiredness or discomfort. The mean total number of sequences performed per infant was of nine (range: 6 to 12) for an overall testing duration comprised between 3 min 27 s and 6 min 54 s per infant.

EEG Recording and Analysis. Continuous EEG acquisition ran on ASAlab 4.7 (ANT) using a 32 Ag/AgCl electrode cap (Waveguard, ANT) according to the 10–10 configuration system (acquisition reference: frontocentral channel AFz, sampling rate: 1,024 Hz, electrode impedance < 15 kΩ). EEG data were preprocessed and a frequency-domain analysis (*SI Appendix, SI Materials and Methods*) was conducted to isolate and quantify both the face-like categorization response (1 Hz and harmonics) and the general visual response (6 Hz and harmonics). Statistical analyses were performed by first identifying responsive channels using *Z*-scores (i.e., signal versus surrounding noise) and nonparametric cluster-based permutation testing (36) and then by comparing the neural responses across odor conditions using repeated-measures ANOVA on the noise-corrected amplitude at identified channels. The lateralization of the face-like–selective response was also investigated with a lateralization index, and the relationship between the face-like categorization response recorded in the baseline odor context and the maternal odor effect was estimated to determine whether the odor effect is mainly driven by infants without a response in the baseline context (*SI Appendix, SI Materials and Methods*).

Data Availability. All EEG datasets and participant information data have been deposited in the Open Science Framework and are freely available at http://doi.org/10.17605/OSF.IO/KF7MU (68)

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