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Tips from the Nose: Odor-driven Visual Categorization in the Developing Human Brain

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Abstract

While humans are usually considered as overly visual, human vision is poor at the beginning of life. In contrast, olfaction is an early-developing sense that promotes adaptive responses and may support visual development. Accordingly, the present chapter reviews recent studies from our group showing that the mother's body odor selectively facilitates face categorization in the 4-month-old human brain. We also reveal that as infants grow up, their ability to categorize faces improves until 12 months of age and becomes progressively independent of the influence of maternal odor. We open with findings in adults, demonstrating that odor-driven visual categorization is still observed for ambiguous stimuli, aligning with the inverse effectiveness principle of multisensory integration. Overall, this body of research exposes the powerful impact of odors on visual categorization, especially how social chemical cues emanating from the mother can drive the categorization of conspecifics from visual inputs in the developing human brain. These findings suggest that odors act as disambiguating cues fostering visual categorization as an inverse function of its effectiveness, and point towards a critical role of multisensory inputs for the acquisition of categories in humans, relying on the ordered development across the senses.

Keywords

Human infant, Face categorization, Maternal body odor, Multisensory perception, Inverse effectiveness, Electroencephalography (EEG), Frequency-tagging

1 Introduction

Smell has long been neglected in humans, while vision is generally considered the dominant sense (Broca, 1879; Darwin, 1871; Huttmacher, 2019). However, a recent surge in research has demonstrated that humans possess a keen sense of smell, with performance sometimes akin to that of other species reputed for their olfactory prowess (e.g., McGann, 2017). In fact, olfaction plays a fundamental role in how humans perceive their environment, as recently highlighted by the Covid-19 pandemic and associated anosmia (Parma et al., 2020). A growing body of research indicates that olfaction can even influence perception in the other senses, including visual perception (e.g., Demattè et al., 2006; Seigneuric et al., 2010; W. Zhou et al., 2010).

The key function of olfaction in the human species is particularly clear at the beginning of life and further extends during different sensitive periods throughout development (Schaal et al., 2020). Olfaction is indeed an early-maturing sense reaching operative functionality from the beginning of the third gestational trimester (Browne, 2008; Schaal et al., 2004). Chemically, odor compounds in the amniotic fluid and in the mother's secretions (e.g., colostrum/milk, sweat from the breast area, etc.) partially overlap (Loos et al., 2019; Porter & Winberg, 1999). Neonates show a strong responsiveness to these odor cues (e.g., Klaey-Tassone et al., 2020), enabling stability and familiarity in a postnatal environment full of sensory novelty.

Unlike olfaction, vision is a late-developing sense in infancy. Visual perception mainly starts to develop from birth onward when newborns are exposed for the first time to a rich and complex flow of visual information. The anatomical development of the visual system in human infants takes longer than the other senses to install (Graven & Browne, 2008) and preterm infants have no pupillary response to light, showing a delayed development compared to the other senses, already reacting to stimuli in utero. Human visual function is thus limited at birth (e.g., poor visual acuity and color vision until 2-3 postnatal months) and follows a protracted development over the first postnatal year (Braddick & Atkinson, 2011).

This ordered sequence of sensory development, common to most vertebrate species, may actually be far from an arbitrary developmental timing across independent and parallel sensory systems (Turkewitz & Devenny, 1993). Sensory ontogeny may be adaptive for the offspring and benefit to perceptual learning, early-maturing senses sustaining later-developing senses. The early onset of the olfactory system therefore put olfaction in an ideal position to mediate perception in the less mature sense of vision.

This chapter aims to outline recent work on the influence of one of the most relevant odors for young infants, their mother's body odor, on their ability to categorize a variety of visual stimuli as faces. We will first describe how maternal chemosignaling actively participates in orienting and regulating infant physiology and behavior early in life. Next, we will portray how one of the most important functions of visual perception – *categorization* – takes time to develop from brain maturation and accumulated visual experience, focusing on the most relevant visual stimuli for young infants: faces. Then, we will survey recent research conducted in 4- to 12-month-old infants to delineate the extent to which the mother's body odor shapes face categorization in the developing brain, as well as experiments conducted in adults to determine whether body odors still influence visual categorization in the mature brain. Finally, we will discuss which mechanisms may underlie the

integration between olfaction and vision and what they may tell us about (multi)sensory development. We will conclude with remaining open questions and suggest directions for future research.

1.1 Mother-to-infant chemical communication

The chemical senses have an early functional onset during the third gestational trimester (Browne, 2008; Schaal et al., 2004). In particular, the olfactory system is a primary medium of communication from the mother to her infant already before birth. The amniotic fluid is filled with odorous compounds conveying information about the mother's physiological state, including both stable (e.g., genetic) and transient information (e.g., emotional reactions), and about external compounds she consumes (e.g., food, cosmetics) (Schaal et al., 2002). Human fetuses use and retain the odor properties of their prenatal environment such that neonates then differentially respond to the odor of their own amniotic fluid (Schaal et al., 1998), or to flavors they have learned from their mother's diet (Faas et al., 2000; Schaal et al., 2000), some of these early preferences lasting long after birth (Hepper et al., 2013; Wagner et al., 2019). The uterine chemical environment therefore provides an early olfactory experience that benefits to the infant after birth. Many odorants experienced in utero are also found in the mother's body secretions, especially from the areolar-nipple and axillary areas (i.e., colostrum, milk, sweat), allowing a transnatal transfer of information (Hartmann et al., 2012; Porter & Winberg, 1999; Spahn et al., 2019).

During the first postnatal months, maternal secretions elicit adaptive behaviors to satisfy physiological needs and promote regulatory functions in her young infant. A few minutes after birth, maternal odor cues from an unwashed *vs.* washed breast guide the neonate towards the nipple to feed (Varendi et al., 1994). Similarly, the mother's breast, presented entirely or partly covered, stimulates breathing and orofacial reactions, while this behavior disappears when the breast is fully covered by a transparent film, i.e., blocking olfactory but not visual cues (Doucet et al., 2007, 2009). The odor of human colostrum/milk is obviously highly attractive in the first hours of aerial life, eliciting positive emotional facial reactions, head orientation and appetitive behavior (Klaey-Tassone et al., 2020; Marlier et al., 1998; Soussignan et al., 1997). Human milk is also attractive to bottle-fed infants who never experienced breastfeeding, revealing its potency to provoke adaptive behaviors even in the absence of postnatal exposure (Marlier & Schaal, 2005).

The mother's scent does not only convey food-related cues, but has a soothing and distress-relieving effect (Zhang et al., 2018, for review). For instance, physiological (e.g., cortisol level, heart rate and oxygen saturation) and behavioral (e.g., crying intensity and duration, motor agitation) stress reactions observed during medical procedures endured in neonatology are reduced in neonates exposed to the odors emanating from the mother. These effects are shown with either pre- (e.g., amniotic fluid) or postnatal odors (e.g., breast milk) and suggest an analgesic effect (Akcan & Polat, 2016; Jebreili et al., 2015; Nishitani et al., 2009; Rattaz et al., 2005). Maternal body odors also convey identifying cues about the emitter that can be actively used by infants. Indeed, while many effects previously described have been obtained using secretions from either the own mother or (an)other mother(s), infants are also able to differentiate between them. For example, neonates

preferentially orient towards their own rather than another mother's odor, whether the scent comes from her breast (Macfarlane, 1975; Russell, 1976), armpit (Cernoch & Porter, 1985; Marin et al., 2015), or uterus (i.e., amniotic fluid; Schaal et al., 1998). Neonates also exhibit more appetitive behavior when exposed to a hospital gown worn by their mother rather than by another mother (Sullivan & Toubas, 1998). Newborns do not only perform odor-based discrimination of familiar *vs.* unfamiliar individuals (i.e., their own *vs.* another mother), they also recognize categories of conspecifics, such as lactating women *vs.* non-lactating women (Makin & Porter, 1989), and species-specific odors, such as the odor of human *vs.* non-human milk (Marlier & Schaal, 2005; Russell, 1976).

At the brain level, preterm and full-term neonates presented with a cloth worn by their mother show an activation of the orbitofrontal cortex (OFC) as assessed by functional near-infrared spectroscopy (Frie et al., 2019). This neural response has been interpreted as an odor-induced state of arousal, in line with the observation that the mother's breast odor triggers eye opening in 3-day-old newborns and may increase visual attention (Doucet et al., 2007). The OFC is also activated by the odor of colostrum in the youngest neonates and this response then progressively decreases as a function of age (Bartocci et al., 2000), suggesting a relationship with their behavioral attraction to colostrum during the first postnatal days (Klaey-Tassone et al., 2020). Similarly, breast milk odor activates the OFC more than formula milk odor irrespective of the infants' experience with formula milk (Aoyama et al., 2010), corroborating behavioral findings (Marlier & Schaal, 2005). Later in the first year, the frontal region of 2- to 9-month-old infants still presents with a larger response to breast milk odor than other odors as measured by scalp electroencephalography (EEG) (Gellrich et al., 2021). Exposure to the mother's odor also decreases the brain response to unfamiliar fearful faces in 7-month-old infants, interpreted as if they were reassured by chemical cues signaling the presence of their mother in an anxious/stressful context (Jessen, 2020). At the same age, a recent study has shown greater brain-to-brain synchrony between infants and unfamiliar women when infants are exposed to their mother's body odor compared to a baseline odor, in association with greater looking time at the unfamiliar woman's face, suggesting that maternal odor promotes infants' interest towards unknown conspecifics (Endevelt-Shapira et al., 2021).

1.2 The early tuning of visual categorization

In contrast to early olfactory learning, the human infant brain only starts to experience a flurry of visual inputs from birth onward. To avoid being overwhelmed by the myriad of inputs coming from the visual surroundings, the infant visual system must progressively go beyond low-level cues (e.g., luminance, contrast, spatial frequencies) and organize visual events into discrete entities according to their meaning. This fundamental function, *visual categorization*, deals with environmental diversity by putting some stimuli into distinct categories (between-category discrimination), while grouping others into the same category (within-category generalization). However, visual categorization is challenging for the infant brain as stimuli belonging to different categories can share some low-level cues, whereas different exemplars from a single category can be widely

variable in appearance. Categorizing the visual environment is therefore one of the most fundamental abilities that infants must acquire during the first months of postnatal life.

1.2.1 An early ability to categorize visual stimuli in infancy

As early as 3 months of age, behavioral studies have documented human infants' abilities to visually categorize stimuli. For instance, when infants are first exposed to several pictures of cats (i.e., familiarization) and then presented with paired pictures of another cat and a dog, they look more at the dog (i.e., novelty preference), suggesting that they recognize the cat as belonging to the category they have been familiarized to (Quinn et al., 1993). It is therefore suggested that 3- to 4-month-old infants are already able to rapidly extract regularities among unfamiliar visual objects (i.e., during the course of an experiment, namely *online category learning*) (Eimas & Quinn, 1994). Over the last three decades, a large body of research using the familiarization/novelty preference paradigm has argued that young infants have either broad (e.g., furniture *vs.* animals) or subtler (e.g., cats *vs.* tigers) categorization abilities, either for abstract/unfamiliar objects or for already-encountered real-life objects (Quinn, 2011, for review).

The neural underpinnings of visual categorization have also been investigated in infancy. In particular, developmental scientists have routinely used scalp EEG as a non-invasive, efficient and relatively inexpensive method to isolate neural markers of visual categorization in human infants (Hoehl, 2016, for review). Electrophysiological studies using event-related potentials (i.e., ERPs) have reported a larger negative ERP component at central scalp locations for novel exemplars when comparing two categories of living beings (Marinović et al., 2014; Quinn et al., 2006) or one living *vs.* one nonliving object category (Elsner et al., 2013; Grossmann et al., 2009), interpreted as sustained attention to novelty (Reynolds & Richards, 2005). It has also been evidenced that the brain response to different exemplars of the same category evolves throughout an experiment, as a neural signature of online category learning (Quinn et al., 2006).

1.2.2 Categorizing conspecifics from visual inputs: the development of face categorization

The ability to categorize visual objects culminates in infants' ability to categorize the face of their conspecifics early on, for which the first year represents a highly sensitive period (Pascalis et al., 2020). Newborns already prefer to track slowly-moving stimuli organized with more features in their upper part, like faces (Johnson et al., 1991; Valenza et al., 1996; see Buiatti et al., 2019, for a neural signature in EEG). However, whether this truly reflects face selectivity, or simply an early preference for stimuli with more elements in the upper visual field, namely top-heavy patterns, has been debated (Macchi Cassia et al., 2004; Turati et al., 2002; Simion et al., 2007, for review). Infants need a few additional months to exhibit preferential looking for faces over other objects (de Heering et al., 2016; Durand et al., 2013). The top-heavy bias becomes selective to faces at 3 months of age (Turati et al., 2005), mirroring the well-known face inversion effect described in adults (Yin, 1969; Rossion, 2008, for review). When faces are embedded in complex visual arrays (Di Giorgio et al., 2012;

Gliga et al., 2009; Kwon et al., 2016) or in naturalistic scenes and sequences (Amso et al., 2014; Frank et al., 2014; Kelly et al., 2019), the ability to detect them mainly improves after 6 months of age (see Leppänen, 2016, for review). Head-mounted cameras provide in situ measures showing that faces are not only the most present visual object in the infant everyday scenes, but that they also benefit from a qualitative advantage compared to the exposure to other visual objects through reciprocal face-to-face interactions (Jayaraman et al., 2015). Thus, maturation and experience are required to tune and refine the visual categorization of conspecifics from their faces (Nelson, 2001; Pascalis et al., 2020; Simion & Di Giorgio, 2015, for reviews).

At the brain level, the emergence of the “face” category has been widely explored by comparing the ERPs elicited by faces from those elicited by other objects. A large body of research has identified distinct neural activity for faces vs. meaningless (Halit et al., 2004; Kouider et al., 2013) or meaningful (Conte et al., 2020; de Haan & Nelson, 1999; Gliga & Dehaene-Lambertz, 2007; Peykarjou & Hoehl, 2013) stimuli after at least 3-4 months. However, it is fair to say that the standard ERP approach is limited to document the development of face categorization in the infant brain¹. Hence, infant ERP studies have often recorded weak and inconsistent neural responses to faces, which are generally dominated by a medial occipital activity driven by low-level image statistics rather than the face category *per se* (see de Haan et al., 2003; Hoehl, 2016, for reviews).

To circumvent these issues, a recent EEG approach, termed frequency-tagging EEG, has been introduced. It capitalizes on the old observation that a periodic sensory input elicits a same-frequency response over corresponding sensory cortices which can be expressed at the exact stimulation frequency and its harmonics (i.e., integer multiples) in the frequency spectrum (Adrian & Matthews, 1934; Norcia et al., 2015, for review; see section 2.1 for details). This approach, actually used for decades in seminal infant studies of the visual system (e.g., Harris et al., 1976), has been recently adapted to investigate high-level vision, especially markers of face perception abilities in the infant brain (e.g., de Heering & Rossion, 2015; Peykarjou et al., 2017, 2022; Poncet et al., 2022). With this approach, a face-selective response has been evidenced at 4 to 6 months of age over the right occipito-temporal cortex, individual responses were quantified, and face selectivity was significant in a majority of infants (de Heering & Rossion, 2015). However, at this age, the face-selective response is low and captured in a single harmonic. The response then increases, becomes bilateral and distributed on several harmonics in 5- (Lochy et al., 2019) and 10-year-old children (Vettori et al., 2019), before being observed on many more harmonics in adults, with the reappearance of the right hemisphere advantage (e.g., Retter & Rossion, 2016; Rossion et al., 2015). This nonlinear evolution of face-selective neural activity reveals the complex developmental pattern of the face categorization system over the first years of life.

¹ ERPs suffer from a low signal-to-noise ratio and are constrained by their sensitivity to (e.g., muscular) artifacts in awake infant studies. ERPs also use post-hoc subtraction between absolute brain responses to transient stimuli, such that face-selective neural activity is indirectly obtained and can be masked by large noise in the subtracted responses, or driven by a subset of stimuli. In addition, the time-windows of ERP components are often difficult to define objectively from brain responses that are heterogenous in terms of shape, latency and polarity across individuals and age groups. Finally, ERP studies generally use a limited set of homogenous and edited stimuli (i.e., segmented from their natural background with identical exposure conditions across category exemplars; see footnote 2), and compare faces to only a few nonface categories.

2 Odor-driven face categorization in the developing human brain

To sum up previous sections, the mother's body odor, henceforth designated as "maternal odor", refers to a mixture of excretions/secretions from the axillary and areolar-nipple areas that elicits differentiable physiological, behavioral and neural responses in infants. Maternal odor is particularly involved in nursing and caregiving, having a specific weight in the sensory bubble surrounding the offspring during the first postnatal months. Aside from these functions, maternal odor is a major sensory control of early social interactions and provides information about what constitutes the body odor of conspecifics. Interestingly, maternal odor also boosts arousal and visual attention early on, allowing the newborn to sample visual cues concurrent to the presentation of the chemical cues. This may be particularly frequent in the very beginning of life, when maternal odor could be a powerful reinforcement during exposure to salient visual information. As a systematically available and co-occurring cue during the infant's experience with conspecifics, whether it is the mother or other conspecifics, maternal odor is therefore in an ideal position to ease the categorization of faces, which takes several years to develop.

A few pieces of evidence tend, indeed, to support a tutoring function of maternal odor in the development of face perception. Seven-month-olds display a reduced neural response to fearful faces in the presence of maternal odor (Jessen, 2020) and infants exposed to maternal odor *vs.* a baseline odor look more at their mother's face at 4 months of age (Durand et al., 2020). Most importantly for our purpose, maternal odor influences the visual exploration of paired pictures of an unfamiliar female face and a car in 4-month-old infants (Durand et al., 2013). In this latter study, infants exposed to maternal odor spent more time looking at the face than infants exposed to a baseline odor whereas equal gazing was found for the car, suggesting improved categorization of the face due to maternal odor. However, although this behavioral effect is important enough to inform about the final output of the cognitive system, it can be due to reorientation of attention following face categorization and it has been described only during pairwise discrimination of a few stimuli. Hence, we aimed at producing direct evidence that maternal odor shapes face categorization (i.e., incorporating both discrimination of faces from many nonface categories and generalization across widely variable individual faces) in the infant brain.

2.1 Measuring maternal odor's influence on face categorization

To measure face categorization in the infant brain and its sensitivity to maternal odor, we conducted several studies relying on scalp EEG and a frequency-tagging approach, which already successfully isolated a face-selective neural response in 4- to 6-month-old infants (de Heering & Rossion, 2015; see section 1.2.2). We exposed infants to a fast periodic visual stimulation presenting streams of various living and nonliving objects (i.e., 170 images depicting plants, animals and man-made objects) at a base rate of 6 Hz (6 images / second; Figure 1a left) and face images (i.e., 66 or 68 images of individual male and female adult faces) were interspersed every 6th image (i.e., at 6 Hz / 6 = 1 Hz). Two distinct neural responses elicited during a single

stimulation sequence were thus tagged in the EEG frequency spectrum: a general response measured at 6 Hz and harmonics (i.e., integer multiples) and a face-selective response measured at 1 Hz and harmonics. The general visual response is common to both face and nonface stimuli, reflecting the brain synchronization to every cue that changes 6 times per second. To emerge, the response to the fast train of images simply requires that infants look at the visual stimulation. In contrast, the face-selective response translates in the frequency spectrum only if the infant brain categorizes faces. It reflects a *differential* response to faces (discrimination from various nonface objects) that is reliably elicited by a majority of face stimuli (generalization across face exemplars). Importantly, we used naturalistic stimuli² (see examples in Figure 1), such that the face-selective response is a signature of rich face categorization devoid of low-level confounds, controlling for category-irrelevant properties by variability rather than elimination or homogenization, as imposed in natural viewing conditions. This is an important aspect to ensure that infants are able to categorize a variety of human faces against many other biological (i.e., animals, plants) or manufactured objects, all embedded in their natural backgrounds, which is not a trivial achievement for their brain.

Frequency-tagged responses thereby provide many advantages when testing young infants. First, brain responses are measured at pre-defined frequencies, making the approach highly objective. Second, stimuli are presented at a fast rate, allowing measurable responses in a few minutes of recording. Third, frequency-tagged responses are of high signal-to-noise ratio with relative immunity to artifacts, reducing experimental attrition. This is due to the frequency resolution obtained by analyzing “long” stimulation sequences (e.g., we used 32-second-long sequences in our studies, leading to a resolution of $1/32 = 0.03125$ Hz, i.e., one value every 0.03125 Hz). Therefore, noise spreads to broad frequency ranges while the signal is isolated in tiny frequency bins associated with little noise. The approach is thus resistant to high-amplitude artifacts such as those generated by infant movements, which usually lead to the rejection of a large number of trials in standard ERP studies and often result in few reliable data during the short testing duration imposed by infants. Fourth, various measurements, including statistical indices, can be derived from the amplitude at the defined frequencies and surrounding noise, allowing individual analysis of a single response. Finally, with frequency-domain representation of the brain responses, there is no assumption as to their properties (e.g., form, temporal dynamics), increasing the robustness of the approach in case of high variability across individuals and age groups. For all these benefits with a difficult-to-test population such as young infants, we used frequency-tagging EEG as a powerful approach to measure face categorization using the same methodology in infants and adults.

During visual stimulation, odors were concurrently presented as context. Such odor delivery does not need an olfactometer inserting tubes in infants’ nostrils, avoiding a considerable challenge to infant compliance, and suits well the 32-second-long stimulation sequences we used. Maternal odor was collected from a t-shirt the mother had worn for three consecutive nights preceding the experiment, to reduce activity-related individual differences. During the days, this t-shirt was stored in a hermetic bag left at ambient temperature. Maternal

² Naturalistic stimuli depict the main item of each stimulus embedded in the original background the photography was taken in, without controlling for viewpoints, luminance, contrast, colors, etc. This is opposed to edited (sometimes referred to as standardized) stimuli which are commonly used in visual experiments, where the item is isolated from its background and generally homogenized across the different exemplars to control for inter-stimulus variability.

odor was contrasted to a baseline odor consisting in an unworn t-shirt with the same storage procedure (Figure 1b left). During testing, the t-shirts were disposed on the infants' upper chest and folded to optimally expose infants to the parts that were in contact with the most odorous areas, i.e., the axillary and breast regions (Figure 1c left).

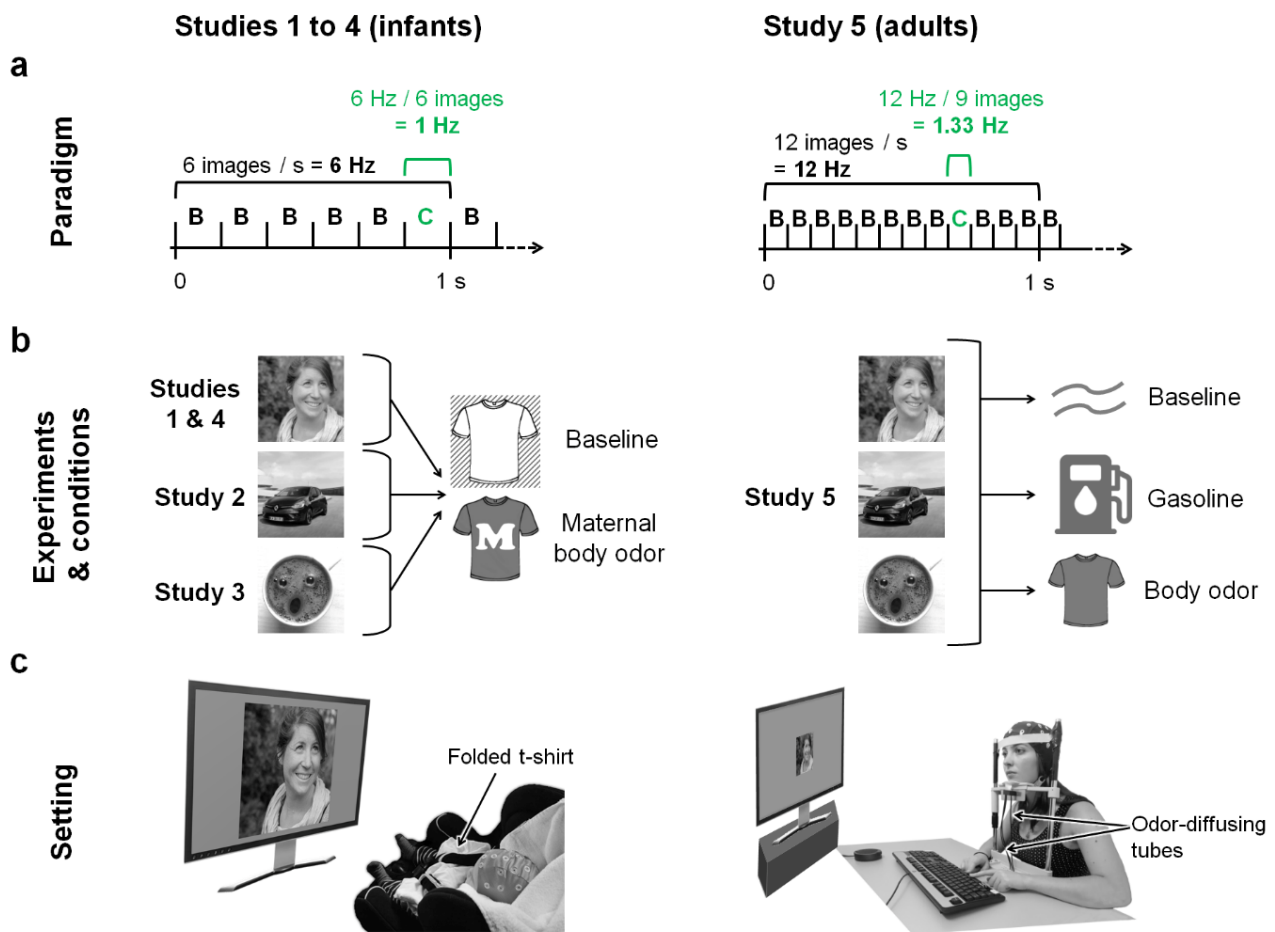


Fig. 1 Measuring body odor influence on face categorization in the infant (left) and adult (right) brains using a frequency-tagging approach in scalp electroencephalography (EEG). (a) A variety of pictures of visual objects were presented at a rapid base rate (e.g., 6 stimuli / s = 6 Hz; referred to as “B”) and various stimuli from a target category were periodically inserted in between (e.g., every 6th stimulus at 6 Hz, i.e., at 6/6 = 1 Hz; referred to as “C”) to isolate a category-selective neural response at the same frequency and its harmonics in the EEG spectrum. (b) In infants, Studies 1 and 4 used human faces as the target category, Study 2 used cars and Study 3 used facelike objects (i.e., nonface objects that elicit the illusory perception of a face in adults). Infants were exposed to maternal odor collected on a t-shirt for three nights or to a baseline odor (unworn t-shirt). In Study 5 (adults), the three visual categories were used and participants were exposed to three odor contexts (scentless mineral oil (baseline), gasoline or axillary sweat from 8 donors (body odor)). (c) During visual stimulation, odors were delivered by disposing the folded t-shirt on the infant’s upper chest in Studies 1 to 4, and using hidden tubes delivering an air-flow under the participants’ head in Study 5. Copyright D. Rekow

To determine whether and how maternal odor selectively shapes face categorization in the infant brain, we conducted a series of four studies (Figure 1b left). Study 1 investigated the modulation of face-selective neural activity in 4-month-old infants exposed to the maternal vs. baseline odor contexts (Leleu et al., 2020). In Study

2, face images were replaced by pictures of cars to test for the selectivity of the maternal odor effect to face categorization (Rekow et al., 2020b). Study 3 explored whether maternal odor is even able to initiate face categorization for ambiguous nonface stimuli, but resembling faces (i.e., objects that elicit illusory face perception – *face pareidolia* – in adults), which are hard to categorize by 4 months of age (Rekow et al., 2021). In addition, to investigate whether the maternal odor effect progressively changes as face categorization develops, Study 4 evaluated the evolution of the face-selective response from 4 to 12 months and its sensitivity to maternal odor (Rekow et al., in preparation).

Finally, we designed a fifth study to elucidate whether the presence of a body odor still influences face categorization in the *adult* brain (Rekow et al., 2022b). We built on previous frequency-tagging EEG studies investigating rapid visual categorization in adults (e.g., Retter & Rossion, 2016) and used a base stimulation rate of 12 Hz rather than 6 Hz, with either faces, cars or facelike objects inserted every 9th stimulus (at 12 Hz / 9 = 1.33 Hz) in dedicated sequences (Figure 1a right). The sets of images from Studies 1, 2 and 3 were used. Three odor contexts were presented during visual stimulation: baseline (i.e., scentless mineral oil), gasoline (diluted by 1‰ in mineral oil) and body (axillary sweat pooled from 8 donors) odors (Figure 1b right). Odors were presented by hidden tubes conducting a low-pressured air-flow diffused just under the participants' head rested on a chinrest (Figure 1c right). Odor intensity was selected following pilot studies that established peri-liminal thresholds and iso-intensity across odors, so that participants remained unaware of the odor diffusion throughout the experiment, as confirmed by a post-testing interview.

2.2 Maternal odor shapes face-selective activity in the 4-month-old brain

In Study 1 (Leleu et al., 2020), we took advantage of the former frequency-tagging EEG study showing rapid face categorization from natural images in 4- to 6-month-old infants (de Heering & Rossion, 2015), and extended this observation in a younger age group of 4-month-old infants ($N = 18$) with a new set of highly variable face images. A face-selective neural response was recorded at 1 Hz (i.e., rate of face presentation in the stimulation stream) over the occipito-temporal cortex, with a larger amplitude in the right hemisphere. Importantly, this response is focal (i.e., recorded over a restricted location of the scalp) and of low amplitude in the baseline odor context, but it is largely increased by the presence of the mother's body odor (Figure 2a left). This larger activation is particularly found over a right occipital electrode (O2 according to the 10–10 classification system), where 17 out of 18 infants show a positive odor effect, i.e., an enhanced face-selective response in the maternal *vs.* baseline odor context. In contrast, the general visual response elicited by the rapid 6-Hz stream of face and nonface images, which results in a medial occipital neural activity, is not affected by concomitant maternal odor cues (Figure 2b left), excluding a mere increase in arousal or visual attention that typically leads to larger brain activity in response to periodic visual stimulation. Overall, this first study reveals that face-selective activity in the 4-month-old brain is actively shaped by the presence of a (maternal) body odor, providing strong support for the fact that chemical cues can tune rapid face categorization in young infants.

Following-up on Study 1, an outstanding issue concerns the selectivity of the olfactory-visual interaction. One could indeed argue from these first observations that the temporal stability of the odor stimulation during a 32-second-long rapidly changing visual stimulation would help the infant brain to detect any visual regularity within the fast stream of pictures, so that any periodically-presented visual object could be better categorized in the presence of maternal odor. Thus, in Study 2 (Rekow et al., 2020b), we tested this alternative hypothesis.

To that aim, we recorded scalp EEG in another group of 4-month-old infants ($N = 18$), but this time, cars were used as the target category presented at 1 Hz within the rapid 6-Hz stream of natural images. Following the same procedure, we exposed each infant to the two odor contexts while recording their visual brain responses. A relatively weak car-selective response was observed at 1 Hz over the right occipital channel O2 in both odor conditions (Figure 2a middle), revealing the 4-month-old infant brain's ability to rapidly assign a series of highly variable exemplars of cars to a single category. However, contrary to the face-selective response measured in Study 1, no significant modulation of the neural categorization response to cars was found in the maternal odor context, which was rather slightly diminished. Similarly, the general visual response to the 6-Hz train of visual stimuli was also immune to the presence of maternal odor, reflecting a similar level of visual attention or arousal in both odor contexts (Figure 2b middle). These findings indicate that the odor effect for faces was not accounted for by the mere temporal stability of the olfactory stimulation, and rather suggest a selective tuning of the infant visual system to categorize congruent inputs such as faces.

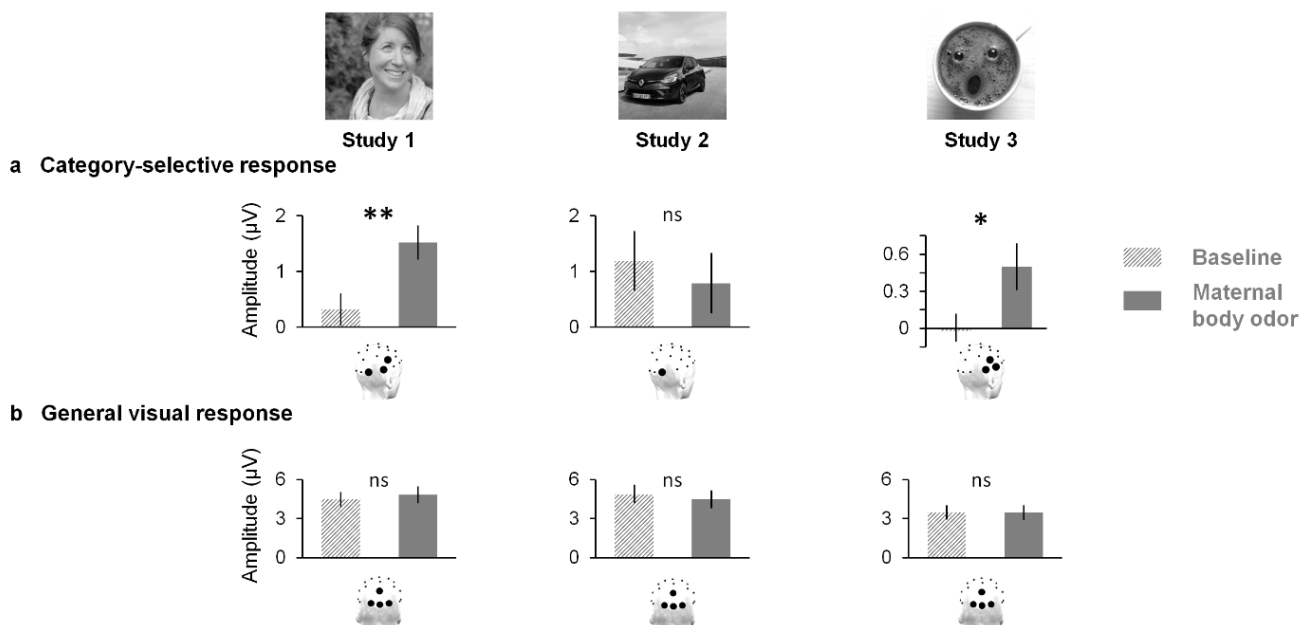


Fig. 2 Maternal odor effect on visual categorization in the 4-month-old brain. (a) Studies 1 to 3 revealed that exposure to the maternal body odor compared to the baseline odor elicits a larger category-selective neural response to both human faces (*left*) and facelike objects (*right*) over right occipito-temporal brain regions (* $p < .05$, ** $p < .01$), while maternal odor does not influence the categorization of cars (*middle*, ns (non-significant): $p > .05$). (b) The general visual response to the rapid stream of stimuli (i.e., recorded at the base rate of stimulus presentation over the middle occipital region) is immune to the presence of maternal odor in the three studies (ns: $p > .05$). Error bars are standard errors of the mean (SEM).

The two first studies have demonstrated a powerful influence of maternal odor on the brain's ability to rapidly categorize a variety of faces at 4 months of age. Does that mean that maternal chemical cues can even *initiate* neural face categorization within the immature infant visual system? In other words, is maternal odor able to trigger a face-selective neural response to stimuli that are hardly categorized as faces from the sole visual input? To answer this question, we used a special type of stimuli instead of genuine human faces: a variety of nonface objects categorized as faces by adults (i.e., inducing face *pareidolia*), namely facelike objects. To our knowledge, this kind of stimuli resembling faces, but depicting many different nonface categories, had not yet been associated with face-selective neural activity in young infants (see e.g. Kobayashi et al., 2012 for evidence of facelike perception in Arcimboldo paintings at 7-8, but not 5-6, months of age).

In Study 3 (Rekow et al., 2021), we recorded scalp EEG in another group of 4-month-olds ($N = 20$) exposed to the same two odor conditions (maternal vs. baseline). Many variable facelike objects (e.g., a coffee cup where the foam makes out a face as in Figure 2, fried eggs of which the yolks evoke eyes, etc.) were used as the target category presented at 1 Hz in the fast 6-Hz streams of other nonface objects. Facelike and nonface stimulus sets depicted the same object categories (e.g., a regular version of a coffee cup without any illusory face was used as a nonface stimulus) to control for the natural properties of the object categories (e.g., shape, color). Hence, a facelike-selective neural response would emerge only if exemplars from different categories (e.g., a facelike plug and a facelike coffee cup) elicit similar neural responses according to their face likeness, and, at the same time, if exemplars from the same categories (e.g., facelike and nonface coffee cups) elicit dissimilar neural responses.

In the baseline odor context, we found a weak neural categorization response to facelike stimuli at 1 Hz in the EEG spectrum over bilateral occipito-temporal regions. Critically, this facelike-selective response is amplified and becomes right-lateralized in the maternal odor context (Figure 2a right). This observation extends our two previous studies, revealing that chemical cues co-occurring with human faces in the infant's experience also shape the categorization of facelike objects as faces in the right hemisphere, which is dominant for this function in humans (Rossion & Lochy, 2021, for review). Importantly, at the individual level, the odor effect is particularly effective in infants with no sign of facelike categorization in the absence of maternal body odor, as they display an odor effect twice as large as the group. In other words, this demonstrates that maternal chemical cues are able to initiate face-selective activity in the infant visual cortex in response to ambiguous stimuli that are hardly categorized as faces based on the sole visual input. In line with our two previous studies, no odor effect was observed on the general response to the fast train of visual stimuli (i.e., the 6-Hz response, Figure 2b right), ruling out a general effect on visual attention or arousal when exposed to maternal odor.

2.3 The effect of maternal odor on face categorization fades during development

Our first three studies have disclosed the early tuning of face(like)-selective activity by chemical stimuli in the 4-month-old developing brain, showing a maternal odor effect on face categorization which is broad enough to occur for any visual input interpretable as a face. They have also shown that the maternal odor effect appears

particularly effective when categorization is demanding for the sole visual system, as revealed by the individual odor effects in Study 3. Thus, given that these studies were conducted in 4-month-old infants, they also suggest that maternal odor is especially effective in fostering face-selective neural activity at an age when face categorization is not fully developed. This would be in line with our main hypothesis that the developmental heterochrony between the two senses favors olfactory-to-visual modulations (see section 1), the early-maturing olfactory system driving perception in the later-developing visual system. Accordingly, we wondered if maternal odor still exerts such an effect on face categorization later on, as the first year of life is marked by dramatic progress in this function (Pascalis et al., 2020). In other words, is the mother's body odor still useful in channeling the infant visual system to respond to faces as face categorization becomes more efficient by itself?

In Study 4, we addressed this question with a cross-sectional approach (Rekow et al., in preparation). We recorded scalp EEG in 4- to 12-month-old infants ($N = 50$, aged from 121 to 374 days old) tested in the same conditions as in Study 1: infants watched 6-Hz streams of natural images with human faces periodically inserted once per second (at 1 Hz) and were exposed to their maternal odor or to a baseline odor using t-shirts. In a first step, we evaluated the development with age of both the face-selective response recorded at 1 Hz and harmonics and the general visual response recorded at 6 Hz and harmonics. This first set of analyses was conducted in the baseline odor condition to measure the visual response without the effect of the congruent maternal odor. It revealed that the face-selective response increases in amplitude with age (Figure 3a left) and becomes more complex, as indicated by a higher number of harmonics in the oldest infants compared to the youngest. This qualitative and quantitative change of the response is not found in the case of the general visual response which remains stable in amplitude and complexity over development (Figure 3b left). In a second step, we analyzed whether maternal odor influences both visual responses (face-selective and general) as a function of age. For the face-selective response, as in Study 1, a positive odor effect was found in the youngest infants, resulting in a stronger amplitude over the right hemisphere in the maternal compared to the baseline odor context (Figure 3a right). However, this effect linearly declines with development, and the oldest infants do not display any positive influence of maternal odor on face-selective neural activity. In contrast, the general visual response remains immune to the presence of the mother's body odor at any age (Figure 3b right), as described at 4 months in our previous studies.

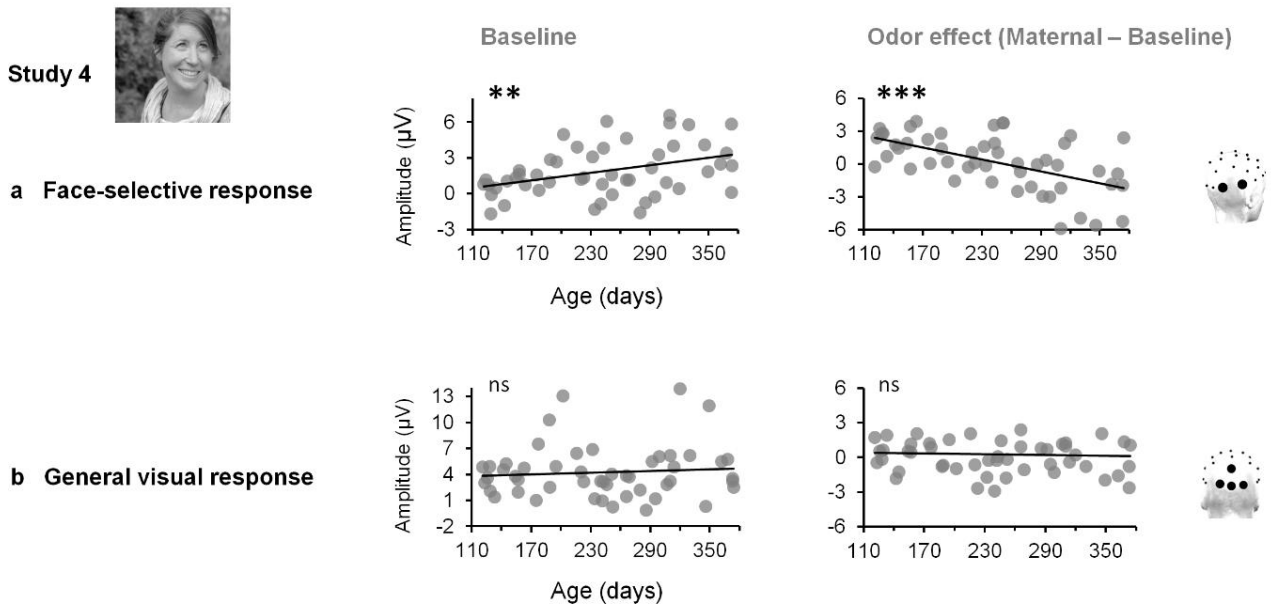


Fig. 3 Maternal odor effect on face categorization between 4 and 12 months of age. (a) The face-selective neural response recorded in Study 4 over the right occipito-temporal region in the baseline odor context (without maternal odor) significantly increases (**: $p < .01$) between 121 days (\approx 4 months) and 374 days (\approx 12 months) of age (*left*). At the same time, the maternal odor effect (amplitude difference of the face-selective response between the maternal and the baseline odor contexts) significantly decreases (***: $p < .001$) over the same region (*right*). (b) The general visual response recorded over the middle occipital region does not increase with age and remains immune to the presence of maternal odor at any age (ns: $p > .05$). Circles represent individual data points.

Overall, this study demonstrates a direct relationship between the strength of the face-selective visual response and the strength of the maternal odor effect. This suggests a developmental trade-off between olfaction and vision, as if the mother’s body odor gradually loses its effect over face categorization in infants as faces become more and more readily categorized from the sole visual input. This supports the view that multisensory inputs help perceiving stimuli as coherent early in infancy, before the age when unisensory inputs become sufficient to elicit accurate perception. This result is more generally in line with the *inverse effectiveness* principle of multisensory integration, whereby the strength of the integration between two senses is higher when unisensory responses are scarce on their own (Regenbogen et al., 2016; Stein & Meredith, 1993).

2.4 Face categorization still relies on body odors under certain circumstances in the adult brain

The aforementioned four studies conducted in infants revealed that mother’s body odor improves face categorization in the developing brain in the form of an increased face(like)-selective response. They also indicated that this intersensory facilitation of visual categorization depends on the brain’s ability to readily categorize faces from the sole visual input, as we found an inverse relationship between the strength of the visual response and the strength of the odor effect, both across individual infants (Study 3) and across ages (Study 4). These latter observations suggest that the inverse effectiveness principle of multisensory integration (Regenbogen et al., 2016; Stein & Meredith, 1993) applies during perceptual development, in line with our main hypothesis

assuming that olfaction is particularly prone to support the visual system early in life (see section 1). In this perspective, one could argue that the human typical adult brain does not rely on odors to visually categorize its environment anymore, as visual categorization is then fully developed and extremely efficient.

Indeed, studies investigating visual categorization with frequency-tagging EEG in adults have shown strong category-selective neural responses to different categories despite the tight constraints put on the visual system (i.e., a single glance at variable naturalistic category exemplars contrasted to many other categories; Jacques et al., 2016; Hagen et al., 2020; Rekow et al., 2020a). For face categorization in particular, a brain response is reliably found, whether stimuli are greyscale (Or et al., 2019), negatively contrasted (Liu-Shuang et al., 2022), low-pass filtered (Quek et al., 2018), or presented for very short durations (Retter et al., 2020). Thus, it was still unknown whether such robust face categorization can be sensitive to the addition of concurrent odor cues. We investigated this question in Study 5 and hypothesized that odors influence face categorization provided the face-selective neural response is not saturated (i.e., at its ceiling level), according to the inverse effectiveness principle. In other words, when the visual input is scarce or ambiguous and therefore difficult to categorize by the adult brain, face categorization would be improved by the addition of congruent body odor cues.

Previous evidence in adults tends to support this hypothesis, as body odors modify our perception and appreciation of conspecifics (e.g., Damon et al., 2021; Spence, 2021, for reviews). For example, in a continuum of faces morphed from neutrality to anger (Mujica-Parodi et al., 2009) or from happiness to fear (W. Zhou & Chen, 2009), a stress odor (i.e., body odors collected during an induced stressful event) reduces the threshold of visual information needed to classify the face as angry (threatening) or fearful (threatened) compared to odors sampled during physical exercise. Likewise, it decreases the proportion of “happy” responses to ambiguous happy faces (i.e., morphed with a neutral face; Zernecke et al., 2011). At the brain level, stress odor also increases an EEG response to ambiguous angry faces and makes it of similar amplitude to the response elicited by full-blown angry expressions (Rubin et al., 2012). Accordingly, Study 5 explored whether body odors act as disambiguating cues for difficult-to-categorize faces in adults.

One way to tackle this issue is to rely on facelike objects that trigger face pareidolia (i.e., the illusory perception of a face), as we did in Study 3 with infants. When various facelike objects are contrasted to similar (i.e., belonging to the same object categories) and equally variable nonface objects in a stream of periodically appearing images, they elicit a lower neural categorization response than human faces (Rekow et al., 2022a). Furthermore, facelike objects elicit individual differences, with some participants spontaneously reporting having seen illusory faces, when others struggle to perceive a face from these ambiguous stimuli. Interestingly, this overt report of face pareidolia is related to the amplitude of the facelike-selective brain response, being larger in “aware” than in “unaware” participants (Rekow et al., 2022a, Experiment 1). We thus chose the facelike category to investigate the body odor effect on face categorization in adults, since face pareidolia is not systematic despite a mature and efficient visual system.

The putative modulation of visual categorization by odors was tested implicitly, i.e., without any instruction and with participants being left unaware of the actual aim of the study. According to earlier studies

investigating rapid face categorization in adults (e.g., Retter & Rossion, 2016), images were displayed at 12 Hz and variable exemplars of either human faces, cars, or facelike objects (in dedicated sequences) were interleaved every 9th stimulus to tag category-selective responses at 1.33 Hz and harmonics in the EEG frequency spectrum. We asked 26 participants to detect briefly appearing white crosses that were superimposed on the stimulation stream. Their scalp EEG was recorded while they were blindly exposed to three odor contexts: a composite body odor, a gasoline odor and a baseline odor (see section 2.1 for details). Since facelike objects were the only ambiguous visual category, we expected to observe that the body odor context enhances the categorization of facelike objects, and that this effect depends on the reported awareness of illusory faces at the end of the experiment.

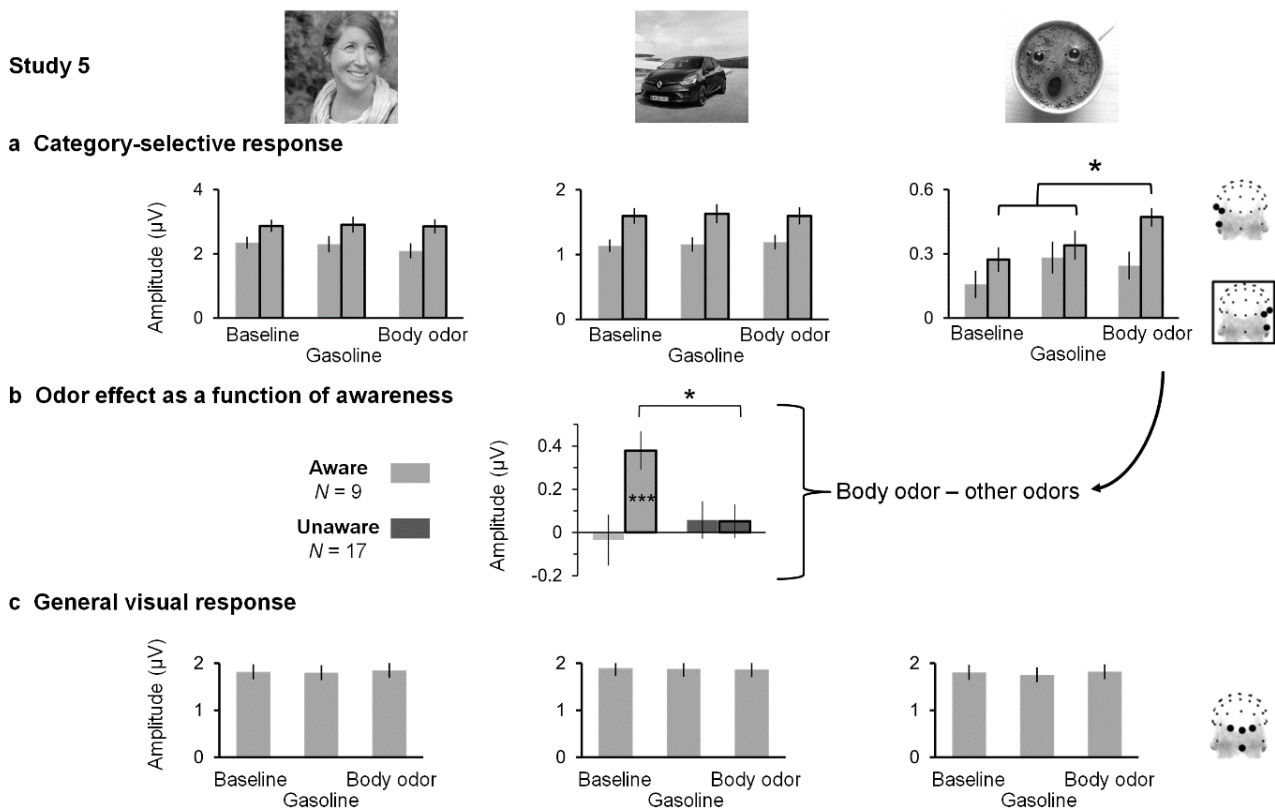


Fig. 4 Odor effect on visual categorization in the adult brain. (a) The amplitude of the category-selective neural response recorded over left and right occipito-temporal regions in Study 5 is large for human faces (*left*), lower for cars (*middle*) and the lowest for facelike objects (*right*). The two former responses are immune to the presence of odor contexts whereas the facelike-selective response significantly increases over the right hemisphere (*: $p < .05$) in the body odor context as compared to the gasoline and baseline odor contexts. (b) The body odor effect on the facelike-selective response (amplitude difference between the body and the two other odor contexts) is driven by 9 out of 26 participants who reported having noticed facelike objects after testing (“aware” participants vs. “unaware” participants; *: $p < .05$, ***: $p < .001$). (c) The general visual response recorded over the middle occipital region is insensitive to the different visual categories and the different odor contexts. Error bars are SEM.

In average, across odor conditions, clear category-selective responses to human faces, cars and facelike objects were measured over the occipito-temporal cortex at 1.33 Hz and harmonics. The largest response was found for human faces, then cars, and the lowest for facelike objects (Figure 4a). When considering the impact of

odor contexts, we observed that odors do not modulate the face- and car-selective responses. In contrast, as compared to the gasoline and baseline odors, the body odor boosts the response to the ambiguous facelike objects over the right occipito-temporal brain region (Figure 4a right). Critically, this increased neural activity in response to facelike objects in the body odor context is systematically found for the 9 out of 26 participants who reported having seen objects resembling faces at the end of the experiment (“aware” participants; Figure 4b). Finally, the general visual response recorded at 12 Hz and harmonics is immune to the different categories presented at 1.33 Hz, and also the different odor contexts (Figure 4c), ruling out any general effect of a given visual category, odor or visual category/odor combination on the attention paid to the rapid visual stimulation. Altogether, these findings disclose a specific influence of congruent odors on the visual categorization of ambiguous stimuli in the adult brain, and point towards a relationship between this odor effect on visual categorization and visual awareness.

3 Discussion

Across the five studies summarized above, we have demonstrated the powerful effect concurrent conspecifics’ chemical cues can exert during visual perceptual development, especially the development of face categorization. At 4 months of age, the mother’s body odor tunes the visual system of her infant selectively towards face(like) stimuli, enhancing the neural activity recorded over the right occipito-temporal region, known to be dominant for face categorization. This maternal odor effect then diminishes progressively over the course of the first year, and is not found in adulthood when face categorization is fully effective on its own. However, in the case of ambiguous stimuli resembling faces, but not always reported as such by adult observers, exposure to conspecifics’ body odor facilitates the perception of a face. Overall, this influence of (maternal) body odor on face categorization reveals that combining socially-relevant congruent stimuli from different senses plays a key role in early perceptual development, and is still effective later in life in case of ambiguous perception. This indicates the importance of multisensory inputs within an ordered developmental timing, when a late-developing sensory system, such as vision, can find support from an early-maturing system, such as olfaction.

3.1 An early perceptual attunement to conspecifics’ odor and face

Our studies have shown that exposure to the mother’s body odor selectively shapes the ability to categorize a variety of unknown human faces against many other living and nonliving categories in the 4-month-old infant brain, an effect that is broad enough to occur for other (nonliving) visual inputs interpretable as faces (facelike objects). How is the perception of the mother’s body odor able to improve the infant’s visual categorization of so diverse and unfamiliar face(like) stimuli? Perceiving our conspecifics is of vital importance from the very beginning of life. In that endeavor, mammalian infants are first equipped with a sensitive olfactory system tuned to attend specific signals or cues from their mother (e.g., Klaey-Tassone et al., 2020; Schaal et al., 2003; Schaal & Al Aïn, 2014). Human fetuses are already exposed to many odors in the womb (Schaal et al., 2002),

some of them being also found in the mother's body secretions after birth (Loos et al., 2014), ensuring trans-natal continuity and familiarity (e.g., Porter & Winberg, 1999). Maternal secretions elicit selective physiological, behavioral and neural responses in neonates (e.g., Aoyama et al., 2010; Marlier et al., 1998; Soussignan et al., 1997), and attenuate their stress reactions (e.g., Rattaz et al., 2005). Maternal odor then benefits from positive reinforcement through nursing and caregiving during the first months, and therefore accompanies the early social interactions between the mother and her infant (Schaal et al., 2020).

In this context, maternal odor stimulates visual arousal at birth (Doucet et al., 2007), thus favoring optimal exposure to the mother's face. Later on, developing infants gradually broaden their social network and are exposed to more and more people, especially to their face during the first year of life (Jayaraman et al., 2015; Rennels & Davis, 2008). Importantly, infants are often held in their mother's arms during social interactions, being simultaneously exposed to her odor and to more or less familiar faces. Exposure to the mother's body odor also reduces the infant's reaction to a fearful face (Jessen, 2020) and appears to promote visual attention towards, and inter-brain synchrony with, unfamiliar conspecifics (Endevelt-Shapira et al., 2021). Therefore, at a perceptual level, sustained co-exposure to both types of stimuli could create, maintain and reinforce a relevant association between chemical and visual stimuli, through associative learning. Being able to learn regularities in the environment and to combine stimuli according to their repeated co-occurrence is a core mechanism of perceptual development. Such statistical learning (Saffran & Kirkham, 2018, for review) is particularly involved in the development of multisensory perception, as infants are extremely sensitive to the spatiotemporal coincidence of events across the senses (e.g., Lewkowicz, 1996). Interestingly, however, odor perception is relatively stable in space and time compared to other sensory perceptions (Sela & Sobel, 2010). Olfactory-visual interactions could thus operate with less spatiotemporal constraints than other intersensory interactions. Rather, odor cues are ideally suited to sustain the development of visual categorization by facilitating the generalization of variable inputs into a single category thanks to the relative stability of odor percepts.

As a result, by 4 months of age, human infants have already been so intensively co-exposed to the mother's body odor and to a variety of faces that the presence of maternal odor cues favors the categorization of visual inputs as faces, even in common nonface objects configured as faces. Years later, children and adults exhibit great sensitivity to fine-grained social cues conveyed by the body odor of conspecifics (de Groot et al., 2017; Lübke & Pause, 2015; Weisfeld et al., 2003), and associations between olfactory and visual information refine. Their combination facilitates the perception of congruent information in adults, such as recognizing the fearful or angry emotion expressed by a face when exposed to a stress odor, especially when the facial expression is ambiguous (Mujica-Parodi et al., 2009; W. Zhou & Chen, 2009). We have shown that this remains also effective for the generic ability to categorize a visual stimulus as a face, since a human body odor still improves the categorization of ambiguous facelike objects in adults. In that case, body odor cues could signal the potential presence of a person (Cecchetto et al., 2020), and even trigger visual imagery (Parma et al., 2017, for review), orienting more systematically towards the "face" interpretation of the visual input.

3.2 Putative mechanisms subtending odor-driven priming of the face category

A main observation in our studies is the fact that (maternal) body odor does neither merely stimulate visual arousal/attention (no effect on the general response to the rapid visual stimulation stream), nor facilitate the categorization of any stable visual object (e.g., periodically presented cars), but selectively enhances the neural categorical response to face(like) stimuli. This indicates an intersensory association relying on the congruency between simultaneous olfactory and visual inputs, like a priming effect of body odor on face categorization, as previously described for other congruent olfactory-visual pairings (e.g., Seigneuric et al., 2010; W. Zhou et al., 2010). This is more generally in line with the view that sensory cues channeled by different senses are combined when they complete each other (Bahrick & Lickliter, 2012; Ernst & Bühlhoff, 2004). Interestingly, we did not find odor effects for incongruent associations (i.e., body odor effect for cars and gasoline effect for face(like) stimuli), contrary to previous reports of odor-driven interference on visual categorization (e.g., Hörberg et al., 2020). Since interference is often observed for an *explicit* decision and the neural activity related to this controlled behavior, the automatic visual categorization we measured in our studies without any explicit behavior may be immune to odor interference. Alternatively, since category-selective responses reflect the direct contrast between the neural activities elicited by the target category and other visual categories, and since incongruency with the target category also means incongruency with the other categories (e.g., a body odor presented during a car categorization sequence is incongruent with both cars and other nonface objects), incongruent associations may cancel each other. Accordingly, it is also worth reminding that category-selective responses include both between-category discrimination and within-category generalization. Hence, regarding the face-selective response, exposure to body odor may improve both the ability to discriminate faces from other visual categories because it is congruent only with faces, and to generalize variable unfamiliar faces into a single category because they share the congruent association with the odor. Moreover, as incongruency with body odor is also shared across the different nonface categories against which faces are contrasted, it may further improve their discrimination from faces.

At the brain level, the repeated co-occurrence of body odors and faces in the social environment could shape a dedicated connectivity between the olfactory and visual systems, so that a body odor would become able to mediate neural activity in the face-selective network and enhance its responsiveness when a face(like) stimulus appears. This is in line with the reentrant signaling hypothesis in the theory of neuronal group selection (e.g., Edelman, 1993). Accordingly, systematic co-exposure to different sensory inputs reinforces bidirectional connections between distinct neuronal groups responding to each input. Experience therefore progressively shapes connections within a large-scale and broad connectivity established during early development, some connections disappearing due to scarce or random co-activation, while others strengthen from repeated and reinforced co-activation.

The existence of such underlying connected network is supported by a convergent line of evidence demonstrating odor-induced neural activity in brain areas typically considered as visual. For instance, activity in the adult right occipital cortex has been consistently reported during the presentation of odors without visual stimuli (Djordjevic et al., 2005; Royet et al., 2001; Zatorre et al., 2000). More specifically, the sole presentation of

body odors activates the lateral fusiform gyrus, a well-known face-selective region of the ventral occipito-temporal cortex (Prehn-Kristensen et al., 2009; Zheng et al., 2018; W. Zhou & Chen, 2008), which is also a downstream recipient of the primary olfactory cortex as revealed by functional connectivity analysis (G. Zhou et al., 2019). More generally, this concurs with large-scale connectivity between distant and typically unisensory brain regions dedicated to the same semantic domain (Mahon & Caramazza, 2011). Recent studies in congenitally-blind people (Mattioni et al., 2020) and early-deaf individuals (Benetti et al., 2021) illustrate how such circuitry shapes the activity of a deprived sensory system. For example, category-selective regions of the ventral occipito-temporal cortex are organized in the same fashion in blind people stimulated with auditory inputs as in sighted individuals stimulated with visual inputs (Mattioni et al., 2020). Hence, it is tempting to speculate that this crossmodal plasticity reflects how perceptual categorization organizes during development, category-selective regions within a given sensory system receiving direct inputs from the other senses that constrain their progressive tuning towards their preferred category.

Another recurrent observation in our studies pertains to hemispheric asymmetry. Both face-selective (in infants) and facelike-selective (in infants and adults) neural responses increase only over the right hemisphere in the presence of (maternal) body odor. This indicates that adding the odor may strengthen the well-known right lateralization of face categorization (Grill-Spector et al., 2017; Hagen et al., 2020; Jonas et al., 2016), even in the infant brain for which the advantage of the right hemisphere is disputed (see Behrmann & Plaut, 2020; Rossion & Lochy, 2021). Right-hemispheric dominance has been related to single-glance perception of the face as a whole, especially for facelike stimuli which are configured as faces without genuine facial features (Caharel et al., 2013; Rossion et al., 2011). Thus, body odor could trigger the perception of a whole face pattern from a single glance at a wide variety of visual stimuli as soon as they are configured as a face. To a larger extent, since the right hemisphere has been suggested to be particularly involved in identifying the odor source, at least in adults (Brand et al., 2001; Royet, 2004), it might be a “hotspot” for integrating social information across the senses with facilitative effects on their categorization. Finally, our findings are also in line with increased brain-to-brain synchrony in the right occipito-temporal region of 7-month-old infants exposed to their mother’s body odor while interacting with unfamiliar women (Endevelt-Shapira et al., 2021), suggesting that maternal odors can promote various prosocial functions, including the right-hemispheric ability to categorize conspecifics from olfactory or visual cues.

3.3 Implications for the development of (multi)sensory perception

Collectively, our studies support our initial hypothesis that olfaction is particularly prone to sustain the development of visual categorization because it is an early-maturing sense compared to vision (Lecanuet & Schaal, 1996), in line with the view that the ordered sequential ontogeny across sensory systems actively contributes to perceptual development (Turkewitz & Devenny, 1993). Indeed, from birth onward, neonates respond to a variety of chemical cues and signals emanating from their mother (e.g., Porter & Winberg, 1999; Schaal, 1988), while visual perception is limited and follows a protracted development over the first year (Braddick &

Atkinson, 2011). The mere ability to categorize a visual input as a face is already difficult for young infants, and takes time to develop. For example, human infants need about 6 months to readily detect faces in naturalistic scenes (e.g., Kelly et al., 2019; see Leppänen, 2016, for review), and the face-selective response tagged in EEG in the 4- to 6-month-old brain is largely immature compared to the response measured in children and adults (de Heering & Rossion, 2015; Lochy et al., 2019; Rossion et al., 2015, respectively). In Study 4, we also informed this neural development, revealing a dramatic quantitative and qualitative evolution of the response between 4 and 12 months. As a result, the maternal odor effect we observed only in the youngest infants³ appears to be particularly effective when face categorization is not fully developed.

Such immature face categorization means that the face category is broadly defined in the 4-month-old infant brain, and face(like) stimuli are still difficult to disambiguate, leading to a lack of sensitivity (some face(like) stimuli are missed) and of specificity (some nonface stimuli are erroneously categorized as faces). The same applies to adults exposed to facelike objects within a fast train of other objects belonging to the same categories, who are inclined to miss some facelike objects and erroneously report faces in nonface objects (Rekow et al., 2022a, Experiment 2). Therefore, (maternal) body odor can be seen as a disambiguating cue that reduces sensory noise induced by the physical variability of the environment, a key function of multisensory integration (Ernst & Bühlhoff, 2004), which has already been reported on several occasions (e.g., for odor effects on facial expression perception; Leleu et al., 2015; Mujica-Parodi et al., 2009; Poncet et al., 2021; W. Zhou & Chen, 2009). This would explain why no odor effect was found for human faces in adults, faces being already easily categorized without the need of another sensory cue (such as a body odor) and under tight visual constraints (e.g., Retter et al., 2020). Likewise, over the first year of life, the odor effect gradually decreases as face perceptual abilities increase, suggesting that maternal odor becomes less relevant for the visual system.

In sum, the odor effect is not observed when face categorization is sufficiently developed to be readily achieved through the sole visual input. This relates to the inverse effectiveness principle of multisensory integration, first described at the level of single neurons in animals (Stein & Meredith, 1993), and further noted in behavioral data of human adults (Regenbogen et al., 2016). This principle states that as the strength of unisensory responses increases, the strength of multisensory integration decreases, following a reverse function. In other words, cues from the different senses compensate one another, helping disambiguate inputs to reach optimal

³ It should be also noted that with frequency-tagging EEG, infants are tested under the same conditions and using the same stimuli as for adults, making infants' data comparable to that of adults but increasing categorization difficulty at such an early stage of development. The maternal odor effect could thus have been also favored by this demanding paradigm for their immature visual system. More generally, one may question the ecological validity of our paradigm since infants rarely see faces so rapidly in their everyday experience. However, while slower modes of visual display better match the natural timing of exposure to a conspecific's face, they are rather limited in terms of measurement validity, especially for visual categorization, as they often rely on a limited set of edited visual stimuli depicting only a few visual categories (see section 2.1 for a discussion of this issue; see also Kominsky et al., 2022, for a recent discussion about the difficult balance between ecological and measurement validity in infant research). Moreover, as mentioned above, we aimed to investigate the development of face categorization using adult performance as reference. Neurotypical adults reach a *plateau* for categorizing natural views of faces after only a short exposure of about 80 ms (≈ 12 Hz of fast periodic visual stimulation; see e.g., Retter et al., 2020). Hence, despite its limitations in ecological terms, our paradigm is well designed to measure the development of adult-like rapid face categorization in the infant brain. Admittedly, future studies should investigate odor-driven visual categorization in other experimental and/or natural designs to further improve the generalizability of our findings.

perception, unless unisensory inputs are already sufficient to elicit a robust percept. In our work, we repeatedly found such an inverse relationship between the odor effect and the strength of the sole visual response, either for individual infants (Study 3), as a function of age (Study 4), or depending on the ambiguity of the visual category (Study 5). In a recent study, we have further addressed the inverse effectiveness of maternal odor on human face categorization at 4 months (Kiseleva et al., in preparation). In a first group of 4-month-old infants, we have replicated our initial observation that maternal odor increases a right occipito-temporal neural response to natural face images (Study 1). In a second group, we replaced the variable naturalistic stimuli by homogenous edited stimuli (i.e., stimuli segmented from their background and always depicted centered and from a full-front view; see footnote 2) to increase both similarity across individual faces and dissimilarity between face and nonface stimuli, thus making rapid face categorization less demanding. As expected, we found that the face-selective EEG response to edited stimuli is larger and more complex (with more harmonics) than to naturalistic stimuli, indicating more efficient categorization. Critically, the response is equivalent in both odor contexts, suggesting that the maternal odor effect has been concealed by an effective categorization from the sole visual input.

From a broad developmental perspective, our findings orient towards a multisensory shaping of knowledge, where inputs from the different senses are merged together into unified percepts, providing the building blocks for the development of semantic memory, language and concepts (e.g., Goldstone & Barsalou, 1998; Murphy, 2002). In this context, we propose that the development of perception, and by extension, memories and concepts, relies on the ability to disambiguate a rich and complex environment by recognizing invariant categories, the combination of information across the senses actively participating in the progressive acquisition of such categories. Later on, as unisensory perception becomes effective on its own, the other senses would be useful when inputs are ambiguous. In other words, perception would function through multisensory integration throughout the life course, but the latter would become evident only when one sense has difficulties to categorize an input by itself. This multisensory account of perception is in line with the observation that many brain regions usually considered as unisensory can respond to stimuli from other sensory modalities (Driver & Noesselt, 2008; Ghazanfar & Schroeder, 2006). It is worth noting that the ability to apprehend and use multisensory inputs along development has long been a matter of debate. On the one hand, the “integration” view suggests that unisensory categories develop first before infants become gradually able to integrate them into multisensory objects (Birch & Lefford, 1963; Piaget, 1952). On the other hand, the “differentiation” view argues that infants build multisensory categories first, before being able to differentiate between unisensory percepts (Gibson, 1969). More recently, intermediate views have been formulated, suggesting that infants are already able to form multisensory percepts early in life, and that multisensory integration further continues to develop (e.g., Bahrack & Lickliter, 2012; Lewkowicz, 2010). The present set of studies favors such a developmental lifespan perspective of multisensory perception, and suggests to consider how unisensory responses are effective on their own to reveal interactions across the senses.

3.4 Conclusions and perspectives

In this chapter, we have reviewed five of our studies showing that a human body odor is able to foster neural activity in face-selective brain regions in response to any stimulus configured as a face, provided that this stimulus is not effectively categorized by the sole visual system (i.e., due to a lack of maturity, or to a scarce or ambiguous stimulus). This suggests that odor acts as a disambiguating cue, which reduces the impact of sensory variance and favors visual discrimination and generalization, following an inverse relationship with the strength of the sole visual response (inverse effectiveness). At the neural level, this is probably subserved by reentrant signaling between olfactory and visual areas through a large-scale connectivity that is shaped during development by the repeated co-exposure to (maternal) body odor and faces. This accumulated experience with co-occurring olfactory and visual stimuli would create an associative learning, such that body odor and faces would become mutually congruent. Accordingly, future studies should test whether faces modulate body odor perception to elucidate how the two sensory systems support each other. Given that olfaction matures earlier than vision, we speculate that visual-to-olfactory influence is not functional early in life, but could certainly gradually appear as the visual system develops. Likewise, it would be interesting to explore whether face categorization is already odor-driven in younger infants. Since maternal odor induces eye opening in neonates (Doucet et al., 2007), maternal odor could trigger visual attention indiscriminately, an effect that could be captured by an enhanced general response to any fast train of visual stimuli in frequency-tagging EEG.

Which odor cues carried by maternal body odor contribute to the odor effects should also be disentangled in future studies. Maternal odor is a complex mixture of compounds pertaining to familiarity/identity, maternity, femininity, humanity, etc., which partially overlap across body regions and conspecifics. Human infants are able to differentially respond to these cues. They discriminate their own from another mother's odor, with odors stemming from different body areas across studies (Marin et al., 2015; Russell, 1976). They also differentiate lactating from non-lactating women (Makin & Porter, 1989), human from non-human milk (Marlier & Schaal, 2005), or early lactation milk from late lactation milk (Klaey-Tassone et al., 2020). However, there is some evidence that infants' looking behavior towards faces is insensitive to the familiarity of maternal odor or to lactating status (Durand et al., 2020). Thus, we can only speculate that some cues, combined or in isolation, are more potent than others (how effective is the father's odor, or the odor of a stranger nulliparous woman?). In adults, we used a composite body odor pooled from males and nulliparous females. Again, a wealth of information related to a variety of states (e.g., emotions) or traits (e.g., identity) emanates from such biological odors and are detected by human adults (de Groot et al., 2017, for review), but we do not know which cues are necessary/sufficient for the odor to be effective on visual perception. At this stage, we can merely speculate that some cues signal that the odor belongs to a human being. Future studies should thus be designed to properly delineate which odor cues sustain the visual system in categorizing faces. More generally, it would be worth determining whether non-body odor cues repeatedly associated with conspecifics during social interactions are also able to shape face categorization. For instance, in our studies, we were only interested in the effect of body odor and asked the mothers to not use cosmetics during odor sampling, but cosmetics can be part of maternal odor in the infants' everyday experience. Future studies should thus investigate whether the odor of cosmetics learned during mother-infant interactions facilitates the infants' ability to categorize faces. If

confirmed, such idiosyncratic olfactory-visual integration would further support our interpretation that the individual experiences of co-occurring sensory inputs drive the development of multisensory perception.

Relatedly, one may also wonder whether our findings can be generalized to any congruent association between an odor and a visual category. According to the title of this chapter, we suggest that odor-driven visual categorization is not restricted to social stimuli but extends to other congruent combinations. Actually, we first used maternal odor and faces in 4-month-old infants because they are arguably the most relevant inputs encountered by infants (Jayaraman et al., 2015; Schaal et al., 2020; Sugden et al., 2014), making them the best candidates to reveal potent odor effects on visual categorization at such early age. Furthermore, there is no other visual category that is familiar enough to infants to be tested with a large and variable stimulus set (see e.g., Werchan et al., 2018 for an intersensory influence in the infant brain with non-social simple stimuli). Unlike infants, adults have become familiar with many odors and visual categories, and a large body of research has described non-social odor effects on visual perception (e.g., Seigneuric et al., 2010; W. Zhou et al., 2010). Hence, in future studies, it would be worth to evaluate, for instance, whether the gasoline odor affects car categorization by using degraded visual stimuli or a challenging mode of stimulus presentation that both hamper visual categorization in adults. This would also further assess the inverse effectiveness of odor cues on vision.

Another outstanding issue stems from the relationship between odor-driven face(like)-selective responses and participants' perceptual awareness, i.e., their subjective experience of a face. In adults, it is remarkable that the odor effect is stronger for participants who are "aware" of the facelike stimuli (who reported face pareidolia at the end of the experiment). This suggests that body odor, by priming face-selective areas to respond to face(like) stimuli, could facilitate the face percept "popping out" of the ambiguous stimulus. This is in line with a strong positive relationship between the magnitude of frequency-tagged category-selective responses and participants' awareness of the stimulus (Rekow et al., 2022a; Retter et al., 2020). However, given that aware participants were identified post-experimentally, an alternative interpretation could be that they are more sensitive to face pareidolia in general, and then more prone to associate body odor and facelike perception. Several elements in our data point towards the first interpretation (e.g., the facelike selective response is of similar amplitude in both aware and unaware participants without body odor), but future studies should directly manipulate awareness in a single group of participants to reach a definitive conclusion. If confirmed, such odor-driven visual awareness would broadly participate in rehabilitating the function of the olfactory system in human cognition. In this context, our findings suggest that the long-granted alerting function of olfaction towards environmental hazards (Herrick, 1933) is not simply a primitive mechanism of survival, but an integral part of an evolved system generating knowledge, and even consciousness. More work is still needed to elaborate on this issue, to shed full light on how chemical cues and signals participate in high-level cognition in human beings.

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