The inverse effectiveness of maternal odor on rapid face categorization in the infant brain

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Par

Madame Anna KISELEVA

The inverse effectiveness of maternal odor on rapid face categorization in the infant brain

L'efficience inverse de l'influence de l'odeur maternelle sur la catégorisation des visages chez le nourrisson

Thèse présentée et soutenue à Dijon, le 21 Décembre 2023

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Title: The inverse effectiveness of maternal odor on rapid face categorization in the infant brain

Keywords: multisensory development, infant brain, maternal body odor, face categorization, frequency-tagging, EEG

Abstract: This thesis examines how the inverse effectiveness principle can be applied to the olfactory-to-visual interaction during infant development using fast periodic visual stimulation (FPVS) with a frequency-tagging approach in scalp electroencephalography (EEG). In particular, we have tried to confirm this principle based on the developmental improvement of vision (Study 1) and different visual demand at a given age (Study 2 and 3) as it was shown that infant visual perception can be facilitated by the reception of odor cues.

We observed that a facilitation effect of maternal body odor on rapid face categorization gradually declines with the progressive maturation of the visual system from 4 to 12 months **(Study 1)**, showing a developmental trade-off between vision and olfaction. This suggests that the strength of the odor effect is linked to the strength of the face-selective response, elicited here using quite complex naturalistic stimuli. Thus, in **Study 2**, we manipulated visual demand (i.e., simplifying the stimuli) in 4 month-old infants and found a stronger face-selective response in the less demanding categorization that led to the suppression of the odor effect. Taking in account the effective face categorization in 12-month-old brain linked with visual development, in **Study 3**, we instead increased visual demand by doubling the image presentation rate. As expected, a weaker face-selective response was measured, however the odor effect did not increase but rather reduced the response, suggesting a sensory overload.

Overall, this dissertation demonstrates for the first time the application of the inverse effectiveness principle to olfaction during perceptual development, through Study 1 and 2. The stronger face-selective response (due to the sufficient maturation level of vision or decreased visual demand) leads to the weakest olfactory-to visual interaction (i.e. intersensory facilitation), however the low face-selective response not always links to the enhanced odor effect: only when visual system is not enough developed in the early infancy.

Titre: L'efficience inverse de l'influence de l'odeur maternelle sur la catégorisation des visages chez le nourrisson

Mots clés: développement multisensoriel, cerveau du nourrisson, odeur maternelle, catégorisation des visages, étiquetage fréquentiel, EEG

Abstract: Cette thèse examine comment le principe de l'efficience inverse peut être appliqué à l'interaction olfacto-visuelle sur le développement du nourrisson en utilisant une stimulation périodique visuelle rapide (FPVS) avec une approche de marquage fréquentiel en électroencéphalographie (EEG). En particulier, nous avons essayé de confirmer ce principe en nous basant sur le développement de la vision pendant la première année de la vie (étude 1) et une demande visuelle différente à un âge donné (études 2 et 3) car il a été montré que la perception visuelle du nourrisson peut être facilitée par la réception de signaux olfactifs.

Nous avons observé qu'un effet de facilitation de l'odeur maternelle sur la catégorisation des visages diminue progressivement avec la maturation du système visuel entre 4 et 12 mois **(étude 1)**, montrant un compromis développemental entre la vision et l'olfaction. Cela suggère que la force de l'effet de l'odeur est liée à celle de la réponse aux visages, ici à partir de stimuli visuels complexes. Ainsi, dans l'**étude 2** manipulant la demande visuelle (en simplifiant les stimuli) chez des nourrissons de 4 mois, nous avons trouvé une réponse sélective aux visages plus forte dans ce cas associé à une réduction de l'effet de l'odeur. Enfin, tenant compte de la catégorisation des visages plus efficace dans le cerveau des enfants de 12 mois en raison du développement visuel, dans l**'étude 3** nous avons au contraire augmenté la demande visuelle en accélérant la vitesse de présentation des images. Cette fois, une réponse sélective des visages plus faible a été observée, mais l'effet d'odeur n'a pas augmenté, mais plutôt réduit, la réponse, suggérant une surcharge sensorielle.

Dans l'ensemble, ce travail de thèse démontre pour la première fois l'application du principe d'efficience inverse à l'olfaction au cours du développement sensoriel. La réponse sélective au visage plus forte (en raison du niveau de maturation suffisant de la vision ou de la diminution de la demande visuelle) conduit à l'interaction olfactive-visuelle la plus faible (c'est-à-dire la facilitation intersensorielle), cependant la faible réponse sélective des visages n'est pas toujours liée à un plus fort effet de l'odeur: seulement quand le système visuel n'est pas suffisamment développé au début de la vie.

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Abbreviations

AF: amniotic fluid

ATL: anterior temporal lobe

ASD: Autism Spectrum Disorders

EC: entorhinal cortex

EEG: electroencephalography

ERP: event-related potential

FFA: fusiform face area

FFT: fast Fourier transform

fMRI: functional magnetic resonance imaging

FPVS: fast periodic visual stimulation

IOG: inferior occipital gyrus

lOT: left occipito-temporal cortex

IRH: Intersensory Redundancy Hypothesis

IS: intraparietal sulcus

latFG: lateral fusiform gyrus

LGN: lateral geniculate nucleus

mO: middle occipital cortex

Nc: negative central component

NIRS: near-infrared spectroscopy

OFA: occipital face area

OFC: orbitofrontal cortex

OT: occipito-temporal cortex

OR: olfactory receptor

OERP: olfactory event-related potential

PPC: posterior piriform cortex

pSTS: mid-posterior superior temporal sulcus

ROI: region of interest

rOT: right occipito-temporal cortex

SC: superior colliculus

SNR: signal-to-noise ratio

STS: superior temporal sulcus

V1/V2/V3: primary/ secondary/third visual cortex

V4: extrastriate visual cortex

V5/MT: middle temporal visual area

V5/hMT: motion-selective occipito-temporal areas

V6/DM: dorsomedial visual area

VOTC: ventral occipito-temporal cortex

Introduction

This dissertation work investigates the one of the rules of multisensory integration as inverse effectiveness. Principally we focused on this principle over early infant development applying it to the olfactory-to-visual interaction, in particular, to the influence of maternal body odor on the rapid face categorization.

Thus, this introduction consists of four main parts:

In the **first section**, we introduce multisensory perception, revealing the multisensory integration rules and underlying brain mechanisms. The **second section** tell us about development of olfactory system, its anatomical and functional specificities, eventually focusing on the maternal body odor. The **third section** follows two major axes: development and neuroanatomy of vision and in particular, face processing. In the **fourth section**, we put together olfactory and visual perception presenting an influence of body odors on the face processing at the behavioral and neural levels across development.

Finally, this literature review will be end by the main research question with following hypotheses and next, by the introduction in the general methodology, since the same method was used for the three presented studies in this dissertation work.

1. «The Merging of the senses»

Every day we perceive a large amount of information coming from our different senses. We are used to handle these signals very efficiently, merging them into unified percepts. Despite the apparent automaticity and easiness of this process, complex neural mechanisms are involved in it. Our environment is so complex and ambiguous that information received from single sensory source sometimes is not reliable enough. That is why perception is an active process, which we can compare with filtering: first, it needs to maximize information coming in from all sensory modalities (sensory combination) and next, to decrease the variance in the sensory assessment to enhance its reliability (sensory integration) (Ernst & Bülthoff, 2004). Moreover, the robustness of perception is also based on an individual's prior knowledge. Through daily experience, our brain builds the most probable interpretations to economize the cognitive cost of sensory processing and the following analytic processes (Gregory et al., 1997).

However, how multisensory perception develops remains unclear. The interaction between innate abilities available from birth and acquired experience have a key-role in perceptual learning (Arterberry & Kellman, 2016), but researchers did not find common ground on whether infants are able to merge their sensory inputs directly after birth or whether this ability is not available in early life and progressively develops until adult age. In his «Principles of Psychology», William James (1890) supposed that young infants experience the world «as one great blooming, buzzing confusion». Later James Gibson (1969) involved the same idea and formulated his *differentiation view* on multisensory perception. It argues that infants first discover complex multisensory blocks and after learn to differentiate sensory units included in their composition. An opposite opinion on this question was proposed by constructivist Jean Piaget (1952). His *integration view* assumes that all sensory systems develop separately and infants need an experience and cognitive maturation to integrate signals from them into multisensory percepts. During the last decades, additional researchers proposed synthetic views, involving both concepts: for them, infants are able to merge senses early in life and this multisensory synergy tunes and shapes by age (Bahrick & Lickliter, 2012; Lewkowicz et al., 2010).

Indeed, many studies already demonstrated the importance of the multisensory properties of the environment in infancy. Early multisensory exposure plays a crucial role for the sensory neural networks formation, decreasing the risk for neurodevelopmental disorders (Duerden et al., 2018; Hüppi et al., 1996; Neel et al., 2019), the level of stress in neonates (White-Traut et al., 2009), and inducing even more deferred outcomes, such as the influence on IQ in adolescents (Allin et al., 2008). However, we still do not know so much on how the different senses do influence each other, and along which mechanisms these reciprocal influences change over development?

1.1 Rules of multisensory integration

The neural process involving a synthesis of information from different sensory modalities we can estimate due to the effectiveness of the stimuli combination vs to the effectiveness of the stimuli separately. For example, the neural response to the event including visual and auditory information could be greater than the response to the event caused by only one type of sensory stimuli. This kind of integration is called multisensory enhancement (Stein & Stanford, 2008).

It is important to note that multisensory integration requires some specific conditions and one of them is temporal synchronization. In other words, onset and offset of two different stimuli should match according to a *temporal rule* (Meredith et al., 1987). Interestingly, this intersensory matching may be perceptually detected very early in development. Neonates and infants between 4 and 10 months of age demonstrate a sensitivity to audio-visual synchrony (Lewkowicz et al., 2010). Neural correlates of this ability have also been reported in 3.5- to 5-month-old infants using electroencephalography (Reynolds et al., 2014) and functional near-infrared spectroscopy (Werchan et al., 2018) during synchronous vs. asynchronous audiovisual stimulations. This process is mediated by low-level, subcortical tecto-thalamo-insular pathways, that explains why this detection is relatively easy and possible from birth (Lewkowicz & Turkewitz, 1980, 1981). However the comparison of the sensitivity to audiovisual synchrony in infants in the first year and adults showed an important difference: the intersensory temporal contiguity window was few times larger in infants (Lewkowicz, 1996), as the latter tend to perceive as coherent temporally various multisensory inputs.

A second specific condition for multisensory integration is spatial coordination between unisensory sources of information. Meredith & Stein (1986) formulated it as the *spatial rule*. For example, Neil et al. (2006) used audio, visual and audiovisual stimuli from different localizations in one year-old infants and adults. From 2 months of age, infants showed a faster behavioral response toward co-localized audio and visual targets than from these dis-localized stimuli, and their performance improved with age. This spatiotemporal overlap between two sensory modalities relies on simple physical relationships, but the role of familiarity of inputs allows infants to more efficiently learn higher-level multisensory associations (Murray et al., 2016). For example, audiovisual integration between human faces and voices appears from a very young age: 3-month-olds can associate them (Brookes et al., 2001), while integrations between more arbitrary and various properties such as color, shape, taste or temperature appear later: only 6- and not 4- month-old infants can link the color of an object with its particular shape (Hernandez-Reif & Bahrick, 2001); 7-month-old infants can learn to associate the color or shape of an object with an arbitrary sound (Bahrick, 1992) or taste (Reardon & Bushnell, 1988) and the ability to associate the color and temperature appears to develops only after 7 months age (Bushnell, 1986). In sum, spatiotemporal relations of separated stimuli from different sensory domains facilitate their multisensory integration, and even more so when the stimuli are familiar and meaningful.

1.2 Brain mechanisms of multisensory integration

A pioneering study demonstrated that combining different sensory stimuli was effective at the level of a single neuron within the cat superior colliculus (SC) (Meredith & Stein, 1983). The SC is a midbrain structure that consists in multisensory neurons processing visual and auditory cues (Stein & Arigbede, 1972). For their integration, these stimuli of different domains must be linked in time. But the conduction speeds of visual and auditory signals being different, their temporal synchronization requires a binding window that lasts several hundred milliseconds. Each multisensory neuron responds to each sensory modality with one receptive field. These receptive fields could overlap in space depending on the location of the stimulation. For example, co-located visual and auditory cues activate both receptive fields, which leads to the enhancement of the multisensory response. This effect is called *superadditivity,* as this multisensory response is stronger than the simple sum of unisensory visual and auditory responses of the same neuron. However, the receptive fields are far from overlapping when the sensory information from different modalities stems come from different source locations. In this case, the response enhancement phenomenon was abolished or even depressed (i.e., *subadditivity*: the multisensory response is weaker than the simple sum of the visual and auditory unisensory responses of the same neuron) (Stein & Stanford, 2008).

However, multisensory integration occurs not only in multisensory cells but also between populations of different neurons. The infant brain is replete with distinct «preliminary» neural networks that represent a common substrate for multisensory integration (Benetti & Collignon, 2022). To form functionally-bound neural maps, different neuronal populations must be activated by synchronized and colocalized stimuli. Thus, those neuronal chains which are synchronously activated in parallel by distinct unisensory sources will become the strongest, conserved networks, while those that do not receive synchronized inputs are progressively eliminated in time. This process of progressive neural selection provides a fundamental basis for perceptual categorization (Edelman, 1987). Later, Edelman (1993) proposed a theory suggesting the ongoing reciprocal signaling between the mapped neuron populations by a process called reentry. Thus, continuous reentry signaling across neuronal maps leads to temporally coordinated synaptic changes that might provide the basis of multisensory integration.

Historically, researchers considered that multisensory processing in humans occurs only in the higher-level associative cortical area, while the information from different sensory modalities is processed first separately in each brain region (e.g., sound cues are processed only in the temporal cortex: Macaluso, 2006). However, recent studies demonstrated alternative views showing that the neocortex is mostly multisensory (Ghazanfar & Schroeder, 2006). Low-level sensory regions provide indeed the feedback for integration as multisensory response could be observed very early in the response formation: i.e., only 40 ms after sensory input (Foxe & Schroeder, 2005; Schroeder & Foxe, 2005). Moreover, other studies confirm that multisensory integration occurs also in the midbrain (Stein & Stanford, 2008) and sensory-specific cortical fields (Calvert et al., 1997; Kayser, 2010; Watkins et al., 2006).

Indeed, effective multisensory integration requires the synergy on low- and high-level brain systems. However, across the lifespan, contribution of these levels could vary. After birth, the infant brain detects rudimentary multisensory correspondences based on low-level cues, such as intensity (Lewkowicz & Turkewitz, 1980), temporal synchrony (Lewkowicz et al., 2010) and spatial co-localization (Neil et al., 2006). At this immature stage, neural tuning is extremely broad reflecting the wide temporal binding window in neonates compared to adults (Lewkowicz, 1996). Unisensory responses in the immature infant brain are weak due to its low maturation level: subcortical regions specialized on simple sensorimotor activity mature before cortical regions responsible for cognitive functions (Murray et al., 2016). Thus, rudimentary multisensory integration could constitute a neuronal basis for more complex, higher-level associative networks. An infant daily experience plays here the crucial role providing multisensory perceptual narrowing (Lewkowicz, 2014; Lewkowicz & Ghazanfar, 2009). Associative learning becomes more and more precise by binding only native multisensory inputs that allows forming narrowly-tuned perceptual categories (Murray et al., 2016) based on brain regions dedicated to the same semantic domain (Mahon & Caramazza, 2011).

Moreover, multisensory integration is characterized by high-level plasticity. The ventral occipito-temporal cortex, which has a category-selective organization, receives direct inputs from the different sensory modalities. Recent studies demonstrated their progressive tuning depending on the type of prevailing sensory information when the activity of the other sensory system was deprived. Indeed, congenitally-blind people receiving auditory inputs demonstrate activation in the same brain regions as sighted participants stimulated with visual inputs (Mattioni et al., 2020), while early-deaf individuals have responses to visual motion in auditory motion-sensitive regions (Benetti et al., 2021). Thus, the absence of unisensory experience (e.g., visual) across development does not disrupt the categorical organization of the ventral occipitotemporal cortex, supporting the idea of an underlying mechanism that is independent on specific sensory modalities (Pietrini et al., 2004; Ratan Murty et al., 2020; van den Hurk et al., 2017; Vetter et al., 2020).

1.3 The intersensory Redundancy Hypothesis (IRH)

The role of multisensory integration in early attention and perceptual learning was specifically studied in the context of the *Intersensory Redundancy Hypothesis* (IRH) proposed by Bahrick & Lickliter (2000) that includes four discussed below predictions. Authors relied on the fact that infants are able to detect common properties across several sensory modalities, which they called *amodal* properties, among which they place synchrony, rhythm, intensity, rate, complexity, variability, etc. These types of information about stimuli can be redundantly specified across cues from distinct sensory domains. They easily attract the attention of infants and favor the detection of highly salient amodal properties in that synchronous bimodal stimulations are more efficient than unimodal stimulation. This first prediction of IRH is called *intersensory facilitation*. For example, 4-month-old infants better discriminated the change in the emotional affect of synchronous audiovisual speech compared to the asynchronous or unimodal speech that was assessed by visual recovery to the test trials after habituation phase (Flom & Bahrick, 2007). The same results was observed for the detection of prosody (Bahrick et al., 2019) and of the tempo of hammer tapping (Bahrick et al., 2002).

Contrary to amodal properties, non-redundant properties are specific to each sensory modality (e.g., the color of an object or acoustic features of a voice). The second prediction of the IRH assumes that modal information is detected easier in unimodal stimulation than in synchronous bimodal stimulation. According to this *unimodal facilitation* prediction, there is no competition for attentional resources from salient intersensory redundancy, thus attention is free to focus on a single modality-specific property. For example, 3- and 5-month-old infants detect the orientation change of hammer only in unimodal visual stimulation compared to the synchronous bimodal condition (Bahrick et al., 2006). The same results occur with face (Bahrick et al., 2014) and voice detection (Bahrick et al., 2005).

Across development, infants' attention, from abstract and general, becomes more and more specific and flexible (Gibson, 1969). With age, infants demonstrate indeed narrowing and differentiation of their perceptions, increasing the efficiency of processing that facilitates detection of amodal and modality-specific properties in both unimodal and bimodal stimulations. Thus, a third prediction of the IRH suggests a *developmental improvement in selective attention*. For example, infants of 8 months of age detect the orientation of the hammer in both unimodal and bimodal stimulation, while in the mentioned above study 3- and 5-month-old infants were not able to detect this non-redundant property in bimodal synchronous stimulation (Bahrick et al., 2006). The same results were noted for synchronous audiovisual speech in 9-month-old infants compared with 5 month-olds (Flom & Bahrick, 2007). A fourth prediction of IRH states that the intersensory facilitation across development depends on *task difficulty and expertise.* Indeed, 3-month-old infants evince intersensory facilitation in a tempo discrimination task during bimodal audiovisual stimulation, but they do not in the unimodal conditions (Bahrick et al., 2002), while at 5 months they demonstrate the stable performance in bi- and unisensory conditions getting without intersensory facilitation (Bahrick & Lickliter, 2004). However, increasing the difficulty of the task induces them to again rely on intersensory facilitation (Bahrick et al., 2010). The same pattern was noted in adults: in conditions of perceptual load, bimodal cues grab spatial attention more effectively than unimodal cues (Santangelo et al., 2008; Santangelo & Spence, 2007; Spence, 2010). Thus, the phenomenon of multisensory integration provides a solid background for the development of perceptual learning and attention tuning.

1 .4 Inverse effectiveness

The above results are in line with the principle of ***inverse effectiveness*** that constitutes the third rule of multisensory integration, besides temporal and spatial synchronization principles (Stein & Meredith, 1993). This inverse effectiveness principle claims that the lower single unisensory responses benefit the most from multisensory integration. Inverse effectiveness was first observed by the Meredith and Stein (1983) on the superior colliculus of the cat. This pioneering study demonstrated at the single neuron level the enhancement of the audiovisual response compared to weak visual and auditory responses separately. Later the principle of inverse effectiveness was generalized to other animal models, such as the mouse (Siemann et al., 2015), guinea-pig (Koehler & Shore, 2013), ferret (Foxworthy et al., 2013), and macaque (Avillac et al., 2007).

In humans, evidence for this principle has also been proven by different methods: using the functional magnetic resonance imaging (fMRI) during non-speech object stimuli presentation (Stevenson et al., 2007), speech and object recognition (Stevenson & James, 2009) and visual event-related potentials (ERPs) during visual speech presentation (Stevenson et al., 2012). Werner & Noppeney (2010) applied the inverse effectiveness principle to audio-visual object categorization, manipulating the informativeness of stimuli and using behavioral measurements and fMRI. Regenbogen et al (2016) showed that peri-threshold multisensory objects accumulated evidence for a correct decision faster than either of the unisensory objects confirming the link between previous findings on a single neuron level with behavioral studies demonstrating multisensory integration.

All studies mentioned above were focused on the integration of visual and auditory stimulations, as auditory and visual modalities have accurate onsets and offsets easily applicable in spatio-temporal synchronization studies. However, the principle of inverse effectiveness has rarely been tested with other sensory modalities. Some studies show visual enhancement of touch in tasks requiring tactile spatial computation near to performance limits (Press et al., 2004). Moreover, further investigations demonstrated the amelioration tactile deficits by viewing the body for the patients suffering a reduced somatosensory sensitivity (Serino et al., 2007). Recently, Ronga et al. (2021) showed spatial modulation of multisensory integration from first hours of life, finding a strong superadditive response for an auditory-tactile bimodal stimulation when the sound source was near to body. However, could the principle of inverse effectiveness apply to a sensory modality that is less pronounced in terms of spatial and temporal features, such as olfaction or taste?

2. A sense of scents: the importance of human olfaction

Olfaction is a grey eminence among of our senses. The importance of odors in humans was neglected by researchers during protracted periods of history of science due to the traditional Western view that the olfactory system has lost its role along evolution (Broca, 1879; Darwin, 1871; Freud, 1905). More recently, the finding of the loss of olfactory receptor genes (by pseudogenization) was even correlated with the acquisition of full trichromatic vision in primates (Gilad et al., 2003), highlighting the alleged general dominance of vision in the human sensorium. This general academic view seems to reflect in part the attitude of people when they are questioned about the importance of the different senses for the everyday realization of their lives. Indeed, Hutmacher (2019) reported that 73% of respondents are scared to lose the sense of vision, while 0% are afraid to never perceive odors. But these latter results stem from the times before the COVID-19 pandemic, which symptoms touching surprisingly olfaction and taste raised general attention to these senses and a renewal of their consideration. Indeed, smell blindness called anosmia can induce increasing discouragement and deep depression that was demonstrated by recent studies (Mathis et al., 2021; Yom-Tov et al., 2021).

However, since the years 1970-2000, research on olfaction, and more specifically on human chemosensory communication, has bloomed (e.g., Doty, 2003, 2015; Engen, 1980; Holley, 1999; Stoddart, 1990; Zucco et al., 2012) showing that olfaction has crucial advantages compared to communication by visual and auditory signals (Lübke & Pause, 2015; Schaal & Porter, 1991). Chemical cues have great specificities (Bushdid et al., 2014), coupled with their low production costs in body odors (Wyatt, 2014). High volatile molecules are effective over long distances, while low volatile molecules demonstrate stability in space and time, both properties that are useful for perceiving scents in absence of their sender. Moreover, in the case of physical barriers, such as dark or noisy environments, olfactory signals can be easily conveyed when other sensory systems are ineffective.

Fortunately, studies of the last decades disclosed that poor human olfactory abilities compared to those of other mammals was a myth (see e.g., McGann, 2017; Schaal & Porter, 1991). Humans are indeed able to detect extremely low odor concentrations (Nagata & Takeuchi, 1990) and they even significantly decrease olfactory detection thresholds with practice (e.g., Dalton et al., 2002). Humans can also discriminate one odorant from another with «just noticeable divergence» (Cain, 1977) and, for some substances, do it even better than dogs and rodents (Sarrafchi et al., 2013; Sarrafchi & Laska, 2017). However, humans do not seem to trust their nose in the traditional Western culture. Self-ratings of olfactory abilities are indeed no correlated with real olfactory detection thresholds (Philpott et al., 2006), because participants base more their responsiveness on vision when they observe perceptual changes (Engen, 1972). Probably, this alleged everyday disconnection from olfactory abilities comes from difficulties in labeling of smell sensations (Lawless & Engen, 1977). However, it is important to note that olfactory abilities continue to play many essential roles in human behavior. Odors modulate the choice of sexual partner (e.g., Wedekind & Füri, 1997), regulate mother-infant relationship (Macfarlane, 1975; Porter et al., 1983; Schaal et al., 1980, 2020; Schäfer & Croy, 2023), warn about danger (Chen & Haviland-Jones, 2000), influence moods (Bensafi et al., 2004; Knasko, 1992; Lundström & Olsson, 2005), cognitive performance (Zucco et al., 2012), and they even change time perception (Baccarani et al., 2021).

2.1 Specificities of olfaction in human development

In the following paragraphs, we will explore special properties of olfactory perception along development, including comparisons with the visual and auditory systems at the anatomical and functional levels, and in terms of plasticity, information properties of stimuli and perceptual attention.

2.1.1 Early maturation

Olfaction is a complex sense based on multi-channel chemoreception. It consists of olfactory and trigeminal subsystems that are interconnected and functionally overlapping. Olfaction becomes functional very early, taking place between touch and vestibular system, and anyway well before vision (Figure 1.1) (Lecanuet & Schaal, 1996). In humans, trigeminal neurons appear by 4th gestational week and they are able to respond to touch stimulation 3 weeks later, while olfactory sensory neurons mature by the 11th gestational week. Thus, at the anatomical level, human olfactory sensory neurons can be seen from early gestation, their ability to process odor cues emerges later in the last trimester (Schaal & Durand, 2012). Floating in the amniotic fluid (AF), the fetus is exposed to odorous compounds which occurrence is regulated by, among other factors, the mother's biological state due to transplacental transfer (Schaal et al., 2002). Specifically, several experiments on the dietary inclinations of pregnant mothers showed that olfaction becomes functional *in utero*. Newborns express preferential or discriminative responses to flavors or odorants which they were exposed to in the intrauterine environment due to the mother-to-fetus transfer (garlic: Hepper et al., 2013; Mennella & Beauchamp, 1993; anise: Schaal et al., 2000; carrot: Mennella et al., 2001; Ustun et al., 2022 and kale: Ustun et al., 2022).

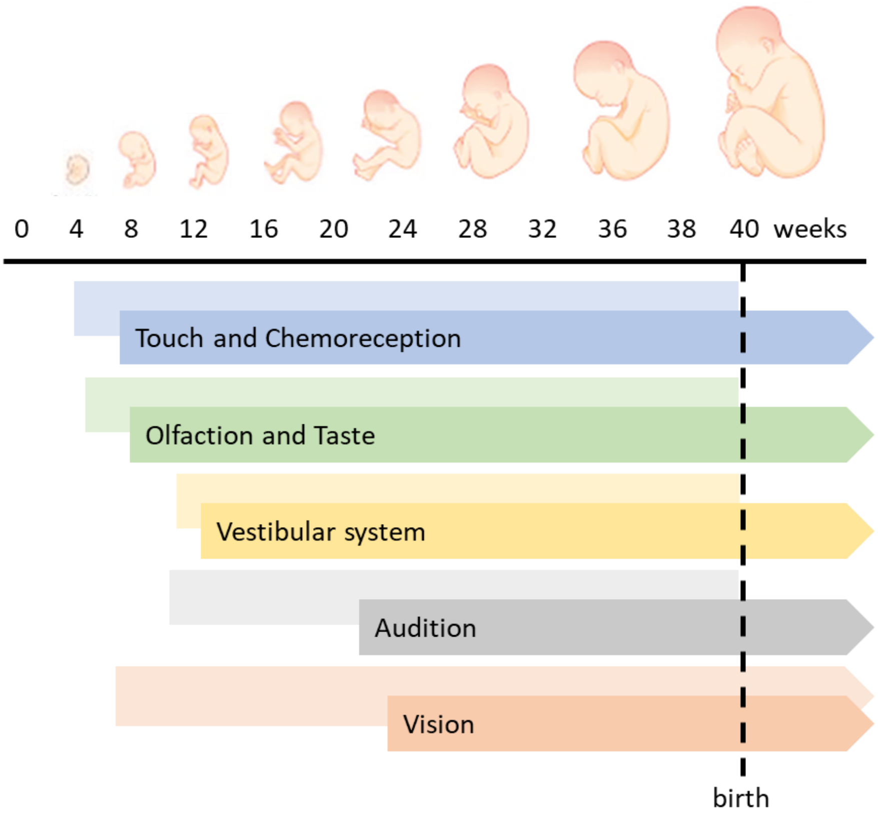

Figure 1.1. Development of sensory systems in humans during gestation. Light bars indicate the emergence and maturation of anatomical structures, while bright bars indicate the functional onsets of senses. Arrows after birth specify the anatomical and functional postnatal development. This figure adapted from (Bremner et al., 2012), original could be found at https://doi.org/10.1093/acprof:oso/9780199586059.001.0001

2.1.2 Plasticity

During early sensory development, in the same line with vision and audition, the fine-tuning of olfaction depends on environmental exposure and perceptual experience (Schaal & Durand, 2012). Thus, neuronal selection and the forming of inter-neuronal networks may follow the same principle as exposed above. However, olfaction is specific in its extremely high susceptibility to the local conditions of the environment, rendering the olfactory context deeply influential on perceptual learning (Bende & Nordin, 1997; W. Li et al., 2008; Rabin, 1988). However, the plasticity of olfaction greatly changes over different developmental stages. The so far most studied sensitive period is situated in early infancy, when the influence of environmental exposure is crucially important for establishing stable odor and flavor preferences (Mennella & Beauchamp, 1998).

2.1.3 The nature of olfactory information

Intensity is one notable amodal property that characterizes information cues from all sensory domains. It may be important for the olfactory modality, as the intrauterine environment of fetuses filters out highly intense odor stimuli (Lecanuet & Schaal, 1996). Therefore, intense odor stimuli elicit avoidance in neonates and infants, much as with visual and auditory stimuli (Lewkowicz, 1991; Lewkowicz & Turkewitz, 1980). The intensity of odor stimuli is an issue for infants, especially regarding their reactivity thresholds for odorants, which can be much lower as compared to adults (Loos et al., 2014). For example, the gas-chromatographic analyses of the AF from mothers who ingested capsules of a powdered cumin demonstrated only non-quantifiable traces of it (Schaal, 2005); nevertheless, both infants and adults were capable to detect such low concentrations of odorants (Schaal & Marlier, 1998). Otherwise, this result also supports the notion that newborns brain can extract odorants encountered prenatally and memorize them until adult stage. Other basic properties of odor percepts are their familiarity/novelty and their hedonic valence. From the earliest stages of development, these properties of odors explain discrimination of iso-intensive stimuli and differential orientation in space leading to effective feeding behavior (Soussignan et al., 1997; Steiner, 1979; Steiner et al., 2001).

2.1.4 Perceptual attention

A capacity of selective attention is crucial to make sense of complex environments, abounding in a multiplicity of sensory cues coming in from different modalities. Due to related sensory complexity, human sensory processing is designed to hit on specific cues selected according top-down (e.g., intentional) and/or bottom-up regulations (e.g., sensory salience). Human sensory systems have different «attentional envelopes» that represent different abilities to change an individual's attentional focus in space and time (Sela & Sobel, 2010). Despite excellent capacities to discriminate odors and perceive very low concentrations, humans are considered poor at localizing odor cues, as compared with visual (Posner et al., 1980) and auditory cues (Salmi et al., 2007). It is important to notice that we consider here olfaction and not trigeminal chemesthesis, the latter being sensitive to high intensity odorants and driving orientation responses based on tactile or tacto-chemical cues in newborns and adults (Rieser et al., 1976). Without respiratory movements (sniffing) or movements of the entire body, humans are incapable to precise if odorants are coming from the left or from the right (Frasnelli et al., 2009; Radil & Wysocki, 1998) or, if they do it, it is slightly better than by chance (Porter et al., 2005). However, newborns demonstrate reliable ability for spatial localization of odor cues of low intensity that, for the most part, stimulates sensory-motor activation (Rosenblatt, 1983; Schaal, 2006). For example, breast odor elicits head orientation ipsilateral to a preferred odor and even favors crawling towards the odor source (Hym et al., 2021; Varendi & Porter, 2001). In addition, relative to control condition, mother's breast odors do also induce longer periods of eyes opening in 2-day-old neonates (Doucet et al., 2007), favoring visually-oriented responses. In adults, some brain-imaging studies with the activation of several brain structures such as piriform cortex and olfactory tubercle involved in olfactory attention, found that olfactory attention allows faster discrimination of odor cues than of visual cues (Spence et al., 2001; Zelano & Sobel, 2005).

Auditory and visual flows of information are, in principle, continuous in time. Although vision is interrupted only by short eye blinks, with an input loss of 250 ms per blink (Caffier et al., 2003), audition cannot be broken up by ear closure (although it can be mechanically). Olfaction is different in this respect: the temporal dynamics of breathing induces periodicity in odor inputs, with more or less regular pauses. In adult humans, such breathing periodicity is less notable because successive sniffs are produced to investigate the olfactory environment (Laing, 1983). This phenomenon is named «change blindness» (Rensink et al., 1997), suggesting that the temporal continuity of sensory input provides a robust focus of attention and therefore uninterrupted awareness of the environment. Change blindness was explained by olfactory habituation at the high cortical level, as this process is absent at the receptor level (Mahmut & Stevenson, 2015). Forster and Spencer (2018) demonstrated «inattentional anosmia» for the detection of coffee aroma. However, brain responses to odorants were nevertheless recorded using fMRI (Sabri et al., 2005) and OERP (Krauel et al., 1999) when odor stimulation cooccurred with an auditory stimulus which participant's attention was directed. Further studies on non-detected odor stimuli found a clear responses in the olfactory epithelium (Hummel et al., 2006) and cortex (Jacob et al., 2001; Sobel et al., 1999). Thus, these results highlight the partly unaware nature of olfactory processing.

2.2 Human olfactory neuroanatomy

The early neuroanatomist Paul Broca (1879) classified humans into the category of «anosmatic» mammals, due to their morphologically-developed frontal lobes and relative small size of olfactory bulbs; therefore, in line with the knowledge of his time, he alleged that our own species relies on odors only marginally in directing its everyday life. As noted above, this view agreed with the discourse of influential thinkers of the 19th century (e.g., Darwin, Freud, James, Haeckel) and their propagators, but the anosmatic status decreed for humans was thereafter toned down to an intermediary «microsmatic» category, taking into consideration that humans take widespread advantage of olfaction in cooking, gastronomy, perfumes and body care. This notion of «human microsmatic» ruled however until recently in psychology handbooks and even contemporary molecular biologists falsely continue to relate the number of expressed olfactory receptors with the prevalence of olfaction in a species natural history. However, McGann (2017) and some others (Candau & Schaal, 2017, 2019; Loos et al., 2023; Schaal & Porter, 1991) have synthetized arguments against that view. Without entering into this debate, the coming section summarizes the anatomical substrate of olfactory processing and how its links with cognitive functions.

2.2.1 Odor processing

As in all mammals, the human olfactory system consists of three of main bilateral structures: the external olfactory epithelium, and within the skull, the olfactory bulb connecting with a complex network of olfactory and multisensory cortices (Figure 1.2) (Mai & Paxinos, 2011). Detection of odorant molecules starts in the nasal cavity through either orthonasal sniffing (Kepecs et al., 2006) or the retronasal flow of odorants stemming in the mouth when eating (Heilmann & Hummel, 2004; Small et al., 2005). Olfactory sensory neurons play also a role of mechanoreceptors activated by inhalation-expiration cycles (Grosmaitre et al., 2007), whereby sniffing shapes neural activity in the olfactory system (Scott, 2006; Sobel et al., 1998; Verhagen et al., 2007). The olfactory epithelium is lined with olfactory sensory neurons that bind odorant molecules on the cilia that terminate their dendrites. Humans have about 12 million olfactory sensory neurons in their nose (Moran et al., 1982), and, when in their mature stage, almost all of them express only one type of olfactory receptor (OR) proteins (Saito et al., 2009). These ciliary OR are more or less specific in their chemical affinity with odorant ligands (Su et al., 2009). Typically, each OR binds with a narrow selection of odorant molecules (Keller et al., 2007; Malnic et al., 1999), although some OR can capture a wide variety of compounds (Grosmaitre et al., 2009). The axons of olfactory sensory neurons form the olfactory nerve, connecting with the olfactory bulb, via the cribriform plate of the ethmoid bone. At variance with other mammalian models (mostly rodents), the human olfactory bulb is organized within fairly greater multiplicity of glomeruli: this spherical structures formed by the fibers and synapses that link olfactory sensory neurons with mitral cells (Murthy, 2011). Each bulbar glomerulus receives input from olfactory receptor neurons that express a single type of OR. Due to this unique pattern of glomerular convergence, the olfactory bulb is considered as a structure where spatiotemporal coding of odors takes place (Leon & Johnson, 2003; Su et al., 2009), despite the difficulty of defining a link between spatiotemporal neuronal activation patterns and specific odorants generating them (Mainen, 2006).

Next, the flow of odor information reaches the primary olfactory cortex via the olfactory tract constituted by the axons of mitral cells. This connectivity is massively ipsilateral, although contralateral projections occur (Savic & Gulyas, 2000; Uva & de Curtis, 2005). The primary olfactory cortex take a part of the ventral temporal lobe, also called piriform cortex, which plays an important role in odor discrimination, classification (Howard et al., 2009; W. Li et al., 2006) and generalization of different odorant types (Barnes et al., 2008). Moreover, posterior piriform cortex (PPC) integrates information about objects from different senses providing multisensory processing (Thunell et al., 2023). Indeed, Porada et al. (2019) demonstrated that visual cues associated with an odor of object activate PPC and this activity increases with the number of sensory modalities providing congruent information.

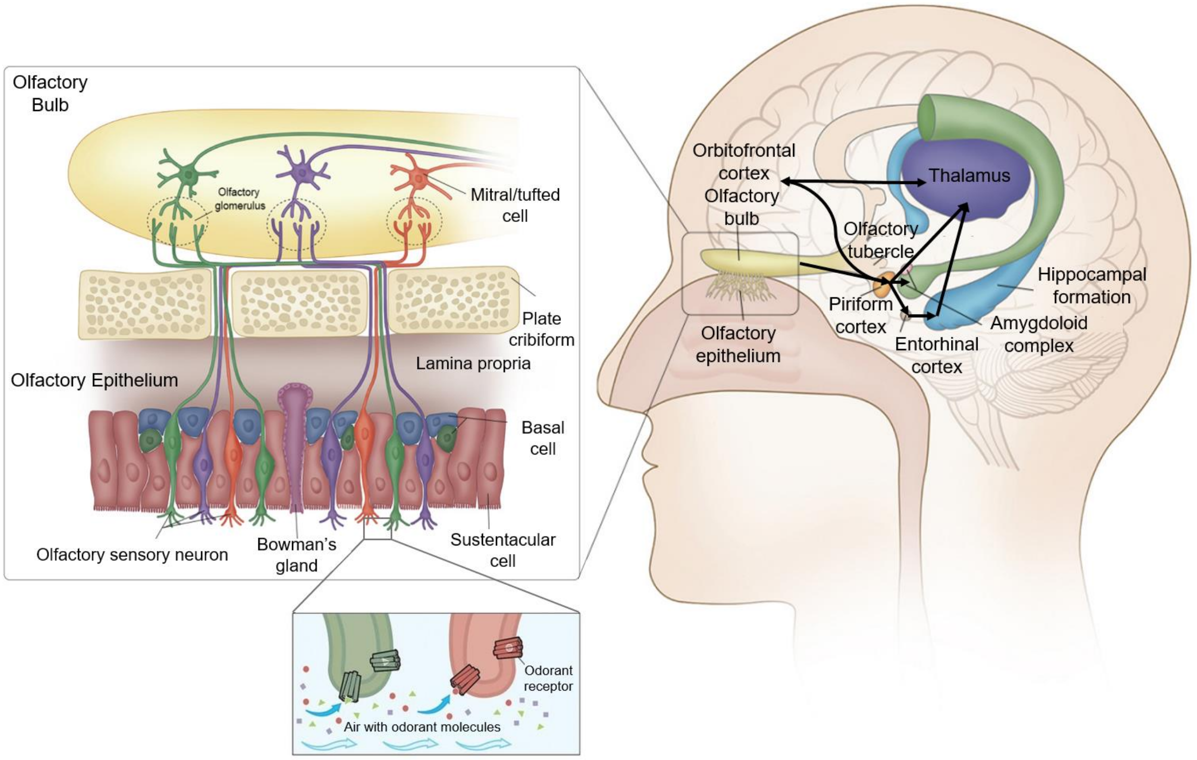

Figure 1.2. Schematic representation of human olfactory system. Molecules of odorant are binded by receptors of the olfactory epithelium. Via the olfactory nerve, receptors axons unit into glomeruli of the olfactory bulb. Information arrive to primary olfactory cortex through olfactory tract. From here, olfactory signals are largely distributed in secondary regions such as the amygdala, the hippocampus with entorhinal cortex, the thalamus and the orbitofrontal cortex. This figure adapted from (Son et al., 2021) and (Rinaldi, 2007). The originals can be found at https://doi.org/10.5483/BMBRep.2021.54.6.055 and https://doi.org/10.1038/sj.embor.7401029.

2.2.2 Roles of olfactory network in the high cognitive functions

Besides the piriform cortex, olfactory neural connections do widely distribute across the orbitofrontal cortex (OFC) and the limbic system. The piriform cortex links directly with the OFC and indirectly via the amygdala, the strategic bridge binding olfactory and neurohormonal information that modulates stress responsiveness, emotional expression and therefore human valenced behavior. Interestingly, neuroimaging studies exposing participants to aversive odors (Zald & Pardo, 1997) and stimuli of high intensity (Anderson et al., 2003) evidenced the essential role of the amygdala in directing responses to stimuli announcing potential risk or real danger (Whalen et al., 2004). The OFC is considered as a secondary olfactory cortex and as a main area of aware processing of olfactory inputs. Li et al. (2010) demonstrated indeed the absence of conscious olfaction in patients with a damaged right OFC, while neural activity was registered in the left OFC during presentation of odor to the left nostril that confirms «blind smell». The OFC is also involved in the learning of new associations involving odors (Rolls et al., 1996) and odor-related object recognition that integrates inputs from other sensory modalities, particularly vision (Zhou et al., 2019). Unlike information from the other senses that relay in the thalamus on their way between periphery and primary cortex (Guillery, 1995), the olfactory tract reaches directly the primary olfactory areas. However, the thalamus finally also receives olfactory input, but through post-cortical connections involving in olfactory attention (Plailly et al., 2008), hedonic processing, olfacto-motor control and odor identification (Sela et al., 2009). The olfactory tubercle receiving direct input from the olfactory bulb is a multisensory integrative center that is involved in reward processes (Ikemoto, 2007), emotional processing and social cognition (Zhou et al., 2019). In particular, the olfactory tubercle provides the sensory convergence of olfactory information with auditory (Wesson & Wilson, 2010) and visual cues: notably, body odors can alone activate the lateral fusiform gyrus that normally responds to the human faces (Zhou & Chen, 2008) as this face-selective brain region forms functional connectivity with the primary olfactory cortex (Zhou et al., 2019).

Olfaction plays also a particular role for the formation of memories (Engen, 2012; Green et al., 2023; Herz, 2016). This engagement of olfaction is already functional in the fetal, neonatal and infant brain (Mennella et al., 2001; Schaal et al., 2000), and promotes autobiographical memories that remain active into childhood and adulthood (e.g., Hepper et al., 2013; Poncelet et al., 2010). Interestingly, as compared to visual and auditory memories, odor-based representations are remembered better and for longer (e.g., Chu & Downes, 2002; Herz, 2004). This performance of olfaction might be related with the direct functional connectivity of the primary olfactory cortex with the hippocampus (Zhou et al., 2021) compared to the other sensory systems, which reach the hippocampus via associative areas. However, it cannot be excluded that this downstream pathway does also occur for the olfactory system, as the hippocampus receives inputs from the OFC via the entorhinal cortex (EC) located in the medial temporal lobe. The EC is considered to be involved in memory consolidation (Hevner & Wong-Riley, 1992) and especially in social memory involved in the recognition of conspecifics (Lopez-Rojas et al., 2022).

Thus, due to the large-scale smell network including the functional and anatomical connectivity with associative cortical areas and limbic system (Zhou et al., 2019), olfaction is strongly involved in the high cognitive functions such as attention, self-control, navigation, decision making, learning, memory and social cognition (e.g., Fischler-Ruiz et al., 2021; Igarashi et al., 2014; Kostka & Bitzenhofer, 2022; Symanski et al., 2022; G. Zucco et al., 2012). In this dissertation work we will particularly focus on the role of smells in the social cognition, which will be reviewed in the next section.

2.3 Odor-based social cognition

Chemosensory communication takes an important part in the social cognition (see Pause, 2017) providing a different levels of recognition including species, classes of conspecifics, and individuals. These processes form a basis for the ontogenetic and phylogenetic survival (Snyder-Mackler et al., 2020). Thus, odors crucially mediate social behavior of humans influencing on the sexual partner selection, family members and friend recognition, besides, providing information about physiological status of odor sender and informing other conspecific about danger or safety (see for review Lübke & Pause, 2015).

In present work we focalize in the mother–infant bonding. It is known that interaction between infant and mother elicits parental involvement in the childcare and protection, feeding behavior stimulation, reciprocal individual recognition and emotional connection (see Porter & Schaal, 2003). We are especially interested in the role of maternal body odors in the normal infant development as the most salient olfactory cues compared to other’s body scents. This distinct status is provided by the fact that infants discover maternal odors even before birth and later, continue to be exposed to them more often due to the mother's caring. In this section, we will describe particularities of maternal odors and their influence on offspring at different developmental stages.

2.3.1 Specificities of maternal odors

Maternal body odor is made up with the mixture of odorant molecules from axillary zone and areolar region of nipple. Moreover, it includes the scents from other sources such as oral and nasal cavity, scalp, neck, hands, feet, genitals and skin in general. There, odors are emitted from the secretions of different types of skin glands (sebaceous, apocrine, eccrine), areolar and Montgomerian. Besides that maternal odor is supplemented by endogenous (milk, saliva, urine, menses, fesses, mucus) and exogenous (diet, cosmetic, pollution) sources (Doucet et al., 2012; Schaal, 2010; Schaal & Porter, 1991). Important to note, the same chemical profile occurs partly already in the prenatal environment, in amniotic fluid, a mixture produced by the mother and the fetus. Thus, transnatal olfactory continuity provides a smooth transition between intrauterine and extrauterine niches in the human newborns (Schaal et al., 2020), as well as in other mammals, thus confirming the same evolutionary mechanisms supporting survival of mammalian infants (Porter et al., 2001; Porter & Schaal, 2003; Schaal, 2010; Schaal & Al Aïn, 2014).

Chemical analyses of the amniotic fluid indicate some resemblance in the prenatal and the postnatal smellscapes to which perinates are exposed, particularly through colostrum and milk (Schaal, 2005, 2016). The amniotic fluid composition in odorants is multiply influenced by maternal genetic determinants, diet and other environmental aspects (cosmetics, tobacco), as well as by the mother's emotions and physical activity and metabolism (Schaal, 2005, 2016; Spahn et al., 2019). In the postnatal environment, the smell of mother's breast attracts the neonates 10 min after birth allowing to find the nipple (Varendi et al., 1994). Components of mothers' diet during pregnancy or during lactation (e.g., anise, carrot, kale) elicits a stable odor preference in few days after birth (Mennella et al., 2001; Schaal et al., 2000; Ustun et al., 2022). However, the infant's odor preferences are highly plastic as a function of their experience with them. For example, while mother's axillary odors induce crying in 3-day-old newborns (Varendi et al., 1998), this behavior pattern changes in two weeks, when newborns start to orient to axillary odors due to coupling with that odor when at the breast (Cernoch & Porter, 1985; see also Delaunay-El Allam et al., 2010 for stable olfactory memory acquired at the brest).

An important stage in transnatal olfactory continuity is the naturalistic birth process. The labor process, with its contractions on the fetal skull, constitutes the last update of AF odor encoding, accompanied by novel sensory experiences of all types for the perinatal infant. The birth-related dramatic change of the environment leads to high arousal levels and increased level of catecholamines (Lagercrantz & Slotkin, 1986) that probably are involved in neonatal olfactory learning. It has been founded that newborns after a Caesarean section do not show a preference few days later for an experimental odor perceived 30 min after being born, while newborns who were born with delivery contractions do learn it (Varendi et al., 2002). The first few postnatal hours are thus especially important for olfactory learning when the brain becomes particularly receptive to all kinds of sensory inputs. Human newborns exposed to an odorant during the first postnatal hour memorize it readily, while newborns exposed to that same odor 12 h after birth do not display any preference for this odor few days later (Romantshik et al., 2007), suggesting that the perinatal hours constitute a sensitive period for olfactory learning, and perhaps for the acquisition of other maternal cues (face, voice, skin). Thus, process of birth contributes to establish a unique neurosensory context promoting learning during the skin-to-skin mother-infant contact (Mizuno et al., 2004) or first breast-feeds (Delaunay-El Alam et al., 2006).

Important to note is the fact that the mother's odor persists in the environment of the offspring despite her physical absence. This stability in the space and time (Sela & Sobel, 2010) is a crucial difference between olfaction and vision/audition, which are abolished in her absence. Thus, maternal odor can remain influential even in periods of separation with the mother. This prolongation of odors in absence of the source is known for long time and used traditionally by parents, as well as institutionally in infant's hospitals (Sullivan & Toubas, 1998; Ybarra et al., 2000) and nurseries. Indeed, breastmilk odor decreases the activation of the hypothalamo-pituitary-adrenal (HPA) axis, therefore leading to decrease cortisol level and induce soothing (Nishitani et al., 2009).

In sum, the relationship between human mothers and infants construes a highly dynamic, but robust, system that is mutually regulated by, among other cues, olfactory signals. On the one hand, newborns are able to discriminate maternal odors (from breast, neck, axilla) compared to those from another mother (Macfarlane, 1975; Schaal et al., 1980) and on other hand mothers can recognize the odor of their own infant (Kaitz et al., 1987; Porter et al., 1983; Russell et al., 1983; Schaal et al., 1980). This reciprocal mother-to-infant link is continuously strengthened by the mother's care, nursing and feeding, which in turn activates the maternal reward system (Lundström et al., 2013) and the infants' prefrontal cortex (Nishitani et al., 2014). Thus, maternal odor can be seen as a crucial stimulus that contributes to initiate multisensory social communication, which nurtures survival in subsequent developmental stages (Schaal et al, 2020).

2.3.2 Influence of maternal odors on the developing human from neonate to adolescent

Studies on premature infants can be extrapolated to infer olfactory abilities and behavior in the intrauterine environment. As we know, Schaal et al. (1995, 1998) first demonstrated the recognition of the familiar amniotic fluid versus an unfamiliar one by both breast- and bottle-fed infants, confirming the prenatal olfactory learning which remains active toward similar odors in the postnatal environment, in particular the odor of the colostrum which is not differentiated from that of amniotic fluid (Marlier et al., 1997) and which preferred (to mature milk) by newborn infants (Klaey-Tassone et al., 2020). In general, the familiarity of maternal odors (amniotic fluid, colostrum, milk, breast) provides a soothing effect on preterm and term-borne neonates (Badiee et al., 2013; Jebreili et al., 2015). Recent findings show in particular that breastmilk odor has an analgesic effect that reduces salivary cortisol level in prematures (Zhang et al., 2018). However, the maturation of the olfactory system, although sufficient for initial functioning in utero, is not finished by the third gestational trimester. For example, late preterm neonates (33-36 weeks) show a unilateral activation of OFC, whereas full-term neonates (37-41 weeks) revealed a bilateral activation when exposed to maternal odor (Frie et al., 2020). Such considerable differences in brain reactivity to odor stimuli may indicate the infants' improvement in olfactory awareness as OFC is involved in the highest associative activities.

As mentioned above, maternal odors noticeably modulate the infant's feeding behavior during the first postnatal months. Breast odor (Doucet et al., 2007) and the amniotic fluid (Contreras et al., 2013; Schaal et al., 1995) elicit appetitive reactions in newborns to such an extent that they drive them to crawl to the source of the odor (Varendi & Porter, 2001). During the first hours after birth, neonates demonstrate head orientation and positive emotional facial reactions to colostrum and milk odor due to their high attractivity (Klaey-Tassone et al., 2020; Soussignan et al., 1997). As breastfeeding is involved in immunity development (Edmond et al., 2006, 2007), the odor of colostrum and milk are very important for neonatal survival. This observation is in line with studies comparing the appetitive value of breast milk and formula milk odor. Porter et al. (1991) demonstrated that even newborns without breastfeeding experience preferred breast milk odor, that was later confirmed by stronger activation of the orbitofrontal cortex (Aoyama et al., 2010). And, interestingly, the odor of colostrum is even more attractive than the odor of breastmilk (Klaey-Tassone et al., 2020). As it noted in preterms, full-term neonates also benefit from maternal odor for reducing distress (Zhang et al., 2018). Breastmilk odor delays the onset of crying (Doucet et al., 2007) and reduces its duration (Mellier et al., 1997), it decreases neonates' motor activity and agitation (Rattaz et al., 2005; Schaal et al., 1980), and finally normalizes salivary cortisol level (Nishitani et al., 2009), heart rate and oxygen saturation (Akcan & Polat, 2016).

This prominent influence of maternal odors continues over the first year. For example, infants between 2 and 9 months have a stronger frontal brain reactivity (measured by EEG) to breast milk odor compared to another arbitrary odor (Gellrich et al., 2021). Further, several studies demonstrated the role of maternal odors in visual perception, notably face processing in 4-month-old infants, in whom they enhance looking time toward faces compared to cars (Durand et al., 2013) and make face categorization more efficient (Leleu et al., 2020), highlighting the social function of this type of odor and its role in multisensory interaction. Important to note, even non-familiar mother's odor can reveal effects similar to those of own maternal odor to favor face perception of own mother in 4-month-old infants (Durand et al., 2020). Jessen (2020), using EEG, further demonstrated that maternal odor decreases brain response for fearful faces in 7-month-old infants, while unfamiliar mother's odor conveyed the same effect although it turned out to be less effective. In the same age group, Endevelt-Shapira et al. (2021) investigated brain-to-brain synchronization between infant and unfamiliar women. They found that maternal odor enhances this synchrony with greater looking time at the unfamiliar woman's face. Taking together, these results in older infants suggest that maternal odor prompts not only the relationship between mother and infant, but also with unknown conspecifics.

Unfortunately, studies are lacking between 1 and 3 years that could shed light on the influence of maternal odor on toddlers. At the next stage, in children aged 3.5–5 years, studies become even rarer, but they show that children remain able to recognize a t-shirt impregnated with maternal odor when presented against t-shirts conveying the odor on unfamiliar women (Roberts & Eryaman, 2017; Schaal et al., 1980). Between 6 and 15 years, using the same t-shirt odor recognition-test, children identified maternal odor more reliably after 9 years old (Weisfeld et al., 2003). Thus, maternal odor recognition in children and teenagers seems increasingly unreliable (Ferdenzi et al., 2010). For example, Johnson (1994) found that daughters between 11 and 21 years recognize the maternal neck odor, but not axillary odor. These inconstancies in results relate probably to methodological issues, to the changing maternal smell through the age, social status, and prevalence of perfumes and to child factors related to the lack of attention and compliance. Finally, in these age groups, maternal odors are perhaps less functionally relevant as children spend less time with the mother (and both parents) in daily life and engage mostly with same-age conspecifics. This hypothesis was confirmed by several studies on siblings' and classmates' recognition. For example, 8-year-olds could detect the t-shirts of their own full siblings (Porter & Moore, 1981) and 4–5-year-olds, particularly girls, can identify classmates via their neck odor (Verron & Gaultier, 1976). In later adolescence, maternal odor recognition seems again to become more important, as a hypothetical driver of incest-avoidance. Compared to 6-8 year-olds, adolescent girls and boys aged 9-15 years reactivate recognition of maternal odor, one study finds (Weisfeld et al., 2003). On the other hand, mothers and fathers preferred the body odor of infant and pre-pubertal children in contrast with those of teenagers (Croy et al., 2017), confirming once more the important social role of communication based on body odors.

3. Gazing through the days: is vision the dominant sense in humans?

Vision has always had a special status among the human senses, both biologically, psychologically and culturally. Vision is indeed certainly the prevalent source of information for human beings. It is estimated to provide over 90% of information in several situations (e.g., driving: Hills, 1980). Moreover, 50% of our cerebral cortex pertain to the processing of visual cues (Milner & Goodale, 2008; Zeki, 1993). This dominant role of the visual system is often explained by the evolution of color perception, with the advent of trichromacy in primates: the ability to sense colors via interactions among three types of color receptors in the retina (Jacobs, 1996). Color vision allowed for a more accurate perception, specifically in the complex diurnal environment, facilitating the detection, categorization and identification of visual cues from objects, foods, conspecifics and landscapes

(Jacobs, 2019). Moreover, the continuously entering flow of visual information necessitates to allocate high levels of attention in both space and time (Posner et al., 1980; Sela & Sobel, 2010).

Visual processing is very predictable: the straightforward structure of the visual receptors in the retina allows them to perceive information depending on wavelength (De Valois & De Valois, 1993), and retinotopic mapping of visual inputs are transferred to the primary cortex (Engel et al., 1997). Furthermore, visual processing operates mostly in states of high awareness (Logethetis, 1998), in contrast with olfaction that functions well without awareness (Shepherd, 2006). Thus, vision seems to us humans to be a most reliable source of information on which we strongly base our daily lives. However, has vision always been so well developed and employed over the different stages of development?

3.1 Visual development in humans

Following an embryological established order across vertebrates (Turkewitz & Devenny, 1993), vision emerges after all the other senses (Lecanuet & Schaal, 1996) (Figure 1.1). Vision takes indeed more developmental time for its protracted maturation, being the only sensory system whose main development falls in the postnatal period, up to 20 years (Braddick & Atkinson, 2011; Graven & Browne, 2008).

3.1.1 Prenatal period

At the anatomical level, the visual system starts developing during the first trimester, much as the other senses: the eyes begin to form in gestational week 5, with the appearance of the primordial retina two weeks later. However, retinal neurons undergo complete myelination at about 3 months (Moore et al., 2008) and its final structural maturation arrives at around 4 months after birth (Mann, 1964). The axons of retinal ganglion cells grow toward the lateral geniculate nucleus (LGN) and start functioning due spontaneous firing between gestational weeks 22-30 that becomes then more and more regular (Graven, 2004). In the striate cortex, the typical laminar structure emerges in the 28th gestational week, however, an adult-level maturation appears only postnatally (Burkhalter et al., 1993). Most visual structures develop in third gestational trimester almost in the absence of visual stimulation however some experiments shows the possibility of light transmission from the external environment to the uterine cavity that can provide kind of visual experience before birth (Del Giudice, 2011). Indeed, behavioral and evoked cortical responses appear first with reactions to light at about gestational week 30 in premature neonates (Ellingson, 1960; Engel, 1964; Taylor et al., 1987). However, at this period, ganglion and bipolar cells, and retinal receptors are not fully mature and the early influence of visual cues, particularly direct light, could be dangerous for the too sensitive visual system as eyelids are still translucent and do not provide protection until gestational week 34 (Fielder et al., 1988).

Important to note, sleep cycles and eye movements during rapid eye movement phases (Hobson, 1995) play a particular role in visual development before and after birth. At 29-30 weeks' gestation, the brain starts indeed to differentiate sleep cycles (Goodman & Shatz, 1993) with regular trains of waves from ganglion cells reaching pons-geniculate-occipital structures and becoming theta waves in the hippocampus. Sleep disruption at these age stages, impair retina-lateral geniculate nucleus-primary visual cortex pathway in the infant brain (Graven, 2004).

3.1.2 Postnatal period

Between the birth and 6 months, the developmental changes of vision are considerable (Maurer & Lewis, 2001). At birth, the visual system consists only of rod receptor neurons and ensuing visual abilities are generally poor during the first weeks. Color vision emerges almost 3 months later when the cone-based photopic system starts its progressive maturation. All colors are then not transcribed in the same time, following a protracted process that begins with red (Franklin et al., 2005; Gerhardstein et al., 1999). At the same age range, Johnson & Mason (2002) found motion detection that is particularly important in the functioning of the visual attention (Wattam-Bell, 1992). Next, visual texture perception appears by 4 months (Atkinson & Braddick, 1992) and binocular interaction (Petrig et al., 1981) with stereopsis (Fox et al., 1980) were investigated in 3–5 month-old infants. These results correlate with the formation of binocular sensitive neurons in the upper cortical layers at this age period (Braddick, 1996) that confirms the emergence of cortical function. Morrone & Burr (1986), using early visual evoked potentials, found that, despite early appearance of orientation-selective neurons during first postnatal weeks, they continue to develop until 6 months to reach adult level even later, a sequence that corresponds with the development of inter columnar connections in the visual cortex (Burkhalter et al., 1993).

The development of the visio-motor system is based on global motion sensitivity supported by the maturation of the cortical dorsal stream and the SC of midbrain (Mays & Sparks, 1980). This process relates to the formation of oculomotor systems that provide the visual information needed for the control of action (Milner & Goodale, 1997) and of visual behavior via spatial attention (Hood et al., 1998). The control of gaze requires saccades and head orientation that mature early (Hainline et al., 1984). From 4 months, infants visually control reaching and grasping objects, and this visio-motor exploration tunes until 2 years of life. Increasing locomotion at the end of the first year promotes the emergence of perception of visual perspective (Kavšek et al., 2009), that involves collaboration of dorsal and ventral visual streams and the development of the SC. Thus, 3D vision appears only at about 1.5 years. Cortical connections in the prefrontal cortex involved in high cognitive functions, such as associative-based perception, discrimination, categorization, identification and memory, takes part of long-term brain development and matures until 5-6 years old (Tucker & Fitzpatrick, 2003).

3.1.3 Plasticity

The visual system is characterized by its high plasticity, attested at molecular, cellular, and systemic levels (in animal models: Hensch, 2005). This was found in studying different types of input anomalies or deprivation. For example, a classical study described how the loss of binocular visual input to cortical neurons results in strabismus (Banks et al., 1975). Deprivation caused by cataract during the first 4 months damages motion sensitivity (Ellemberg et al., 2002), face recognition (Geldart et al., 2002; Grand et al., 2004), and integration of geometric forms (Putzar et al., 2007). But visual disruptions beyond 4-6 months do not lead to so strong disorders (Ellemberg et al., 2002), pointing a critical period for the development of normal visual functions. Prolonged deprivation induces the degeneration of cortical visual processing. Following-up a patient who was blind between 3 and 40 years, Fine et al. (2003) showed no recuperation of capacities to perceive contrasts, faces, perspectives after corneal transplantation. However, other cases of visual deprivations showed recovery of several visual functions, including high level of visual processing, after 20 years of vision training (Ostrovsky et al., 2006). These studies highlight the importance of visual experience during sensitive periods for the optimal deployment of vision. Moreover, visual plasticity often leads to cross-sensory transfers between vision and touch (Held, 2009) or audition (Mattioni et al., 2020), where vision «teaches» the other senses, thus engaging the lifelong capacity for perceptual learning (Levi & Li, 2009).

3.2 Neuroanatomy of visual processing

The visual tract consists of eyes with photoreceptors, neural pathways via the LGN through the thalamus and SC in the midbrain to the visual cortex (Figure 1.3) (Graven & Browne, 2008). The visual signal is light reflected by objects that hits the eye through the cornea, focused by the lens and projecting onto the retina, the light-sensitive layer at the back of the eye. The conversion of light into neuronal impulses (transduction) carried out by retinal photoreceptors detecting the photons. These receptors are of two types: rods and cones. Rods line the peripheral parts of the retina and respond to dim light providing the night vision, while cones concentrate in the fovea, where acuity sensitivity to colors are the highest. Cones are of three kinds, tuned to red (60%), green (30%) and blue (10%) according to target wavelengths (e.g., red cones are sensitive to the red light). Thus, the response ratio of the three types of cones provides color vision (Bowmaker & Dartnall, 1980). From the photoreceptors of the retina, the neural signals are transmitted via synapses from the bipolar cells to the retinal ganglion cells, which long axons form the optic nerve. Retinal ganglion cells are sometimes called a third type of photoreceptors because, despite their negligible contribution to vision, they support perception of the circadian rhythm and the pupillary light reflex (Foster et al., 1991) and they are rudimentary visual brightness detectors mediating conscious and unconscious vision (Zaidi et al., 2007). In addition, amacrine and horizontal cells located between photoreceptors and ganglion cells, transmit neural impulses laterally from receptive fields sensitive to motion or colors (Tovée, 2008).

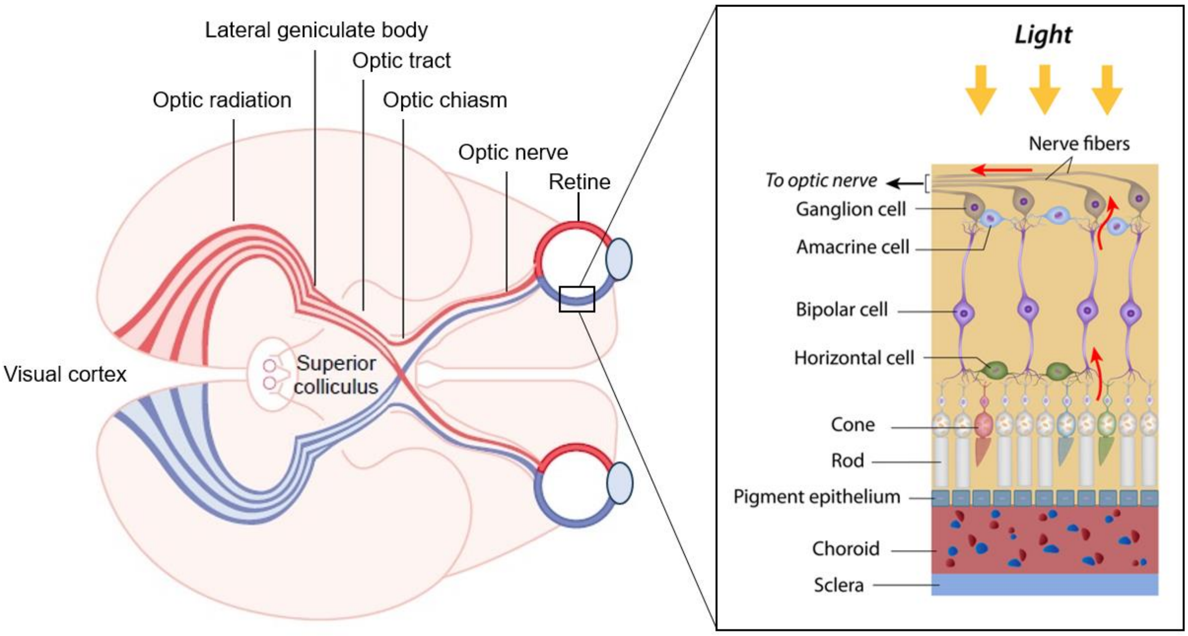

Figure 1.3. Schematic representation of human visual system. Visual inputs arrive into the eye where the photoreceptors of the retina detect the photons and transduce them into neural signal. Next, this neural information is conveyed from the temporal retina zone via the optic nerve arrive to the ipsilateral lateral geniculate nucleus, while information from the nasal retina areas first crosses in the optical chiasma to go to the lateral geniculate nucleus of the thalamus by contralateral way. In addition, part of the neural information follows toward the superior colliculus in midbrain. Finally, the visual signal arrives ipsilaterally through radiation into the primary visual cortex situated in the occipital zones and to the higher cortical levels of the secondary visual cortex. This figure adapted from (Polyak, 1941).

The optic nerves from each eye partly intersect at the optic chiasma: axons from the temporal retinal zone keep the direction and go in ipsilateral regions, while axons from the nasal retinal area arrive to contralateral regions. Thus, visual information from each hemifield can be exposed to conjoined processing. Next, 90% of axons receiving inputs from ipsi- and contralateral connections go to the LGN in the thalamus via the optic tract, and only 10% of axons arrive to the SC in the midbrain involving in the control of eye movements (Nolte & Sundsten, 2002). After the LGN in both hemispheres, visual information projects ipsilaterally in radiation to the primary visual cortex, represented by the striate cortex (V1) on bilateral occipital regions.

Following the retinotopic organization, visual information is presented to the V1. This area is involved in the bottom-up saliency map formation that responds to the most salient visual features, such as color and orientation, to guide attention via eye movements (Li, 2002). Next, visual inputs follow to the hierarchical organization of the cortex that consists of V2, V3, V4, V5/MT and V6/DM areas (i.e., the secondary or extrastriate visual cortex). The difference between visual processing in the primary and secondary cortices is that V1 neurons respond only to a segment of a particular orientation according to its retinotopic location, while neurons in the visual association cortex are responsible to perceiving the complete object (e.g., a human face). Mishkin & Ungerleider (1982) described the ventral and the dorsal visual streams that reflect increasing complexity of neural representation. The ventral stream (so-called «What?» pathway) localizes in the inferior temporal cortex (through V2 and V4 areas), and responds to object features, such as color, texture, shape and size. The dorsal stream («Where?» pathway) takes the part from extrastriate regions via the parietal area toward the prefrontal cortex (including V2, V5/MT and V6/DM areas) and is involved in the spatial attention detecting the motion and spatial relationships between objects, and also controlling eye and head movements.

Thus, visual processing allows us to transform the various scattered cues into accomplished concepts. In humans it plays an important role in the conspecific recognition basing on the face categorization. Our brain discriminate the faces from other elements of visual environment organizing them in distinct category with different but related facial exemplars. Indeed, the faces may strongly differ from each other due to the divers morphological features and physiological states. Perception of these specific cues provides so called «social vision» that take a prominent part in the conspecific recognition and in social cognition in general (Stolier & Freeman, 2016). In the next section we will present a review of anatomical and functional organization of face processing through the development with particular focus on the face categorization.

3.3 Face to faces: social role and specificity

Faces are probably the most salient visual cues processed by the human brain (although complex landscapes and impressionistic master works are not the easiest to process), and they are salient from birth despite aforementioned relative immaturity of the system (Reynolds & Roth, 2018). Conspecific recognition is crucially important for a hyper-social species such as our own (Snyder-Mackler et al., 2020). Communication, care, protection, food searching, cooperation, mating, fighting and escaping all depend crucially on this ability (Holt-Lunstad et al., 2010). The mechanism of face perception is so powerful and robust that some researchers even suppose that responsiveness to faces may be unlearned or «innate»: human newborns who had not seen a real face followed with head and eyes a moving face-like stimuli (Goren et al., 1975; Johnson & Morton, 1991). However, following formation of face processing is exceedingly susceptible to environmental influences. Experimental restrictions of visual development (in animal models) or pathological absence of visual experience indeed support the view that face processing needs protracted period of stimulation to improve after birth and to be attuned over time to environmental affordances (Pascalis et al., 2011).

Faces are quite complex visual stimuli which provide a lot of different information, such as the species, race, gender, age and identity among kin and non-kin individuals (Klein et al., 2009). Faces also reflect the emotional and physiological states of individuals, which perception is crucial for selective communication with conspecifics (Lee et al., 1998). Face processing follows different stages and is carried out on different levels. The simplest stage is face detection among surrounding objects or discrimination between persons. In presence of multiple faces, humans generalize them across different exemplars and build categories. This categorization process is fast, automatic and follows an all-or-none principle (Retter et al., 2020) because it is based on the treatment of common traits. In the same time as it creates categories, face identification requires process of individuation in binding specific traits to a given individuum. This individuation process follows face categorization and seems to take more time and cognitive resources (Bruce & Young, 1986).

3.3.1 Neuroanatomy of face processing

The neural architecture dedicated to face processing was investigated a lot during last decades through functional neuroimaging (Puce et al., 1995; Sergent et al., 1992) and intracranial electroencephalography (Allison et al., 1994; Rossion et al., 2018). Researchers emphasized the ventral occipitotemporal cortex (VOTC) as the face-selective region in the brain. Specifically, the VOTC of the right hemisphere is more concerned by face processing (Rossion et al., 2018), although bilateral activation was also found depending on individual traits and age (Lochy et al., 2019).

3.3.1.1 Stages of processing in face perception

The core system of face processing includes the occipital face area (OFA) localized in the inferior occipital gyrus (IOG), the fusiform face area (FFA) in the lateral fusiform gyrus (latFG) and the superior temporal sulcus (STS) (Figure 1.4) (Haxby et al., 2000). First, visual information from faces arrive to the OFA that is involved in the early sensing of facial features, providing effective face detection (de Vries & Baldauf, 2019; Liu et al., 2010). Next, sensing of unique identity takes place in the FFA (McCarthy et al., 1997) after the analysis of the featural and configural aspects that links to holistic processing (i.e., face perception as integral and unbroken whole: Tanaka & Gordon, 2011). On the same processing stage, the STS is sensitive to the changeable aspects of faces, such as gaze direction (Campbell et al., 1990; Marquardt et al., 2017) and facial expressions (Grill-Spector et al., 2017). However, these hierarchical relationships between the elements of core system of visual analysis proposed by Haxby et al. (2000) do not seem to be so evident. For example, Rossion et al. (2003) demonstrated the preferential activation by faces in the FFA in absence of any feedforward inputs from the lesioned area which corresponded to OFA in a patient with propagnosia. Thus, FFA and OFA can be activated in parallel and, moreover, OFA can receive information from FFA that confirms that these two areas have rather reentering connectivity than hierarchical organization (Rossion, 2014).

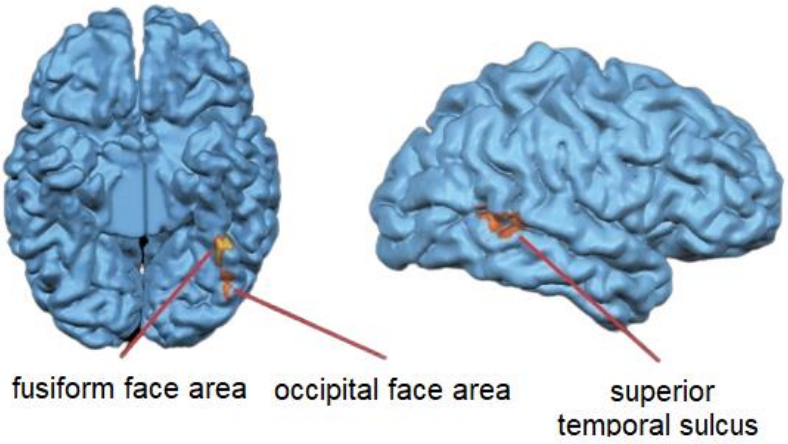

Figure 1.4. The core system of face processing represented by occipital face area (OFA), fusiform face area (FFA) and the superior temporal sulcus (STS).

Further, the anterior temporal lobe (ATL), intraparietal sulcus (IS) and amygdala, as parts of the limbic network and auditory cortex, form an extended system of visual analysis (Haxby et al., 2000). ATL is crucial for semantic memory, especially relating to social and individual aspects such as personal identity and biographical information. In this area, researchers noted a high (around 40%) number of face-exclusive responses without reaction to objects or houses (Jonas et al., 2016). Indeed, recent studies based on intracerebral recording (Hagen et al., 2020; Quian et al., 2023) confirmed that face-selective neuron populations are mostly isolated from other category-selective neurons in the VOCT despite the observed earlier overlaps (Haxby et al., 2001). IS is involved in spatial attention and memory transferring information about gaze direction and head orientation to parietal neural systems (Harries & Perrett, 1991). In general, the functions of STS and IS are overlapping, especially in the detection of gaze direction, although not in the detection of non-speech mouth movements that links only to STS (Puce et al., 1998).

The perception of emotions is an important part of face processing. Recognition of negative emotions (e.g., fear, anger, disgust) is especially linked to activation in the amygdala and insula, highlighting an essential role of quick reading of these emotions for adequate social communication (Breiter et al., 1996; Morris et al., 1996; Phillips et al., 1998). The processing of lip movements provides effective speech comprehension and improves hearing accuracy even in people without auditory troubles. Moreover, dissociation between lip movements and speech leads to sensory disorientation (Mcgurk & Macdonald, 1976). In the absence of speech lip-reading evokes activation in STS and even auditory areas that provides brain coordination between visual and auditory responses during multisensory processing (Calvert et al., 1997). Interestingly, recent studies on humans and non-human primates provided anatomical and functional evidence for a third visual pathway involved in the processing of the social dynamic cues, such as eye, lips and body movements (Pitcher & Ungerleider, 2021). This pathway starts in V1, goes through V5/hMT (motion-selective occipito-temporal areas) to finally project onto the mid-posterior superior temporal sulcus (pSTS).

3.3.1.2 Specificity of face processing network in infancy

As was mentioned above, infants manifest their visual preference for faces very early (Goren et al., 1975). However, this precocious perception is characterized by coarse configuration in newborns (Johnson et al., 1991), corresponding to the activation of the subcortical pathway (LGN, amygdala, SC, pulvinar: Johnson & Morton, 1991; Johnson et al., 2015). It seems that the immature infant brain has an optimal organization for sufficient processing of basic facial configuration (e.g., top-heavy patterns: Cassia et al., 2004). Indeed, 1-5 days after birth newborns demonstrate a haemodynamic response over bilateral posterior temporal cortex viewing a dynamic face but not a moving arm (Farroni et al., 2013). Besides, the strength of this activation is strongly correlate with number of hours after birth that indicates the importance of face-to-face interaction for its inducing. Later, at 4 months, infants start to perceive facial features that correlate with the maturing ventral pathway, which includes the FFA. Indeed, Deen et al. (2017), using fMRI to investigate 4-to-6-months-olds, found a functional organization of the face-selective areas similar to that of the adult brain. Interestingly, at this developmental stage, the face-specificity was not found after presentation of faces versus objects, probably due to incomplete brain maturation: at this age, infants do probably not perceive faces in a holistic way that becomes established only after 6 months (Hayden et al., 2007; Quinn & Tanaka, 2009; Schwarzer et al., 2007). These results are in line with the activation of the dorsal pathway, which maturation is delayed in comparison to the ventral pathway (Livingstone & Hubel, 1988).

Interestingly, the right hemispheric dominance for face perception mentioned above changes with age. In the EEG study of de Heering & Rossion (2015) on 4-to-6 month-old infants, a clear face-selective response was found in the right occipito-temporal cortex (rOT), while Lochy et al. (2019), using the same paradigm, showed bilateral occipito-temporal response in 5 year-old children. Later, in adults many studies show again a right hemispheric dominance for face perception (Grill-Spector et al., 2017; Rossion et al., 2015; Sergent et al., 1992). Thus, face-specific lateralization follows a non-linear trajectory of development. Moreover, face processing is affected by many parallel brain processes. One of them is the visual processing of words that involves the left hemisphere. Behrmann & Plaut (2020) supposed that increasing reading abilities could reinforce the right lateralization of face processing over age, and notably in adults. Indeed, preschool children only starting to learn reading, their lateralization for face processing is not yet prominent. Lochy et al. (2019) evidenced a positive relationship between grapheme-phoneme recognition and right lateralization for faces in 5-year-olds, but no correlation between left-hemisphere lateralization for letters and right-hemisphere lateralization for faces, that was found by Dundas et al. (2014) in 7-12 year-old infants. Thus, word processing rather contributes to the development of brain lateralization; however, this mechanism appears to be more complex than a direct influence considering initial right hemispheric dominance of face processing in early infancy (de Heering & Rossion, 2015).

3.3.2 Development of face perception

From earliest age, infants show particular favor to gaze at faces. Indeed, newborns prefer face-like objects (e.g., with top-heavy patterns imitating eyes/nose/mouth) compared to non-face stimuli (Johnson & Morton, 1991; Turati et al., 2002), are sensitive to face attractiveness (Slater et al., 2000), capable to recognize their own mother's face in contrast to non-familiar women (Bushneil et al., 1989), and even they can imitate facial expressions (Meltzoff & Moore, 1977). Di Giorgio et al. (2012) realized a series of experiments showing monkey faces versus human faces to newborns: interestingly, they did not demonstrate the typical preference for human faces, but could discriminate monkey from human faces, and, like human faces, inversed monkey faces affected their visual preference (Cassia et al., 2004). Newborns need, however, a long period of maturation of face perception, which is deeply attuned by daily experience with faces indicating that the face-processing system of newborns, despite wide-ranging initial competences toward faces, is broadly-tuned and very flexible.

Indeed, Quinn et al. (2002) showed that 3-to-4-month-old infants are capable to make a difference between female and male faces, preferring female ones. Other studies found a preference according to the primary caregiver: infants raised by the father preferred male over female faces, and vice-versa, highlighting that infant's social interactions and not innate mechanism shape the preferences that arise at this developmental stage. The role of daily experience in face perception was also found by infants' race recognition. Already by 3 months, they discriminate different races with a preference for the own one; by 6 months, however, the range of discriminated race faces narrows down, to finally result in only being able to discriminate faces of own race by 9 months of age (Kelly et al., 2007). This trend of face narrowing is probably related to the different stages of face processing: at 3 months, infants perceive only facial features, while at 9 months they holistically perceive faces from their own-race, becoming better in the recognizing face identity, while keeping the perception of facial features for other race faces that leads to simple face detection. Confirming the plasticity of this process, Sangrigoli et al. (2005) showed that infants from a given race adopted in the families of another race changed their discrimination in adopting to the new environment. In the same line with this face perception plasticity issue, Scott & Monesson (2010) found even more surprising results: taking into account that between 6 and 9 months infants lose the ability to discriminate monkey faces, they hypothesized that the perceptual narrowing could be avoided in giving individual name to each monkey. Indeed, after 3 months of training, 9-month-old infants demonstrated a neural specialization in the monkey face identification. Thus, authors confirmed that the representation at the individual level is crucial for face discrimination.

3.3.2.1 Formation of face categorization

Categorization is a fundamental cognitive function that allows to structure various percepts coming from the complex sensory environment into distinct categories, according to their similarities or other common criteria. Categorization optimizes memory, learning, decision making and communication (Medin & Smith, 1981; Rosch, 1975). Infants need to learn this ability from birth to efficiently perceive salient objects as a function of increasing daily experience.

Many studies focused on the ontogeny of generic categorization, and they demonstrated that infants are capable to build several categories from early developmental stages (Mareschal & Quinn, 2001), such as humans, animals, and different kinds of objects (Quinn, 2011). Their methodological basis is often relying on visual preference tasks, which put some limits for the estimation of categorization. As objects are the units of perception and categories represent their cognitive integration, behavioral measurements do probably reflect only some perceptual features linked to visual characteristics (e.g., same appearance) and not to semantic aspects based on earlier experience. Thus, infants may employ a dual-process framework, including perceptual learning and the activation of conceptual knowledge that is progressively enriched by everyday experience (Mandler, 2000; Oakes et al., 1996; Quinn & Eimas, 2000). Indeed, Peykarjou et al. (2023) due to the frequency-tagging approach in EEG showed the development of rapid object categorization across different ages observing the first signs of this process from 4 months, while only at 11 months infants used high-level visual cues demonstrating the same neural pattern as adults and 5-6 years old children.

Thus, studies on face perception that discovered gender (Quinn et al., 2002) and race (Kelly et al., 2007) categories formation before 6 month probably more take in account the faces discrimination than a categorization that request the generalization across multiple exemplars. Moreover, researchers use sometimes too simplified visual cues lacking the naturalistic representation. In contrast, using more challenging perceptual task in which the faces were presented in complex visual scenes demonstrated different results: effective face recognition was observed only after the age of 6 month (Frank et al., 2009; Kelly et al., 2019; Leppänen, 2016). Thus, applied visual stimuli play a prominent role in obtained results and its interpretation and become a source of debates about ecological and measurement reliability in the infant studies (Kominsky et al., 2022).

Despite the apparent functional simplicity of face detection in a rich visual environment including non-human objects, animals, nature elements, etc., its operation is not so evident for the immature infant brain. To process faces qualitatively and rapidly infants need indeed 1) to discriminate them from the background and other objects, and 2) to generalize faces across one category despite their variable appearances. In the next section, we will review brain imaging studies, based on electroencephalography (EEG), near-infrared spectroscopy (NIRS) and functional magnetic resonance imaging (fMRI), that shed more light on the face categorization process over different developmental stages.

3.2.2.2 Neural signatures of face categorization

Although behavior is the ultimate variable to understand the meaning and function of any perceptual/cognitive function, the recording of the EEG has some advantages over behavioral paradigms (Pauen & Peykarjou, 2021). First, it has a high temporal resolution in the order of milliseconds (Luck, 2005), allowing the precise measurement of the brain response after stimuli presentation. Second, it makes possible short presentation times of stimuli, thus increasing the number of trials and collecting more data despite infants' short attentional capacity. Third, this method is applicable to all ages allowing to employ the same paradigm across the lifespan to investigate the development of face categorization.

Based on event related potentials (ERPs), researchers have defined four face-selective components of the neural response to faces in the infant brain: P1, N290, P400 and Negative central (Nc) (de Haan et al., 2003). N290 and P400 are integrated together during development, and they are equivalent to the N170 component in adults (Bentin et al., 1996). The amplitude of N290 detected in the posterior area of the right hemisphere is greater for faces compared to visual noise already in infants of 3 months of age (Halit et al., 2004). The N290, similarly to the adult N170 (Guy et al., 2016) is sensitive to the face inversion effect (Halit et al., 2003) and to face category measured in contrast to cars in 3-month-olds (Peykarjou & Hoehl, 2013), to toys between 3 and 12 months (Conte et al., 2020), and to monkey faces in 9-month-olds (Scott et al., 2006). Moreover, compared to the P1 and Nc, the N290 demonstrates the most consistent pattern in development from 5 to 10 months, the variation of which depends more on individual factors (Di Lorenzo et al., 2020). The other component, P400, detected over the occipital zone probably plays a role in novelty detection demonstrating greater amplitude to novel faces compared to familiar ones (Key et al., 2009). Moreover, the P400 is also involved in face categorization as its latency is shorter for faces than for toys in 6 month-olds (de Haan & Nelson, 1999).

Interestingly, Marinovic et al. (2014) using an oddball paradigm showed activation of the other neural component, Nc, for humans versus animals in 7- but not in 4-month-olds. Thus, neural correlates of face processing change across development. Twelve months-old infants exhibit adult ERP patterns for upright and inverted human faces (Halit et al., 2003). Interestingly, the preference for the mothers' faces vs stranger women's face also changes over age: N290 and P400, which are normally larger for mother face at 6 month olds (de Haan & Nelson, 1997) and later between 1.5 and 2 years, become larger for stranger women's face between 3.5-4.5 years old (Carver et al., 2003). In a recent study, Xie et al. (2022) assessed how visual representations of different categories including faces develop in the brain: testing 6-to-8-month old infants and adults, they confirmed that both groups partly share visual category representations, however, visual response appears faster in adults than in infants and reflects more complex encoding of visual features.

However, the standard ERP approach appears limited for the of brain face categorization activity (e.g., face-selective response could be masked by the noise; poor homogeneous sets of visual stimuli are often used). Moreover, generally recorded medial occipital activity reflects the processing of low-level image proprieties rather than face categorization (Hoehl, 2016). An alternative solution was found in using the frequency-tagging approach, consisting to couple the advantage of high time resolution of EEG with the fact that periodic sensory inputs elicit cortical responsiveness on the same frequency (Adrian & Matthews, 1934; Norcia et al., 2015; see section 4.3.2 for details). This method was used for many decades in studies on the visual system (Harris et al., 1976), and was recently adapted to the detection of neural markers of face categorization in adults (Liu-Shuang et al., 2014; Quek & Rossion, 2017; Rekow et al., 2022; Retter et al., 2020; Rossion et al., 2015) and infants (de Heering & Rossion, 2015; Leleu et al., 2020; Peykarjou et al., 2017; Poncet et al., 2022). Important to note, frequency-tagging EEG allows to display sets of various faces and objects that lead to not only discrimination of face patterns against distracting objects, but also generalizing individual face features across multiple exemplars. Thus, faces regularly inserted among a string of objects in the visual sequence elicit a face-selective response in the brain on a precise frequency.

A pioneer study on infants demonstrated a face-selective brain response over the right occipito-temporal cortex in 4-to-6 month-olds (de Heering & Rossion, 2015). Across development, the face-selective response becomes stronger in amplitude and deploys more complex and bilateral distribution in the brain, as shown in 5- (Lochy et al., 2019) and 10-year-old children (Vettori et al., 2019), before the adult stage, which demonstrates the right hemisphere advantage again (Rossion & Lochy, 2021). Importantly, in this approach, the face categorization task is implicit, avoiding any instructions in infants and allowing the completion of orthogonal tasks during the experience in adults.

NIRS measurements could be complementary to the EEG as they provide better spatial resolution and, in the same time, keep freedom of movements in young infants. Backing on this method, Csibra et al. (2004) demonstrated occipital responses in 4-month-old infants to real faces compared to the scrambled faces. Next, Otsuka et al. (2007) testing 5-to-8-month-olds found a different brain signal at the level of adult STS for upright faces relative to objects, but not for inverted faces, also supporting early face categorization in the infant brain. Carlsson et al. (2008) investigated the difference between perception of own mother face and the face of an unknown female in 6- to 9-month-old infants and showed the higher activation in the right fronto-temporal cortex following the display to the mother's face.

Results obtained through fMRI appear more controversial to estimate the period in infancy when brain zones involved in face categorization become adult-like. Moreover, due to the constraint to fix head position during recording in the fMRI apparatus, this approach was not so adapted to investigate brain responses at early age, jumping directly to older children. Thus, Golarai et al. (2007) studied recognition of faces and objects in children (7–11 years), teenagers (12–16 years) and adults using fMRI and found the same pattern of FFA activation in all age groups with three times larger activation in adults. However, Scherf et al. (2007) obtained not so evident results of face-, object-, and place-selective activity in the ventral visual cortex in children (5-8 years), adolescents (11-14 years) and adults. Interestingly, children expressed the same pattern of brain activation for objects and places as adults, but not for faces. In contrast, adolescents confirmed the adult pattern of face-selective activity, but in a more right lateralized distribution. Deen et al. (2017) demonstrated that the visual cortex of awake 4–6-month-old infants already responds to faces versus naturalistic scenes with similar spatial distribution as adults (ventral, lateral face regions and STS). Finally, Kosakowski et al. (2022) confirmed these results on 2-to-9-month-old infants, finding the same global category organization in the visual cortex for the faces, body parts, scenes and objects as in adults.

Summing up, we may conclude from this set of studies comparing children and adults, that, due to various methods and paradigms, the neural substrates for face categorization seem to be functional over first year of life but need a great deal of maturation.

4. Multisensory face processing: the guiding role of olfaction

To sum up previous sections, odors may be ideal stimuli to create sensory contexts capable of modulating face processing. First, olfaction has anatomical and functional advantages over vision in terms of precociousness in development (Lecanuet & Schaal, 1996; Turkewitz & Devenny, 1993); thus infants have full experience of smells over their first year, notably when they learn to see and to understand the visual world (Braddick & Atkinson, 2011). Second, in contrast with the extremely dynamic visual environment and related efforts of attention they necessitate, the olfactory environment is stable (within the temporality of the visual stimuli) leading odorscapes that are relatively constant in space and time (Sela & Sobel, 2010); while this particularity may involve restrictions on olfactory awareness, odor can anchor visual attention either as stimuli which are congruent with the visual inputs (e.g., association between maternal odor and human face) or as context that induce moods making infants prone to attend other stimulations, both features being crucial for perceptual learning and memory. Third, odors may be more robust and reliable source of sensory information because they are less ambiguous than complex visual cues. For example, facial expressions are fakeable (Aviezer et al., 2017; Barrett et al., 2019) as they are partially controlled by the individual, while the emission of natural body odors is involuntary and basically honest. Finally, as already noted before, odors can persist in the environment after their source has faded, so that they can re-evoke on their own entire visual memories of scenes, objects or persons.

Despite these listed advantages of olfactory pertaining to vision and the proven role of effectiveness of olfactory cues for conspecific communication (Köster, 2020; de Groot et al., 2017; Lübke & Pause, 2015; Schaal et al., 2020; Loos et al., 2023), this topic of multisensory functioning was poorly investigated as compared to auditory-visual integration (e.g., Bahrick & Lickliter, 2012; Lewkowicz et al., 2010). In next paragraph, we will review some studies on the influence of maternal body odor on face perception in infancy. Next, we will focus on the series of studies on odor-driven face categorization assessed by the frequency-tagging EEG approach that served as the base for this dissertation work.

4.1 Maternal odors and face perception in infancy

From birth, maternal odors convey non-specific arousal effects which affect the visual system. For example, in a naturalistic experiment run at the time of breastfeeding, the exposure to the mother's breast odor increases the duration of eye-opening in 3 day-old newborns (Doucet et al., 2007), promoting the infant's exploration of the immediate visual environment, among which significant stimuli are the mother's breast and face. At later age, in 4-month-old infants, Durand et al. (2013) found that the restitution of the maternal odor collected on a t-shirt increases the duration of infants' visual fixation on an unfamiliar female face rather than on a non-visual object (a car). These results can be multiply interpreted, either in terms of the infants' perception of a semantic congruence between socially-relevant cues in both maternal odor and in faces, or as the perception of a «surprise» induced by sensing the mother's odor in presence of an incongruous face identity. If the first case applies, it is unclear whether the mother's odor influence on infant face perception is specific to given mother-infant dyads, or whether the odor of every mother (unrelated, but postparturient and possibly lactating) can induce visual interest in infants. It is already known that 4-month-olds look more at the face of unfamiliar women compared to own mother's face (Bartrip et al., 2001). However, this pattern changes in presence of a maternal odor (originating in the infant's own mother or in an unfamiliar mother), as infants then look more toward own mother's face presented simultaneously with another mothers' face (Durand et al., 2020).

Jessen (2020) used the odor of own and non-familiar mothers as well as no odors context in an EEG study measuring ERPs to happy vs. fearful faces in 7-month-old infants. They found that the infants' brain response to fearful faces, i.e. a strong Negative Component (NC), decreased in the presence of own mother's odor becoming a similar to the response to happy faces. The same tendency, but with an decrease of smaller magnitude, was noted in the odor of the non-familiar mother. In line with earlier studies on the soothing effect of maternal odor (Schaal et al., 1980; Badiee et al., 2013; Jebreili et al., 2015; Zhang et al., 2018), the attenuated brain response to fear faces was interpreted as resulting from the strong calming effect of the mother's odor on infants. The more moderate impact of the unfamiliar mother's odor may be caused by odor properties that are common to all females in early mothering stage, due to specific neuroendocrine and physiological mechanisms. Important to note, the maternal olfactory effect could be provoked even in the physical absence of mother, only by restituting her sole body odor. Endevelt-Shapira et al. (2021) investigated brain-to-brain synchrony based on EEG during face-to-face free interaction between infants and their own or stranger's mothers. First, authors showed a higher connectivity between the right central cortex (adult) and the right occipito-temporal cortex (infant) in the own mother-infant compared to the stranger's mother-infant condition. And next, when maternal body odors were added during stranger's mother-infant interaction, their interbrain synchrony was increased compared to the no odors control context. Thus, maternal body odors gave a large impact on the infant's social behavior enhancing visual attention, positive arousal, safety and engagement.

In sum, maternal odor, with a hypothetical graded efficiency from own mother's odor to unfamiliar odor, may promote communication with their offspring, in directing the latter's attention towards them and most probably, in the same time, in sending non-specific cues which operate as non-specific «safety signal».

4.2 Odor-driven face categorization

The studies mentioned above relied on discrimination/preference tasks between the two images presented on a screen (e.g., face versus car). However, this paradigm is not the easiest to directly measure category-specific processing. Adapting the method of de Heering et Rossion (2015), Leleu et al. (2020) used a frequency-tagging approach coupled with EEG in infants facing visual stimulation. But they innovated in questioning the potential effects of running such an experiment in an odor context known to strongly impinge on infants, as outlined in the previous sections. Thus, 4-month-old infants were exposed to their own mother's body odor (the odor collection method, borrowed from Durand et al. 2013, consisted in requiring mothers to wear a t-shirt for 3 consecutive nights) altering with a control odor (baseline odor of t-shirt) while they watched a naturalistic non-edited faces among a visual stream of living and nonliving objects. In this paradigm of implicit rapid face categorization, infants need first to discriminate the faces from the objects, and second to generalize them as belonging to the same category despite different identities, points of view, expressions. This frequency-tagging approach allows to isolate brain responses matched with the different frequencies of stimuli presentation. For example, Leleu et al. (2020) displayed 6 images per a second including 1 face. Thus, the general visual response was measured at the 6-Hz base rate (6 images/second). The target faces were inserted every 6th stimuli, leading to a face presentation rate of 1 Hz (i.e., at 6 Hz / 6 = 1 Hz) resulting in a brain face-selective response measured at this frequency of interest (Figure 1.5A).

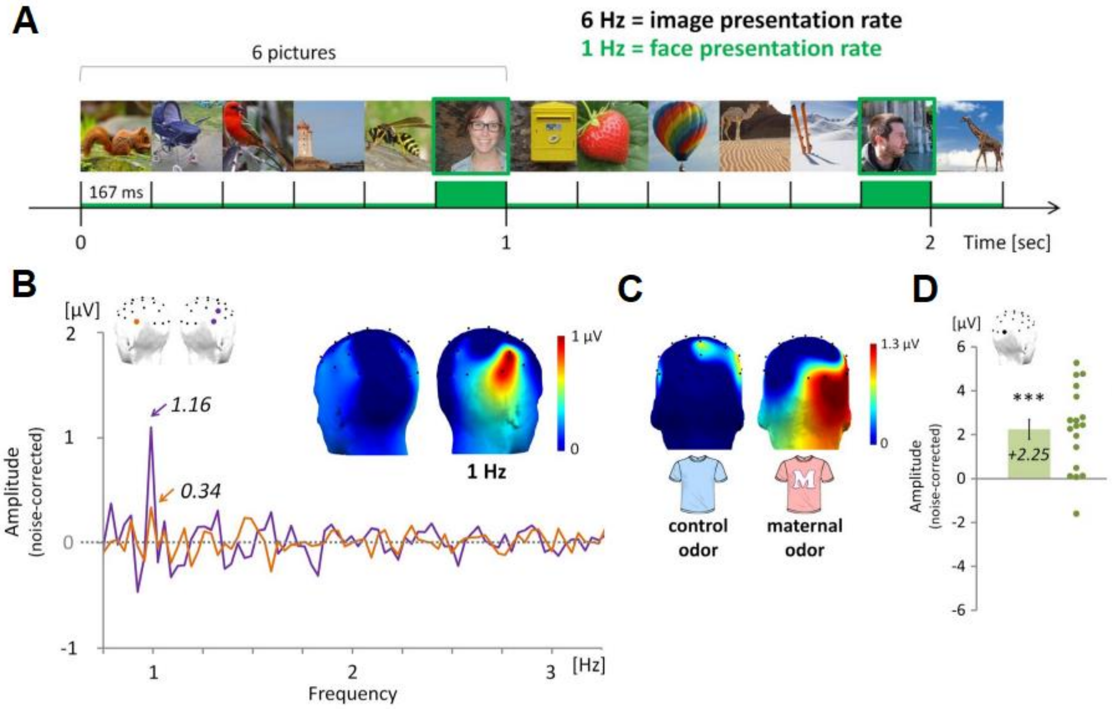

Figure 1.5. Methodology and main results from Leleu et al. (2020). A. Extract of fast periodic visual stimulation with images presented at 6 Hz base rate and faces at 1 Hz. **B.** Amplitude of face-selective response on the EEG spectrum averaged across the maternal and baseline odor contexts. On the frequency of interest (1 Hz), we see a significant peak over the occipito-temporal cortex for the right (in purple) but not for the left hemisphere (in orange). **C.** Head topographies show the distribution of the face-selective response in baseline (blue t-shirt) and maternal (rose t-shirt) olfactory contexts. A significant increase of face-selective response is found over the right occipito-temporal cortex in the maternal odor context. **D.** the Odor effect (i.e., maternal minus control odor) on the face-selective response over electrode O2 (right hemisphere). Original figures at https://doi.org/10.1111/desc.12877

The results were as follows: firstly, a significant face-selective response was recorded over the right occipito-temporal cortex (rOT) regardless of the odor context (Figure 1.5B, purple peak at 1 Hz), which is considered to represent the neural signature of face categorization in the 4-month-old infant brain. Secondly, this face-selective response was relatively weak in the baseline odor context, while in the presence of maternal odor, it was increased over the rOT (Figure 1.5C). The difference in magnitude of the face-selective response between the maternal and baseline odor contexts was called the odor effect (Figure 1.5D).

Replacing faces by cars, Rekow et al. (2020) investigated the selectivity of the brain response to categories of objects different from faces. As for faces, they found a car-selective brain response that confirmed the capacity of 4-month-old infants to build different visual categories. The presence of the maternal odor did not increase the selective brain response to cars, in contrast with faces, highlighting the effect of semantic congruency between stimuli which convey meaning as the mother's odor and face.

When cars were replaced with face-like objects (i.e. objects which easily induce illusory faces, also named pareidolia), infants of the same age were capable to categorize images of this category and demonstrated significant increase of face-like-selective response in the presence of maternal odor (Rekow et al., 2021). This brain activity was found over the rOT as in the aforementioned face categorization study. Thus, 4-month-olds use maternal odor to categorize entities bearing social cues, such as real faces and face-like objects. Moreover, the general visual response reflecting common visual activity over the middle occipital cortex was immune to the influence of maternal odor in all three experiments. These results support the notion of a specific influence of maternal odor on face categorization than rather than a non-specific effect that would simply increase visual attention.

The rapid face categorization was studied in parallel in adults (Rekow et al., 2022), in combining in a single study the three previous infant experiments involving face-, car- and face-like categorization. In these adult studies, the frequency of visual stream was adapted (Retter et al., 2020) in presenting 12 images per second (12 images/second = 12 Hz), while faces were inserted every 9th stimulus with a frequency of 1.33 Hz (12 Hz / 9 = 1.33 Hz). The olfactory contexts were chosen according to semantic congruency with the visual stimuli (body odor for faces; gasoline for cars), and with the baseline odor they were alternatively presented in each type of visual stream. In all three cases, adult participants expressed a robust category-selective brain response across the odor contexts. But, in contrast with 4-month-old infants, they did not show significant odor effects for face categorization in any odor context.

It is much probable that a mature visual system and visual expertise allow to efficiently categorize faces or objects without any involvement of olfactory cues. The face-selective brain response was equally strong in the body and baseline odor contexts keeping its right occipito-temporal dominance. The categorization of cars was not significantly influenced by any of the odor contexts;

however, compared to the other categories of visual stimulations, the face-like-selective brain response was weakly increased over the rOT in the presence of body odor. Interestingly, the participants who self-reported seeing pareidolia showed a significant odor effect (89%) compared to unaware participants (whereas, only 15% of subjects in an additional group reported face-like objects in a behavioral experiment without olfactory stimulation).

Thus, body odor appear to convey powerful cues guiding visual attention toward particular category of visual stimuli, even influencing aware perception of illusory objects that evoke ambiguous faces. We suppose that, even in expert visual brains such as those of adult participants, this type of illusory visual stimuli do not contain sufficient information for an efficient categorization as faces; additional sensory cues such as body odor facilitate this process. Taken together, these results are in line with the principles of inverse effectiveness: unisensory percept of ambiguous stimuli benefit most from additional contributions of other senses in the process of multisensory integration (Stein & Meredith, 1993).

4.3 Hypotheses and methodology

Previous studies on face categorization confirm that, among other sensory modalities, olfaction can facilitate visual processing. However, evidence from studies on auditory-visual integration (Bahrick & Lickliter, 2012), suggest that this intersensory facilitation seems to decline through early development, depending on sensory maturation and the acquisition of perceptual expertise of the participants. Evidence for a converging trend in olfacto-visual integration was noted: the facilitation effect of body odor on the categorization of face was found in 4-month-old infants, but not in adults; in contrast, both infants and adults were sensitive to the effect of a congruent odor when the objects to categorize were ambiguous face-like objects (Rekow et al., 2022).

In terms of the above mentioned principle of inverse effectiveness, this would mean that : (1) the face-selective response in the baseline odor context *(unisensory visual response)* was strong enough to reflect efficient face categorization due to the advanced visual development of adults; (2) the face-selective response in the body odor context *(multisensory response)* remained a similar amplitude as unisensory visual response; (3) the difference of brain response between these two types of contexts, that we call the odor effect, *(intersensory facilitation*) appeared negligible. Thus, the *strongest response based on unisensory stimulation benefits less from multisensory integration*. In the case of ambiguous visual stimuli (face-like objects), the unisensory visual input is not effective enough to be classified as a face, unless it is integrated with an additional cue from another sense. Then only, it elicits a strong multisensory response and, therefore, a significant odor effect.

However, between 4-month-old infants and adults, we have a large research gap. The principle of inverse effectiveness involving olfacto-visual interaction was never investigated in infancy. Thus, our

main hypothesis states that odor-driven face categorization follows the inverse effectiveness principle across development.

4.3.1 Predictions

Indeed, the compensatory mechanism across the senses seems to be flexible for perception. It activates only when one of the sensory systems is not sufficient in the case of early maturation stage or too high perceptual demand. To investigate that, we follow two main axis of present research: **(1) declining of intersensory facilitation for odor-driven face categorization across 1st** year that is based on progressive maturation of vision and **(2) dependence of intersensory facilitation on the visual demand at given age** to which infants are exposed.

To test these predictions, we conducted three studies including different age groups:

In **Study 1**, we assess the effect of the odor context on visual categorization of faces in the background of the protracted development of vision over first year of life. In theory, the progressively improving visual system should ameliorate face categorization between younger (4 month-old) and older (12 month-old) infants. Thus, we predict a progressively **increasing face-selective response based on vision alone and a decreasing odor effect as vision become efficient on its own between 4 and 12 months.**

In **Study 2** and **3**, we go steps further in investigating the mechanism of inverse effectiveness ween olfaction and vision in different age groups in controlling of the visual demand to which infants are exposed. **Study 2** will be focused on **4 month-old infants** who have a weak face-selective response that is boosted by maternal odor, as shown with naturalistic non-edited images that are representative of the complex visual environment and which is demanding for the visual system (Leleu et al., 2020). Here, we aim to 1) to replicate this study using various sets of naturalistic images and 2) to use the **visually-simplified stimuli** predicting an **increase of the unisensory face-selective response**, which reflects a lower demand of visual perception. In addition, according to the inverse efficacity principle, we expect that **this less demanding visual categorization task will also be less dependent on the maternal odor effect**

According to the prediction from **Study 1**, we consider that, by the end of first year, the unisensory face-selective response is strong enough to categorize highly-variable face stimulations. Thus, **Study 3** will focus on **12-month-olds** in presenting them a task in which the visual demand for face categorization is enhanced by speeding the rate of face image presentation. For this more demanding face categorization task, we expect to find a **decreasing unisensory face-selective response** and **an increasing odor effect** (Figure 1.6).

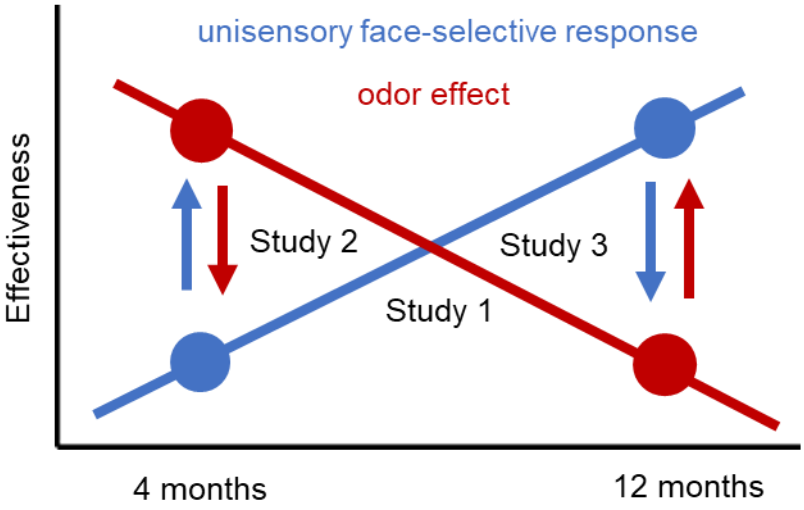

Figure 1.6. The principle of inverse effectiveness adapted to the odor-driven face categorization across the first year of life. In **Study 1**, we predict that the unisensory face-selective response increases while odor effect decreases progressively in 4-to-12-month-old infants due to the developmental improvement of face categorization. In **Study 2**, the controlled reduction of the visual demand should make the face categorization task less demanding, with an ensuing increase of the unisensory face-selective response and decrease of the odor effect in 4-month-old infants. By contrast, in **Study 3**, we enhance the visual demand of the face categorization and expect decrease of unisensory face-selective response and increase of the odor effect in 12 month-old infants.

4.3.2 Methods

The method used in all studies presented in this dissertation will consist frequency-tagging by fast stimulus presentation coupled with EEG, a face categorization measurement at the brain level which is adapted to the abilities of early infancy. EEG is not invasive and allows the direct assessment of brain activity in real-time. EEG electrodes placed on the scalp record synchronized synaptic activation in cortical neuronal networks, which due to high temporal resolution allow to track neural responses during/after external stimulation. Despite its rough spatial resolution, EEG can engender topographical source localization of this brain activity (Jackson & Bolger, 2014).

The analysis of electrophysiological responses can be performed not only in time, but also in the frequency domain. Brain activity synchronizes under periodical stimulation at the frequency given by the stimulation period (Adrian & Matthews, 1934). The fast periodic visual stimulation (FPVS) oddball paradigm is based on the nested presentation of two types of visual streams designed at fast and at low frequency rate. The category of interest (e.g., faces) is periodically inserted at low rate among various categories of objects displayed at fast rate. For example, the base rate represents F = 6 Hz (i.e., 6 images per second, duration of stimuli = 1/F = 1/6 = 163 ms). Faces (i.e., category oddball) are periodically inserted every 6th stimuli, thus face presentation rate F/n = 6/6 = 1 Hz (1000 ms between each face) (Figure 1.7A). Thus, the frequency-tagging-EEG approach allows to dissociate two brain responses elicited by two different stimulation streams: 1) the target category-selective response (faces) reflects high-level visual categorization and 2) the general visual response that corresponds to the processing of low-level visual cues (e.g., contrast, luminosity) and arises in middle-occipital cortex (Regan, 1966).

The EEG category response, defined in amplitude, reflects the differentiated electrophysiological activity which is specific to the oddball versus base properties (Rossion et al., 2020) (Figure 1.7B). The neural mechanisms driving frequency-tagged responses seem to be based on nonlinear interactions between neural events with partial time overlap (Retter & Rossion, 2016). Due to the complexity of brain responses, we visualize their amplitude distribution across harmonic frequencies after a Fast Fourier Transform (FFT) that serves to make subsequent analyses in the frequency domain (Figure 1.7C). Thus, the brain responses occur not only at the stimulation rate F, but also at higher frequencies (i.e., 2F, 3F, etc.) (Figure 1.7D). Thus, harmonics represent multiple integers of the stimulation frequency and for the correct estimation of the brain response we need to sum all harmonic amplitudes (Retter et al., 2021) (Figure 1.7E).

Overall, frequency-tagging EEG has multiple advantages (Rossion et al., 2020). First, it is a valid measurement of face-selective responsiveness that emerges through the process of discrimination from other categories, and allows generalization across different face exemplars demonstrating resistance to the low-level visual cues. Second, the possibility to predefine the frequency of interest and to next measure brain response at this frequency and its harmonics leads to a paradigm of high objectivity (Retter et al., 2021). Third, the frequency-tagging approach is sensitive: it resists to artifacts and provides a high signal-to-noise ratio (SNR) as the brain response is concentrated at definite frequencies compared to the noise spread across random frequencies (Norcia et al., 2015; Regan, 1989). In addition, high frequency resolution (e.g., 1/30 = 0.033 Hz) allows to collect a big amount of data in short testing time that is crucial for low attention span of infants. Fourth, the electrophysiological measurements using this approach are stable and reproducible on the group and individual level showing a high reliability (Dzhelyova et al., 2019). Moreover, the face-selective response reflects automatically and can be measured implicitly, which again is advantageous to study preverbal or non-verbal organisms (infant, anesthetized persons). Fifth, the possibility to use the same sets of stimuli and parameters of stimulation allows to apply this approach across different developmental stages, such as infants (de Heering & Rossion, 2015; Leleu et al., 2020; Rekow et al., 2021), children (Lochy et al., 2019; Vettori et al., 2019) and adults (Rekow et al., 2022; Rossion et al., 2015). Finally, the whole test apparatus, target stimuli, and procedures can be used to measure brain responsiveness in changing contexts. In our case, the stream of visual stimulation mentioned above will be played to participants in contrasted olfactory context (here, within-subject alternation of t-shirts impregnated with maternal skin secretions against the baseline odor of a non-worn t-shirt).

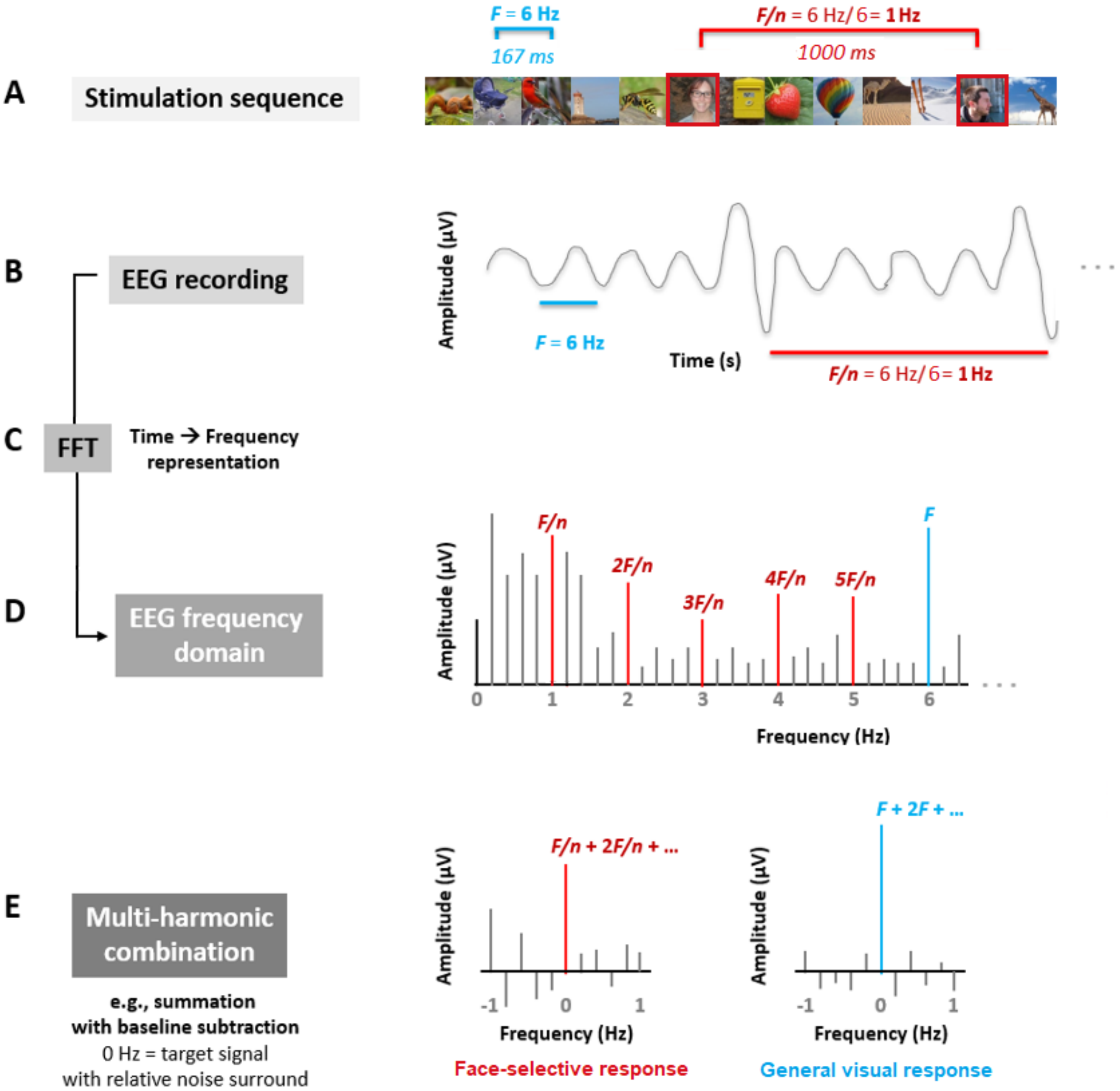

Figure 1.7. General methodology of frequency-tagging EEG studies. A. Excerpt of oddball fast periodic visual stimulation (FPVS) with 6 images per second (F = 6 Hz, duration of each stimuli 167 ms) including faces (F/n = 1 Hz, 1000 ms between faces). **B.** During the EEG recording in time domain, neural responses appear to each stimuli presentation, with a differential response to the periodic oddball (low rate stream = F/n = 1 Hz) compared to the base images (fast rate stream = F = 6 Hz). **C.** Transformation of EEG signal from time into frequency domain occurs using Fast Fourier Transform (FFT). **D.** Amplitude spectrum of the EEG signal. The peak of general visual response at F = 6 Hz (blue) and face-selective response spread across the stimulation frequency F/n = 1 Hz and following harmonics (multiple integers): 2F/n, 3F/n, 4F/n, and 5F/n (red). **E.** The sum of amplitudes at each harmonic (e.g., F/n+2F/n+3F/n+... etc and F+2F+3F+... etc., for face-selective (red) and general visual response (blue), respectively) results in the multi-harmonic combination at the frequency of interest (1 or 6 Hz) with surrounding frequency “noise” amplitudes. Adapted from Rossion et al. (2020). The original can be found at https://doi.org/10.1016/j.neuropsychologia.2016.07.028

Experimental part

Thus, the frequency-tagging EEG approach seems very relevant to the investigation of the inverse effectiveness principle on olfacto-visual interaction in infancy. The objective measurement of rapid face categorization will allow us precisely estimate both the unisensory visual and the multisensory olfactory-visual responses that correspond to the face-selective neural activity in the baseline and maternal body odor context, respectively.

The experimental part consists in three studies, according to our predictions. In **Study 1,** we will focus on a large age group of infants aged 4 to 12 months to explore how the unisensory face-selective response increases due to the developmental improvement of visual perception . On the other hand, we predict that the earlier intersensory facilitation (i.e., odor effect) found in 4-month-old infants (Leleu et al., 2020) will progressively decrease with age as the visual system becomes effective on its own, suggesting a developmental trade-off between vision and olfaction. In **Study 2** and **3,** we will test the principle of inverse effectiveness not in terms of developmental perceptual improvement over a period of 8 months, but in controlling the perceptual demand in two different age groups. In **Study 2,** we will decrease the demand of the visual task, supposing to find then an enhanced face-selective response that does not necessitate additional sensory cues (viz., maternal body odor) at variance with previous study 1 imposing a high-demand visual task in 4-month-old infants. Therefore, the reduced difficulty of the visual task is expected to lead to the suppression of intersensory facilitation by olfaction. Finally, **Study 3** will focus on 12-month-old infants who benefit of improved visual abilities due to the protracted visual development over 1st year (Pascalis et al., 2011). In this age group, we aim thus to increase the demand of the visual task to assess its effects on both the face-selective response and strength of intersensory facilitation (i.e., odor effect). If the principle of inverse effectiveness applies here, we expect the re-emergence of a strong facilitation of the visual task by the olfactory context.

Study 1. Olfactory-to-visual facilitation in the infant brain declines gradually from 4 to 12 months

This section corresponds to the article:
Rekow, D., Baudouin, J.-Y., Kiseleva, A., Rossion, B., Durand, K., Schaal, B., & Leleu, A. (2023). Olfactory-to-visual facilitation in the infant brain declines gradually from 4 to 12 months. *BioRxiv, 556823*. https://doi.org/10.1101/2023.09.08.556823

Abstract

During infant development, intersensory facilitation declines gradually as unisensory perception improves. However, this developmental trade-off has been mainly investigated using audiovisual stimulations. Here, fifty 4- to 12-month-old infants were tested to determine whether the facilitating effect of their mother's body odor on neural face categorization, as previously observed at 4 months, decreases with age. In a baseline odor context, results revealed a face-selective electroencephalographic (EEG) response that increases and changes qualitatively between 4 and 12 months, marking improved face categorization. At the same time, the benefit of adding maternal odor fades gradually with age, indicating an inverse relation with the strength of the sole visual response, and generalizing to olfactory-visual interactions previous evidence from the audiovisual domain.

1. Introduction

From birth onward, human infants must navigate a complex multisensory environment and learn to form coherent percepts from a variety of sensory inputs. While the development of multisensory perception has long been debated (i.e., unisensory perception either preceding (Birch & Lefford, 1963; Piaget, 1952) or following (Gibson, 1969) multisensory perception), it is now generally admitted that infants can bind inputs across the senses at an early age, and that such intersensory integration improves and refines throughout development (Bahrick & Lickliter, 2012; Lewkowicz & Bremner, 2020; Murray et al., 2016 for reviews). Evidence accumulated so far indicates that the early emergence of multisensory perception is a function of principles that govern how inputs are integrated in the nervous system of numerous species.

A basic principle upon which infants rely to merge sensory inputs is *spatiotemporal coherence*. First described at the single-neuron level in nonhuman models (King & Palmer, 1985; Meredith et al., 1987), this principle ensues from the fact that the sensory features of an object do not occur arbitrarily, but are correlated in space and time. As a result, when auditory and visual stimuli are presented at same *vs*. different locations, human infants exhibit faster behavioral responses to stimuli coming from the same location already at 2 months of age (Neil et al., 2006). Likewise, when the temporal synchrony between a visual object and a sound is manipulated, neonates and infants aged up to 10 months evince distinct behavioral (Lewkowicz, 1996; Lewkowicz et al., 2010), autonomic (i.e., heart rate; Curtindale et al., 2019) and neural (Hyde et al., 2011; Werchan et al., 2018) responses to synchronous compared to asynchronous audiovisual stimulations. Strikingly, sensitivity to audiovisual synchrony is observed for both veridical (e.g., a ball bouncing up and down and a sound signaling the impact) and arbitrary (e.g., a human face and a tone) associations (Lewkowicz, 1996; Lewkowicz et al., 2010). This indicates a rudimentary ability to detect the synchronous onsets and offsets of concomitant inputs, forming a broadly tuned perceptual system that assembles simple events from their simultaneous occurrences in the physical environment (Murray et al., 2016).

Such early sensitivity to overlapping inputs has been proposed to support efficient perceptual learning, providing the scaffold on which more complex multisensory features can be integrated (Murray et al., 2016). This process would be particularly important during the initial learning of a specific domain, when intersensory correspondence between some features is still arbitrary for young infants (Lickliter & Bahrick, 2004, for review). In particular, the intersensory redundancy hypothesis (Bahrick & Lickliter, 2000) suggests that redundant information across several modalities (so-called amodal properties) grabs infants' attention, renders inputs more salient and helps to bind features across the senses, leading to *intersensory facilitation* toward redundant information. For instance, during synchronous or collocated audiovisual stimulations, infants are able to discriminate tempos (at 3 months; Bahrick et al., 2002), rhythms (at 5 months; Bahrick & Lickliter, 2000), trajectories (at 4 months; Bremner et al., 2012), prosodies (at 4 months; Bahrick et al., 2019) or emotions (at 4 months; Flom & Bahrick, 2007), while they fail during unisensory, asynchronous or dislocated stimulations.

Interestingly, however, intersensory facilitation becomes less effective during development when unisensory perception improves. For instance, when exposed to audiovisual displays, young infants detect a change in the tempo and rhythm of a moving hammer at 3 and 5 months respectively, but they fail when the sole visual stimulus is presented (Bahrick et al., 2002; Bahrick & Lickliter, 2000). In contrast, older infants discriminate tempos and rhythms (at 5 and 8 months, respectively) from both unisensory and multisensory stimulations without any sign of intersensory facilitation (Bahrick & Lickliter, 2004). Remarkably, this developmental pattern can be reversed by task demand, as a more difficult tempo discrimination task leads 5-month-olds to perform like 3-month-olds, i.e., losing their discrimination ability with unisensory inputs and showing intersensory facilitation (Bahrick et al., 2010). Altogether, these findings are in line with another well-known principle of multisensory integration, *inverse effectiveness*, whereby the strength of the integration increases as unisensory responses decreases. First described in nonhuman models (Meredith & Stein, 1983), and later observed in human adults using behavioral (e.g., Regenbogen et al., 2016), neuroimaging (Stevenson & James, 2009) and electrophysiological (Stevenson et al., 2012) approaches, this principle can be transposed to multisensory development, as intersensory facilitation is particularly effective when unisensory perception is not fully developed.

So far, the principles subtending multisensory development were mainly investigated using auditory and visual stimuli, which are bound by a precise spatiotemporal synchrony. However, intersensory influences in early infancy can also occur for less space- and time-locked senses, such as olfaction (Sela & Sobel, 2010). For example, 3-month-old infants look longer at a smiling face associated with a pleasant rather than an unpleasant odor (Godard et al., 2016). At 4 months, exposure to the mother's body odor increases looking duration at a face as opposed to a car (Durand et al., 2013), and at the mother's face as opposed to a stranger's face (Durand et al., 2020). At the same age, maternal odor facilitates the categorization of a variety of faces, as indexed by a larger face-selective electroencephalographic (EEG) response over the right occipito-temporal cortex (Leleu et al., 2020; Rekow et al., 2020). Similarly, when common objects configured as faces (i.e., facelike objects eliciting *face pareidolia* in adults) are rapidly presented among non-facelike objects belonging to the same categories, adding the mother's body odor initiates a facelike-selective EEG response in 4-month-olds (Rekow et al., 2021). Later on, at 7 months, exposure to the mother's odor also reduces the brain response to fearful faces (Jessen, 2020), and favors interbrain synchrony with, and visual attention to, an unfamiliar woman with whom the infant interacts (Endevelt-Shapira et al., 2021).

In most of these studies, odors were presented as contexts for long durations (i.e., several tens of seconds) and without clear spatial location. This indicates that despite a loose spatiotemporal relation between the two inputs, odors are prone to influence visual perception in infants. Does that mean that olfactory-to-visual facilitation does not rely on the same principles than other intersensory facilitations? Here, we address this question by investigating whether the maternal odor effect observed on neural face categorization at 4 months (Leleu et al., 2020; Rekow et al., 2020, 2021) follows the inverse effectiveness principle as applied to perceptual development, i.e., intersensory facilitation declining as unisensory perception develops. Indeed, the aforementioned studies used a rapid mode of visual stimulation together with a variety of naturalistic stimuli, making face categorization demanding for the 4-month-old brain. In adults, who effectively categorize genuine human faces from the sole visual input, there is no such improvement with a body odor, except for the less effective categorization of ambiguous facelike objects (Rekow, Baudouin, Durand, et al., 2022). Therefore, these findings suggest that the impact of a concurrent body odor progressively fades as the ability to categorize faces develops.

To tackle this issue, we used a cross-sectional design and a frequency-tagging EEG approach. We tested fifty infants, aged from 4 to 12 months, while they were exposed to fast streams of images presented at 6 Hz (6 images/s), with human faces inserted every 6th image to tag a face-selective neural response at 1 Hz and harmonics (i.e., integer multiples) in their EEG spectra. During visual stimulation, infants were alternatively exposed to a maternal or a baseline odor context. In a first set of analyses, we examined the development of the face-selective response measured in the baseline odor context to determine whether face categorization becomes more efficient with age. In a second step, we analyzed the evolution of the maternal odor effect on face categorization as a function of age, hypothesizing an odor effect for the youngest infants that gradually disappears for the oldest infants. Finally, we conducted the same analyses on the general visual response to the fast train of images (6 Hz and harmonics) to assess whether the putative decline of the odor effect with age is selective to face categorization.

2. Material and methods

2.1 Participants

Fifty-two healthy infants aged 4 to 12 months were recruited by mail from the local birth registry to participate in the study. Parents were informed about the objectives and methods of the study before they agreed to participate in signing a written informed consent. None indicated their infants having any sensory (e.g., visual, olfactory), neurologic, or psychiatric disorder. Procedure of testing was conducted according to the Declaration of Helsinki and approved by a French ethics committee (CPP Sud-Est III - 2016-A02056-45). One infant was excluded from the final sample due to less than two sequences per condition (see below) and another infant because of too noisy EEG data. The final sample was thus composed of 50 infants (26 females) whose age covered a large range (121–374 days, mean age ± SD: 242 ± 78 days, Figure 2.1A). Sample size was estimated a priori by considering a moderate relation between the age of the infants and the maternal odor effect (R^2 = 0.20), a significance level α = .05 (two-tailed), and a power 1-β = .90, leading to a sample size N = 50.

2.2 Visual stimuli

Natural colored images of various nonface objects (animals, plants, man-made objects; N = 172) and human faces (N = 68, 34 females) were used (Figure 2.1B). Images were cropped to a square and resized to 400 × 400 pixels. In the cropped images, items appeared at variable locations and the original background was preserved, so that physical cues were highly variable across stimuli and barely informed about the visual category. Stimuli were presented in the center of a 24-inch LED screen (refresh rate: 60 Hz, resolution: 1920 × 1080 pixels, background: 128/255 in grayscale) at a viewing distance of 57 cm, subtending 24 × 24° of visual angle.

2.3 *Odor stimuli*

Following previous studies, two odor stimuli were used: the mother's body odor and a baseline odor (Durand et al., 2013; Leleu et al., 2020; Rekow et al., 2020, 2021). Both odors were delivered using white cotton t-shirts. T-shirts were first laundered using a scentless hypoallergenic powder detergent (Persavon, France). One t-shirt was sent to the mother of each tested infant in a zip-locked hermetic plastic bag. Instructions were enclosed for the collection of her body odor, specifying to wear the t-shirt on bare skin during the three consecutive nights preceding the experiment and to refrain from using odorous soap or perfume before wearing it. During the collection period, mothers had to store the t-shirt in the hermetic bag at room temperature (away from any heating device). The odor of an unworn t-shirt (stored in a similar plastic bag in our premises) was used as the baseline odor.

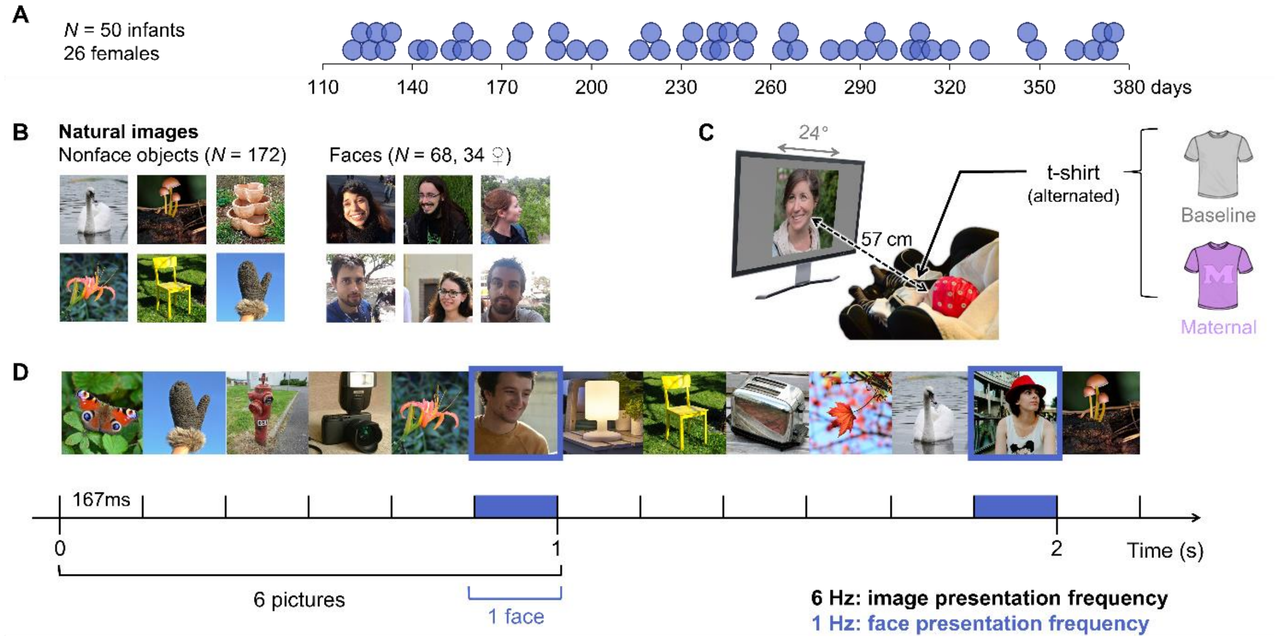

Figure 2.1. Participants, stimuli and procedure. A. Age distribution of the 50 included infants. Circles represent individual participants as a function of their age (in days) at the time of testing. **B.** Examples of the natural images of control objects and faces used as stimuli. **C.** Infants were equipped with an electrode cap and seated at 57 cm in front of the stimulation screen. Before a series of 2 sequences of visual stimulation (36 s each), a folded white t-shirt imbued with the odor (either maternal, depicted in violet, or baseline, depicted in grey) was placed on their chest. T-shirts were alternated every 2 sequences. **D.** Extract of 2.167-s of the 34.5-s-long clip of visual stimulation. Each stimulus lasted 167 ms and was directly followed by another stimulus, resulting in a fast 6-Hz rate of image presentation (6 images/s). A face was presented every 6th stimulus, thus corresponding to a 1-Hz face presentation frequency (1 face/s).

2.4 *Procedure*

Procedure was identical to that of the aforementioned infant frequency-tagging EEG studies (Leleu et al., 2020; Rekow et al., 2020, 2021). Testing took place in a light- and sound-attenuated room equipped with an air-renewing system. To additionally reduce olfactory noise, the room was aired between testing sessions and experimenters did not use odorous products prior to, or during, the session. Each infant was equipped with an electrode cap and seated in a baby car seat in front of the screen behind occluding blinds to minimize visual distractions. Parents were asked to stay at a minimal 2.5-m distance away from their infant and to refrain from interacting with them except in case of manifest distress. A webcam allowed to monitor the infant and to launch the visual stimulation when the infant looked at the screen. The t-shirts were manipulated by the experimenters using dedicated disposable nitrile gloves (Schield Scientific, The Netherlands). To deliver the odors, they were folded backward (sleeves folded over the front) to expose the infant to the breast and axillary areas, and disposed on their upper chest while being maintained by the seat belts (Figure 2.1C). One t-shirt corresponding to one odor condition was placed just before the beginning of a sequence of visual stimulation (see below), and the two odor conditions were alternated every two sequences. Odor presentation order was counterbalanced across infants, and a minimum interval of 1 min was introduced at each change, taking the form of a break of visual stimulation for the infant.

Sequences of periodic visual stimulation were presented at a fast rate of 6 Hz (6 images/s) without inter-stimulus interval, such that each stimulus lasted 167 ms (i.e., 1 s/6) on the screen. Face images were inserted among nonface stimuli as every 6th stimulus, i.e., at a rate of 6 Hz/6th = 1 Hz (i.e., 1-s interval between each face, Figure 2.1D). As a result, we tagged two distinct neural responses at different frequencies in the EEG amplitude spectrum: a general visual response at 6 Hz and harmonics (i.e., integer multiples) and a face-selective response at 1 Hz and harmonics. The general visual response comprises the neural activity elicited by the rapid change of stimuli 6 times per second, and is mainly sensitive to the variations of low-level physical cues (e.g., local cues, contrast). In contrast, the face-selective response captures the neural activity selectively elicited by the face images, i.e., a direct differential response to faces against many living and non-living categories, insensitive to low-level cues (already captured by the general visual response) and generalized across variable individual faces.

Each sequence of visual stimulation lasted 34.5 s and was composed of a pre-stimulation interval (0.5 s), a fade-in of ramping-up contrast (0 to 100%, 1.833 s), the full-contrast stimulation segment (31.167 s), a fade-out of decreasing contrast (100% to 0, 0.833 s) and a post-stimulation interval (0.167 s). The 68 face images were randomly split into two sets of 34 faces (17 females) and counterbalanced between sequences, therefore all individual faces were presented equally across the two consecutive sequences of one odor condition, and contrasted to the same set of 172 nonface stimuli. If needed, short sounds were used to reorient infant's attention to the screen (sporadic and non-periodic, thus not contaminating the frequency-tagged EEG responses with auditory-evoked potentials). The experiment stopped when the infant manifested disinterest or fatigue, or at parental demand. Infants were included in the final sample if they achieved at least 2 valid sequences per odor condition (i.e., no premature abortion and presence of a general visual response, see next section).

2.5 *EEG recording and preprocessing*

EEG was recorded from a 32-Ag/AgCl-electrode cap (Waveguard, ANT Neuro, The Netherlands) according to the 10–10 classification system (acquisition reference: AFz, electrode initial impedance < 15 kΩ, sampling rate: 1024 Hz). EEG analyses were run on Letswave 6 (http://www.letswave.org/) carried out using Matlab 2017 (MathWorks, USA). Left and right mastoid electrodes (M1 and M2) were too noisy and thus removed from montage before preprocessing. In a first step, individual EEG data were preprocessed and cleaned of artifacts, blind of the condition (see Supplementary Method for details). After preprocessing, the final number of epochs ranged between 2 to 8 per infant, with an overall rejection of 18 epochs out of 398 (i.e., 4,5%). The remaining average number of epochs was (mean ± SD) 3.64 ± 1.52 and 3.74 ± 1.65 for the baseline and maternal odor conditions, respectively. After this cleaning step, remaining epochs were sorted according to the odor condition and averaged together in the time domain to obtain a single 32-s-long epoch per condition for each infant. These data are made available in the public repository associated with this manuscript (https://osf.io/twyp5/?view_only=ccada0e1575046499fae51301f08afdc).

2.6 Frequency-domain analysis

A fast Fourier transform was applied to the two epochs (one per condition) for each infant and raw amplitude spectra were extracted for all electrodes with a frequency resolution of 1/32 = 0.03125 Hz. Given the steep power-law function of the EEG spectrum, a baseline correction was first applied to remove background noise and lead to a notional amplitude of zero in the absence of frequency-tagged responses. At each frequency bin, noise was defined as the mean of 6 neighboring bins and subtracted out. These bins were selected among the 10 surrounding bins (5 on each side: ± 0.15625 Hz) after the exclusion of the 2 immediately adjacent (one on each side, in case of spectral leakage) and the 2 extreme (minimum and maximum) bins (to avoid including signal and potential outliers in noise estimation). Next, we estimated the range of significant harmonics separately for the general visual response (6 Hz and integer multiples) and the face-selective response (1 Hz and integer multiples) using *Z*-scores calculated on the average of all electrodes, infants and odor conditions. Z-scores were computed as the difference between the amplitude at the frequency of interest and the mean amplitude of 20 neighboring bins, divided by their standard deviation. These bins were selected among 22 surrounding bins beyond those used for baseline correction (11 on each side: from ± 0.1875 Hz to ± 0.5 Hz) after the exclusion of the two extreme bins. Harmonics were considered significant when their *Z*-score was > 1.64 ($p < .05$, one-tailed, signal > noise). The range of significant harmonics was defined until *Z*-scores were no longer significant. For the general visual response, 6 consecutive harmonics were significant (i.e., until 36 Hz, all *Z*s > 5.06, Table S1, Appendix 1), and significance reached the 7th harmonic for the face-selective response (i.e., 7 Hz, all *Z*s > 2.15, Table S1, Appendix 1), excluding the 6th harmonic which corresponds to the general visual response (i.e., 6 Hz).

Electrodes of interest were then identified on the responses summed across significant harmonics and still averaged across infants and odor conditions. For each brain response, the *Z*-scores of all individual electrodes were calculated and considered significant when $Z > 2.93$ ($p < .05$, one-tailed; signal > noise, Bonferroni-corrected for 30 electrodes). For the general visual response, every individual electrode showed a significant response (all *Z*s > 17.6, Table S2 Appendix 1). Therefore, we kept the 4 best electrodes that were all located over the middle occipital cortex (Oz: $Z = 168$, O2: $Z = 133$, POz: $Z = 122$ and O1: $Z = 102$). For the face-selective response, 11 electrodes showed a significant response (all *Z*s > 3.20, Table S2. Appendix 1). We considered the 4 best electrodes excluding the midline, which corresponded to 2 left and 2 right homologous occipito-temporal electrodes (P8: $Z = 19.5$, P7: $Z = 13.1$, O1: $Z = 5.31$ and O2: $Z = 4.38$). For both responses, electrodes of interest matched those reported in previous frequency-tagging EEG studies investigating face categorization in infants (de Heering & Rossion, 2015; Leleu et al., 2020; Rekow et al., 2021).

Subsequent analyses were completed for both the face-selective response and the general visual response, but in separate pipelines. In a first step, the development of each neural response as a function of age was characterized in the baseline odor context. A repeated-measures ANCOVA was run on individual amplitudes with *Age* as a continuous factor, and *Electrode* (either P7, P8, O1, O2 for the face-selective response or POz, Oz, O1, O2 for the general visual response) and *Harmonic* (1st, 2nd, 3rd, 4th, 5th and either 6th for the general visual response or 7th for the face-selective response) as within-subject categorical factors. *F* values and partial eta squared (η_p^2) are reported, and significance threshold was fixed at $p < .05$. Sphericity was assessed using Mauchly's test and whenever it was violated, the Greenhouse-Geisser correction was applied (corresponding effects are reported with adjusted degrees of freedom and epsilon coefficient ε). Given our aim to characterize the development of the neural responses, we focused on the main effect of *Age* and its interactions with the other factors. Contrasts were used to decompose significant interactions. Then, another repeated-measures ANCOVA with the *Age* and *Electrode* factors was conducted on individual amplitudes summed across harmonics with (a) significant effect(s) involving *Age*. Finally, to assess the evolution of the number of significant harmonics as a function of age, *Z*-scores, as defined above, were calculated for each infant, electrode and harmonic, considering the 4 electrodes and the 6 harmonics defined at group level for each response. The maximum number of significant harmonics (i.e., $Z > 1.64$, $p < .05$, one-tailed, signal > noise) for at least one electrode was extracted for each infant and submitted to a linear regression with *Age* as a continuous factor. R^2 and *F* values are reported, and significance threshold was fixed at $p < .05$. For all these analyses, the effect of *Age* is illustrated with the predicted outcomes from the regression line equation at X = 120 days (4 months) and X = 360 days (12 months), and with the data averaged for the 25 youngest infants (4-8 months) and the 25 oldest infants (8-12 months). Means and standard errors of the means (SEM) are thus reported for these two subgroups but were not submitted to significance testing.

In a second step, we analyzed the difference between the two odor conditions as a function of age. As for the previous analysis, a repeated-measures ANCOVA was first computed on individual amplitudes using the *Age*, *Electrode* and *Harmonic* factors, with the addition of *Odor* (maternal, baseline) as a within-subject categorical factor. Again, *F* values and η_p^2 are reported, the Greenhouse-Geisser correction was applied whenever necessary, and significance threshold was fixed at $p < .05$. Here, given our aim to determine whether maternal odor exerts an influence on the visual responses and, if so, whether this effect declines as age increases, we focused on effects involving the *Odor* factor and its interaction with the *Age* factor. Significant interactions were decomposed using contrasts. As for the first step of analyses, another repeated-measures ANCOVA with the *Age*, *Electrode* and *Odor* factors was conducted on individual amplitudes summed across relevant harmonics. For illustration purposes, predicted outcomes of the *Odor* × *Age* interaction are reported together with data averaged for the youngest and oldest infants (see above). Finally, we computed a lateralization index by considering raw amplitudes summed across harmonics at electrodes O1 and O2 (since O2 is the only electrode showing a significant decrease of the odor effect with age, see Results). Amplitude at O1 was subtracted from amplitude at O2 and then divided by the sum of the two electrodes to reflect the advantage for one hemisphere expressed in %, with positive and negative values corresponding to right- and left-lateralized responses, respectively. We calculated the index for each infant and each odor context and submitted individual odor effects (maternal minus baseline odor) to a linear regression with *Age* as a continuous factor.

3. Results

3.1 Face-selective neural activity progressively increases and refines with age

To delineate the development of the ability to rapidly categorize human faces within a fast train of natural images between 4 and 12 months of age, a first set of analyses was conducted in the baseline odor context. Visual inspection of the EEG spectrum revealed that the periodic appearance of face stimuli at 1 Hz within the rapid visual stimulation elicits a clear response at the same frequency and harmonics over the occipito-temporal cortex for both the youngest (4-8 months) and the oldest (8-12 months) infants. Descriptively, this face-selective response is larger for the oldest infants for the 1st, 2nd, 4th and 5th harmonics, while lower for the 3rd and 7th harmonics. Summed across these 6 harmonics, the overall response is larger (+128%) for the oldest (2.60 ± 0.47 µV) than the youngest (1.14 ± 0.31 µV) infants (Figure 2.2A).

The analysis of individual amplitudes extracted for each harmonic at occipito-temporal electrodes (P7, P8, O1, O2) revealed a significant main effect of *Age* (F (1, 48) = 8.41, p = .006, η_p^2 = .149), qualified by a significant *Harmonic* × *Age* interaction (F (1.9, 90.3) = 5.54, p = .006, η_p^2 = .104, ε = .38). A significant effect of *Age* was found for the 1st (F (1, 48) = 6.03, p = .018, η_p^2 = .112) and 2nd (F (1, 48) = 12.01, p = .001, η_p^2 = .200) harmonics, the face-selective response increasing as a function of age for both of them (Figure S1, Appendix 1). No effect of *Age* was found for the other harmonics (all Fs < 2.18, ps > .14). The analysis on the sum of the two first harmonics also yielded a significant main effect of *Age* (F (1, 48) = 11.17, p = .002, η_p^2 = .189). The predicted face-selective response combined across these harmonics is 10 times larger at 12 months (i.e., 360 days: 2.61 µV) than 4 months (i.e., 120 days: 0.26 µV) (Figure 2.2B left), and its mean amplitude measured for the youngest infants (4-8 months) is 0.80 ± 0.28 µV, as opposed to 2.11 ± 0.37 µV for the oldest infants (8-12 months). In sum, there is a strong increase of the face-selective response between 4 and 12 months that is mainly driven by the two first harmonics. The outcomes of these ANCOVAs are reported in Table S3 (Appendix 1).

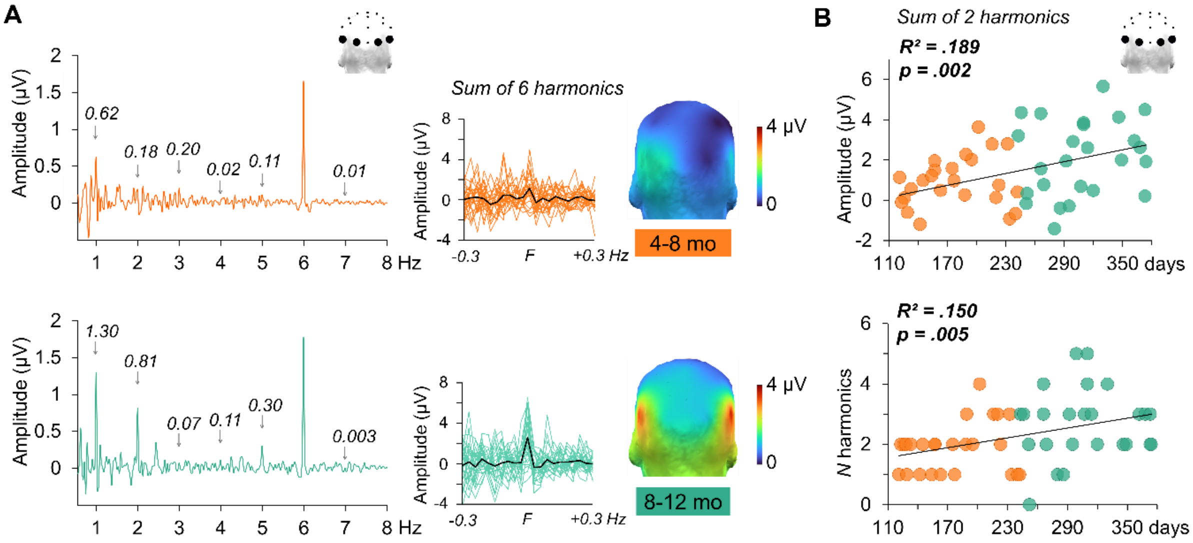

Figure 2.2. The development of the face-selective response with age. A. Amplitude spectra recorded in the baseline odor context for the youngest (orange: 4-8 months, top) and the oldest (green: 8-12 months, bottom) infants averaged for the 4 occipito-temporal electrodes (P7, O1, O2, P8). The face-selective response is captured at 1 Hz and harmonics (until 7 Hz) excluding the 6th harmonic (6 Hz) which corresponds to the general visual response. The smaller spectra represent the summed amplitude of the response, with the average group-level activity in black and individual spectra in color. Head maps show the topography (posterior view) of the summed response. **B.** Amplitude of the face-selective response summed across the 2 first harmonics (top) and maximum number of significant harmonics (bottom) as a function of age. Each circle represents individual infant data depending on their subgroup (orange: 4-8 months, green: 8-12 months).

We also determined whether the number of significant harmonics evolves between 4 and 12 months. We extracted the maximal range of significant harmonics for each infant (Figure 2.2B right), and found an effect of *Age* (R^2 = .150, F (1, 48) = 8.48, p = .005) showing that the number of harmonics increases significantly as age increases (predicted number: from 1.62 harmonics at 120 days to 2.92

harmonics at 360 days). On average, the youngest infants (4-8 months) have 1.88 ± 0.17 significant harmonics compared to 2.68 ± 0.18 for the oldest infants (8-12 months). Overall, all infants but one (i.e., 98% of infants) present at least 1 significant harmonic. Hence, the face-selective response does not only increase with age but also complexifies, being distributed on more harmonics in the oldest infants.

3.2 The influence of maternal odor on the face-selective response gradually declines with age

The second objective was to estimate whether the influence exerted by maternal odor on the face-selective response evolves with age. In line with a previous study conducted at 4 months (Leleu et al., 2020), visual inspection of topographical head maps suggested a larger response over the right occipito-temporal cortex in the presence of the mother's body odor compared to the baseline odor, especially for the youngest 4-8-month-old infants (Figure 2.3A). Indeed, their face-selective response increases with maternal odor at both electrodes O2 (from -0.19 ± 0.34 µV in the baseline odor context to 1.12 ± 0.37 µV in the maternal odor context) and P8 (from 1.06 ± 0.45 µV to 1.76 ± 0.40 µV). In contrast, for the oldest infants (8-12 months), the response increases only at P8 (from 3.42 ± 0.74 µV to 4.20 ± 0.94 µV) and decreases at electrode O2 (from 1.06 ± 0.39 µV to 0.13 ± 0.38 µV). In addition, for both age groups, the face-selective response decreases with maternal odor at the two left-hemispheric electrodes, although to a lesser extent than the right-hemispheric increase (mean across O1 and P7, respectively from 1.16 ± 0.30 µV in the baseline odor context to 0.78 ± 0.33 µV in the maternal odor context at 4-8 months and from 1.97 ± 0.41 µV to 1.58 ± 0.43 µV at 8-12 months).

We analyzed individual amplitudes extracted for each harmonic and each odor context and found a marginal *Harmonic* × *Odor* × *Age* interaction (*F* (2.3, 110.8) = 2.65, *p* = .067, η_p^2 = .052, ε = .46) qualified by a significant *Harmonic* × *Odor* × *Electrode* × *Age* interaction (*F* (5.0, 241.7) = 4.28, *p* < .001, η_p^2 = .082, ε = .34). Decomposition of this interaction revealed that the *Odor* effect and its modulation by *Age* are limited to the two first harmonics, since no other harmonics evinced a significant effect involving these factors (all *F*s < 2.50, *p*s > .081). For the 1st harmonic, we found significant *Odor* × *Electrode* and *Odor* × *Electrode* × *Age* interactions (both *F*s (3, 144) > 4.31, *p*s < .006, η_p^2 > .083). For the 2nd harmonic, there was a significant *Odor* × *Age* interaction (*F* (1, 48) = 6.12, *p* = .017, η_p^2 = .113).

When the face-selective response is summed across these two harmonics, the analysis yielded a significant main effect of *Odor* (*F* (1, 48) = 5.15, *p* = .028, η_p^2 = .097) and several interactions including the *Odor* factor, especially the *Odor* × *Electrode* × *Age* interaction (*F* (3, 144) = 3.35, *p* = .021, η_p^2 = .065). Contrasts indicated that the *Odor* × *Age* interaction is actually limited to the right occipital electrode O2 (*F* (1, 48) = 21.83, *p* < .001, η_p^2 = .313), which shows a predicted increase of amplitude of +2.40 µV in the maternal *vs*. the baseline odor context at 4 months (120 days), compared to a reduction of -1.95 µV at 12 months (360 days) (Figure 2.3B). The youngest infants (4-8 months) have a mean odor effect of +1.31 ± 0.32 µV as opposed to -0.93 ± 0.56 µV for the oldest infants (8-12 months). The three other electrodes displayed neither the main effect of *Odor* nor its modulation by *Age* (all *F*s < 1.58, *p*s > .21), despite a positive odor effect on average for P8 (+0.74 ± 0.42 µV) and negative odor effects for P7 and O1 (-0.32 ± 0.36 µV and -0.46 ± 0.38 µV, respectively). The outcomes of the ANCOVAs are reported in Table S4 (Appendix 1).

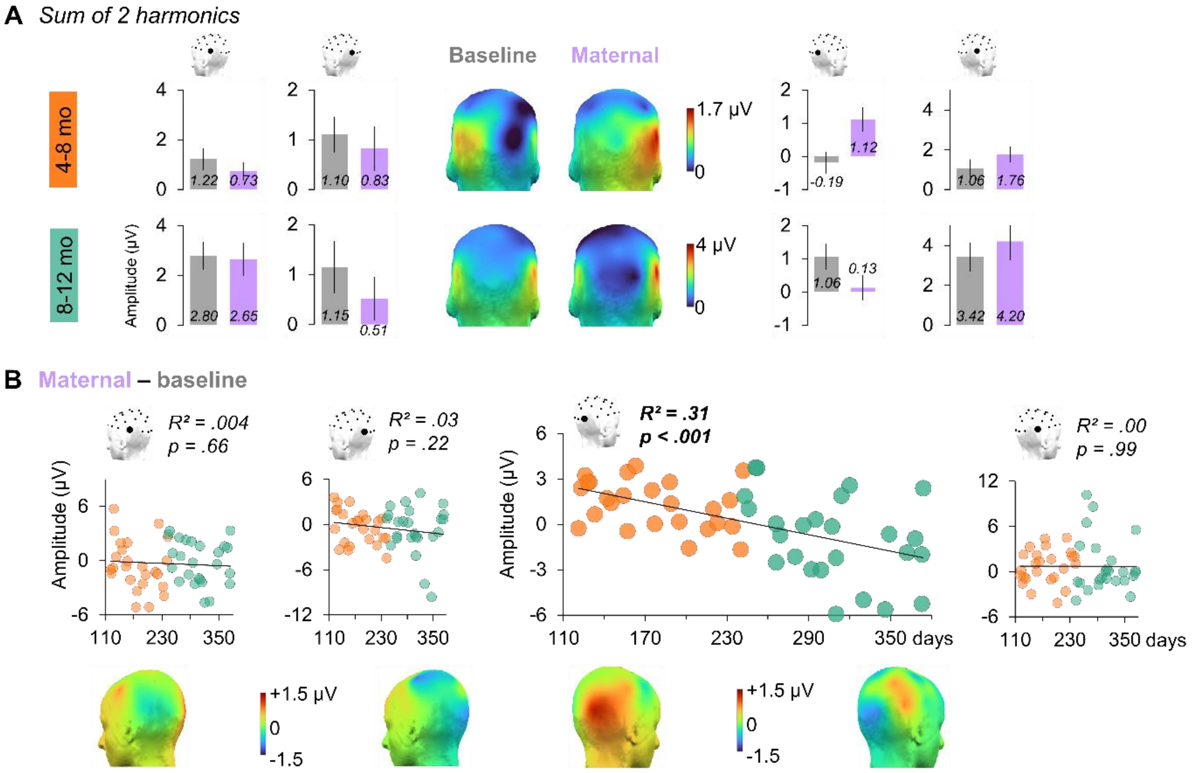

Figure 2.3. Maternal odor effect on the face-selective response. A. Amplitude of the face-selective response summed across two harmonics at each occipito-temporal electrode (from left to right: P7, O1, O2, P8) for the youngest (4-8 months, top) and the oldest (8-12 months, bottom) infants in the baseline (grey) and maternal (violet) odor contexts. Head maps show the topography (posterior view) of the response in each odor context and for each subgroup. **B**. Maternal odor effect (amplitude of the face-selective response in the maternal minus the baseline odor context) at each occipito-temporal electrode as a function of age. Each circle represents individual infant data depending on their subgroup (orange: 4-8 months, green: 8-12 months). Below are head maps showing the topography (lateral views) of the effect for the youngest (4-8 months) and the oldest (8-12 months) infants.

Finally, to further confirm the lateralization of the maternal odor effect as a function of age, we computed a lateralization index between O1 and O2 (with positive and negative values corresponding to right and left hemisphere advantages, respectively) and calculated individual odor effects (maternal minus baseline). We found a significant effect of *Age* (R^2 = .103, *F* (1, 48) = 5.54, *p* = .023) confirming the increase of the face-selective response over the right hemisphere with the mother's body odor at 4 months (predicted index at 120 days: +24.9%) that progressively declines (predicted index at 360 days: -7.5%). The mean odor effect on the index is +17.1 ± 5.4% for the youngest infants (4-8 months) as opposed to -0.3 ± 7.2% for the oldest infants (8-12 months). Hence, in essence, the presence of the mother's body odor strongly increases the face-selective response recorded over the right occipital cortex at 4 months, this odor effect gradually declining with age. At 12 months, the odor effect reverses, the face-selective response decreasing over the right occipital region to become restricted to more anterior occipito-temporal locations.

3.3 *No change of the general visual response with age and in the presence of maternal odor*

The same analysis pipeline as for the face-selective response was applied to the general visual response to the rapid stream of natural images (6 Hz and harmonics). Inspection of the EEG spectrum recorded in the baseline odor context indicated a clear response at 6 Hz and harmonics over the middle occipital cortex at all age (Figure S2A. Appendix 1). This response is descriptively larger for the youngest (4-8 months) than the oldest (8-12 months) infants for the 2nd, 3rd and 4th harmonics and lower for the 1st, 5th and 6th harmonics, leading to an overall response (summed across the 6 harmonics) of 4.36 ± 0.57 µV for the youngest infants and 4.15 ± 0.65 µV for the oldest infants (Figure 2.4A). The general visual response is not different between the two odor contexts for the youngest infants (mean amplitude in the maternal odor context: 4.36 ± 0.61 µV) while slightly larger with the mother's body odor for the oldest infants (4.67 ± 0.71 µV).

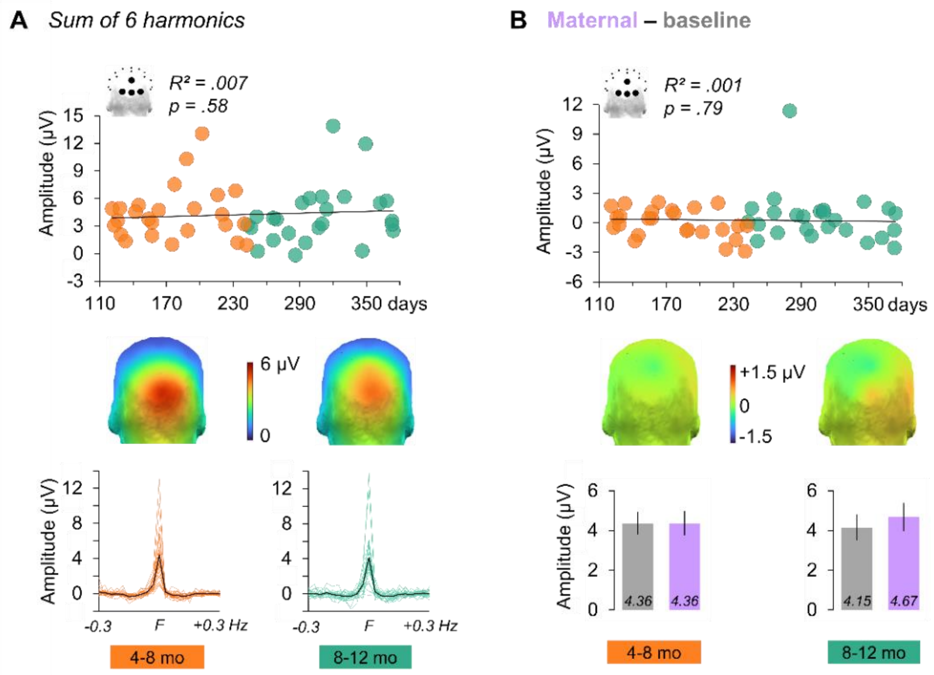

Figure 2.4. No effect of age and maternal odor on the general visual response. Amplitude of the general visual response averaged for the 4 medial occipital electrodes (Oz, POz, O1, O2) and summed across six harmonics (from 6 to 36 Hz) as a function of age in the baseline odor context (**A**) and for the difference between the maternal (violet) and the baseline (grey) odor contexts (maternal odor effect, **B**). Each circle represents individual infant data depending on their subgroup (orange: 4-8 months, green: 8-12 months). Head maps show the topography (posterior view) of the response. The small spectra in A represent the mean response of each subgroup in black and individual spectra in color. Bar graphs in B depict the mean amplitude of the response for each subgroup and each odor context.

The analysis of individual amplitudes extracted for each harmonic at medial occipital electrodes (O1, O2, Oz, POz) in the baseline odor context did not reveal a significant effect of *Age* (*F* (1, 48) = 0.32, $p = .58$, $\eta_p^2 = .007$, Figure 2.4A) or any interaction involving this factor (all *F*s < 1.90, *p*s > .16). Similarly, the maximum number of significant harmonics remains stable as a function of age (mean number across infants: 5.0 ± 0.16 significant harmonics), as revealed by a non-significant linear regression ($R^2 = .009$, *F* (1, 48) = 0.45, $p = .51$, Figure S2B, Appendix 1). Finally, the analysis including the *Odor* factor did not reveal a main effect or interaction with this factor (all *F*s < 0.46, *p*s > .60), for a mean odor effect (maternal minus baseline) across infants of +0.26 ± 0.30 µV for the summed response across harmonics (Figure 2.4B). Since one infant has an odor effect of +11.3 µV whereas the remaining 49 infants have an effect comprised between -2.96 µV and 2.46 µV, we reran the analyses without this outlier. The updated analysis did not change the conclusions (all *F*s < 0.98, *p*s > .32), for a mean odor effect across infants of +0.04 ± 0.20 µV. The outcomes of these ANCOVAs are reported in Table S5.

4. Discussion

By using frequency-tagging EEG to measure rapid face categorization in fifty infants aged from 4 to 12 months, we hereby identify that a face-selective neural response recorded over the occipito-temporal cortex develops as a function of age, both quantitatively (larger amplitude) and qualitatively (distributed on more harmonics in the EEG spectrum). Most importantly, by exposing the infants to their mother's body odor or a baseline odor, we also replicate previous evidence of a larger face-selective response over the right hemisphere in the presence of the mother's odor for the youngest infants (Leleu et al., 2020; Rekow et al., 2021), and further demonstrate that this maternal odor effect gradually declines as face categorization develops (with age). Critically, the general response to the rapid stream of visual stimulation recorded over the middle occipital cortex is immune to the presence of maternal odor, excluding a mere influence on visual attention or general arousal. Overall, we provide conspicuous evidence that during early perceptual development, intersensory facilitation between olfaction and vision decreases as visual perception develops, extending previous findings with audiovisual stimulations (Bahrick et al., 2004) and generalizing them to olfactory-visual interactions.

4.1 The development of rapid face categorization between 4 and 12 months

A first major achievement of the present study is to delineate the development of rapid face categorization in the infant brain between 4 and 12 months. Face perception in general follows a well-documented protracted development in infancy (Pascalis et al., 2020), several abilities improving during the first year of life, such as the discrimination of facial identities (Sugden & Marquis, 2017, for a meta-analysis) or expressions (e.g., Poncet et al., 2022 for recent evidence with frequency-tagging EEG). At birth, infants already orient toward simple face-like stimuli (Johnson et al., 1991), an inborn ability that may be driven by an early preference for basic configurations of visual features (Simion et al., 2007 for a review). Then, between 3 and 4 months, infants exhibit preferential looking for a face over one other object (e.g., a car; de Heering et al., 2016; Durand et al., 2013). Similarly, several EEG studies have measured the event-related potentials elicited by face *vs.* nonface stimuli and identified distinct neural activity for faces from 3-4 months (see de Haan et al., 2003 for review; see also Conte et al., 2020, for recent evidence). However, when testing infants in more complex visual settings, such as a face presented among several nonface objects (Di Giorgio et al., 2012; Kwon et al., 2016) or in more naturalistic stimuli (Frank et al., 2014; Kelly et al., 2019), rapid face detection as measured by eye-tracking mainly improves from 6 months of age (Leppänen, 2016 for review), highlighting that younger infants difficultly track faces in rich environments. At the neural level, previous infant studies have also used frequency-tagging EEG to measure the rapid (i.e., at a glance) categorization of faces contrasted to many other living and nonliving nonface categories within a set of highly variable naturalistic stimuli (de Heering & Rossion, 2015; Leleu et al., 2020). They have identified an occipito-temporal face-selective response already at 4-6 months, which is relatively small (about 1 µV), focal and captured in a single harmonic. Similar studies in children and adults have shown that the face-selective response becomes larger and distributed on several harmonics at 5 (Lochy et al., 2019) and 10 years of age (Vettori et al., 2019), before being observed on even more harmonics with a large occipito-temporal topography in adults, for an overall amplitude of about 4 µV (e.g., Jacques et al., 2016; Rossion et al., 2015). Thus, extending these studies, here we reveal that the frequency-tagged face-selective response progressively increases between 4 and 12 months, with a predicted amplitude of 0.26 µV at 4 months to 2.61 µV at 12 months. Moreover, though here the bulk of the response concentrates on the two first harmonics, which both show a strong effect of age, the number of significant harmonics also increases between 4 and 12 months (predicted number of 1.62 at 4 months to 2.92 at 12 months), indicating that the brain response complexifies (multicomponent waveform in the time domain, see Retter et al., 2021), despite a much lower number of harmonics than in adults (e.g., Jacques et al., 2016; Rossion et al., 2015). Hence, altogether, these findings demonstrate that the ability to rapidly categorize a variety of faces within naturalistic stimuli follows a gradual development during the first year. Future studies should pursue these efforts to delineate the development of face-selective neural activity beyond 1 year of age.

Remarkably, the qualitative and quantitative changes of the face-selective response between 4 and 12 months may reflect improved categorization abilities for both faces and nonface items. In frequency-tagging paradigms of rapid categorization (e.g., Barbero et al., 2021; Jacques et al., 2016; Rekow, Baudouin, Brochard, et al., 2022; Rekow, Baudouin, Durand, et al., 2022), the category-selective response is a direct differential response reflecting the discrimination of the target category from the other categories displayed in the sequence (i.e., distinct neural activity), and the generalization of this discrimination to different exemplars of the target category (i.e., reliable distinct neural activity during the whole sequence). Hence, the observed larger amplitude of the response as age increases, suggests that infants become better at discriminating faces from other objects and at generalizing this response across the variable natural images of faces, which depend on both the accurate recognition of face stimuli (high rate of hits among the 34 faces within a sequence) and the absence of face-selective activity for nonface stimuli (low rate of false alarms among the 172 nonface objects). In other words, improved face categorization does not only imply that faces become more familiar to infants and have a higher chance to be perceived as faces, but also that nonface objects become more familiar to infants and have a lower chance to be *misperceived* as faces. Finally, it is worth noting that this developmental pattern is specific to the face-selective response, as the general visual response does not change with age, in line with previous studies at various ages (de Heering & Rossion, 2015; Leleu et al., 2020; Lochy et al., 2019; Vettori et al., 2019). Given that the general response reflects basic visual function in response to the fast train of images (i.e., detection of changes between 2 successive stimuli), this suggests a selective perceptual improvement based on infants' experience and irrespective of the mere maturation of the visual system, likely driven by the sheer ubiquity of faces in the infants' environment (Jayaraman et al., 2015).

4.2 The mother's body odor fosters face categorization in the youngest infants

A second major achievement of the study is to replicate the maternal odor effect on face-selective neural activity previously found at 4 months for both genuine human faces (Leleu et al., 2020) and naturalistic face-like stimuli (Rekow et al., 2021). In line with these studies, the effect is observed over the right occipital cortex, dominant for face categorization (Rossion & Lochy, 2021 for review). Other studies have also found that maternal odor modulates both behavioral and electrophysiological responses to facial information in young infants (Durand et al., 2013, 2020; Endevelt-Shapira et al., 2021; Jessen, 2020). The mother's body odor is a salient chemosensory stimulus that accompanies infants from the very beginning of life and promotes specific physiological, behavioral and neural responses already in neonates (Schaal et al., 2020 for review). By stimulating eye opening at birth (Doucet et al., 2007), maternal odor favors optimal exposure to the mother's face during nursing and caregiving. Later on, infants are often carried by their mother while engaged in social interactions, leading to co-exposure to the mother's odor and to various (un)familiar faces. This repeated co-occurrence of both sensory stimulations in the infants' environment could generate a relevant association, leading to intersensory facilitation, as previously observed for audiovisual associations (e.g. Hyde et al., 2011; Lewkowicz et al., 2010; Neil et al., 2006).

Interestingly, compared to auditory and visual perception, odor perception is less sensitive to spatiotemporal precision (Sela & Sobel, 2010). This reduced spatiotemporal constraint could make odor cues particularly prone to foster the development of visual categorization by supporting the generalization of variable inputs into a single category. At the neural level, a dedicated connectivity could be shaped by the recurrent association between the mother's odor and faces, so that the former would be able to boost the sensitivity of the face-selective network through reentrant signaling (Edelman, 1993). Such connectivity is supported by a body of research in adults revealing that the sole presentation of odors activates the right occipital cortex (e.g., Royet et al., 2001), and body odors in particular elicit neural activity in the lateral fusiform gyrus (e.g., W. Zhou & Chen, 2008), which is part of the face-selective network and is also functionally connected to the primary olfactory cortex (G. Zhou et al., 2019). Finally, it is also important to note that the odor effect is not driven by a mere enhancement of arousal or attention, as the general response to the rapid stream of visual stimulation remains unaffected by the presence of the mother's body odor (Leleu et al., 2020; Rekow et al., 2020, 2021). This dissociation between the face-selective and general visual responses as a function of age reminds that the frequency-tagging approach allows to isolate and characterize distinct responses at different frequencies simultaneously within the same stimulation sequence.

4.3 Olfactory-to-visual facilitation declines gradually as a function of age

Importantly, according to our main hypothesis, we found a gradual decline of the maternal odor effect as a function of age. The odor effect observed at the right occipital electrode O2 is the strongest for the youngest infants, and progressively decreases and reverses as age increases, such that the face-selective response becomes restricted to occipito-temporal sites in the presence of the mother's body odor for the oldest infants. This supports prior studies in the audiovisual domain reporting intersensory facilitation in younger but not in older infants when unisensory perception has improved (Bahrick et al., 2004; Bahrick & Lickliter, 2000, 2004), and extends them to olfactory-visual interactions. Such developmental trade-off between olfaction and vision for efficient categorization relates to the inverse effectiveness principle whereby multisensory integration decreases as unisensory responses increases (e.g., Meredith & Stein, 1983; Regenbogen et al., 2016; Stevenson et al., 2012). This presumably stems from the fact that a key function of multisensory integration is the disambiguation of otherwise ambiguous unisensory events (Ernst & Bülthoff, 2004), as already reported in infants (Phillips-Silver & Trainor, 2005; Scheier et al., 2003), or in adults for odor effects on the perception of ambiguous facial expressions (e.g., Forscher & Li, 2012; Leleu et al., 2015; Poncet et al., 2021; W. Zhou & Chen, 2009). Similarly, in adults, a composite body odor pooled from 8 unfamiliar donors favors the categorization of ambiguous face-like objects while it does not influence human face categorization (Rekow, Baudouin, Durand, et al., 2022), which is readily achieved without another sensory cue and under tight visual constraints in the adult brain (e.g., Retter et al., 2020). Hence, the presence of maternal odor cues may help the infant brain to disambiguate inputs to reach optimal face categorization, unless visual inputs are sufficient to elicit a robust percept as face perceptual abilities improve over the first year of life. Future studies should investigate this interpretation by increasing, for instance, face categorization demand at 12 months of age, to determine whether intersensory facilitation from the mother's odor reappears, as previously observed with audiovisual stimulations (Bahrick et al., 2010).

Alternatively, during development, maternal odor may become less associated with the face category in general. Early on, infants are already able to differentiate their own from another mother's odor (e.g., Cernoch & Porter, 1985; Russell, 1976; Schaal et al., 1998). Thus, as face perceptual abilities develop, the mother's body odor may be specifically associated with the recognition of her face, while the association with other faces weakens. In the same vein, the femininity of the mother's odor may gradually become recognized by older infants and selectively associated with the categorization of female faces. This putative developmental shift is in line with previous evidence in the audiovisual domain that multisensory perception is broadly tuned during the first months and then gradually narrows toward more specific associations (Murray et al., 2016 for review). Maternal odor could even be progressively dissociated from the perception of faces, as the proportion of faces in the infant's visual environment linearly decreases during the first year while the proportion of other body parts, especially hands, increases (Fausey et al., 2016). However, accumulating evidence shows that human odors are still associated with faces in adulthood (see Damon et al., 2021 for a recent review), indicating that body odor influence on face perception is not restricted to the maternal odor effect in the youngest infants.

Another non-mutually exclusive interpretation could be that maternal odor progressively loses the ability to trigger face categorization because its composition changes between 4 and 12 months. The mother's body odor is a mixture of several compounds conveying a variety of cues about her traits (e.g., identity, femininity, humanity) and states (e.g., maternity, emotions). In particular, certain cues emanating from milk can be discriminated by infants, who differentiate human from non-human milk (Marlier & Schaal, 2005), lactating from non-lactating women (Makin & Porter, 1989), or early from late lactation milk (Klaey-Tassone et al., 2020). Given that young infants are generally more often breastfed than older infants, feeding status is a candidate factor for the maternal odor effect. However, when adding the feeding factor to the analysis, there is no evidence for an interaction between feeding and age, and no interaction with the odor effect (Table S6 and Figure S3, also for the absence of significant interactions with the infants' sex, Appendix 1). For other cues, such as the familiarity of the odor, there is no clear evidence in the literature, as previous infant studies about odor-face interactions that compared the own and another mother's odor did not systematically evidence a comparable effect (Durand et al., 2020; Jessen, 2020). Finally, as mentioned above, a composite body odor pooled from males and nulliparous females is able to foster face perception in the adult brain (Rekow, Baudouin, Durand, et al., 2022; see also Cecchetto et al., 2020; Wudarczyk et al., 2016 for other non-maternal body odors), revealing the potency of a human odor beyond maternal cues, at least in adulthood. Therefore, future studies should carefully characterize the chemical profile of the mother's odor as a function of age, and delineate which cues carried by this odor facilitate face categorization in the youngest infants.

4.4 Conclusions

To conclude, we have shown that the mother's odor effect on neural face categorization previously reported at 4 months (Leleu et al., 2020) gradually decreases with age as face-selective activity amplifies. This suggests that face categorization relies on maternal odor cues in developing infants until the visual system becomes able to readily achieve categorization by itself, generalizing previous evidence in the audiovisual domain that intersensory facilitation declines as unisensory perception improves (Bahrick et al., 2002; Bahrick & Lickliter, 2000, 2004). From a broad developmental perspective, our findings favor a multisensory view of knowledge acquisition (Gibson, 1969). However, this does not mean that perception strictly develops from multisensory to unisensory abilities, a large body of research having shown intersensory facilitation in adults when unisensory inputs are scarce or ambiguous (e.g., for odor-face association Forscher & Li, 2012; Leleu et al., 2015; Poncet et al., 2021; Rekow, Baudouin, Durand, et al., 2022). We thus support a lifespan view of multisensory perception (Bahrick & Lickliter, 2012; Murray et al., 2016; Lewkowicz & Bremner, 2020 for reviews), in which intersensory facilitation at any age is a function of how unisensory perception is effective on its own. In this context, early infancy would represent a key period of multisensory development, when the perceptual system is still immature and highly naïve toward the environment, while progressive maturation and experience would then reduce the need to bind multisensory cues for effective categorization in the environment.

Study 2. Olfactory The inverse effectiveness of olfactory-to-visual facilitation in the 4-month-old brain

This section corresponds to the article:
Kiseleva, A., Rekow, D., Schaal, B., & Leleu, A. (Submitted). The inverse effectiveness of olfactory-to-visual facilitation in the 4-month-old brain.

Abstract

To navigate their environment, infants rely on intersensory facilitation when unisensory perceptual demand is high, a principle known as inverse effectiveness. Given that this principle was mainly shown using audiovisual stimulations, here we aim to determine whether it applies to olfactory-to-visual facilitation. We build on previous evidence that maternal odor facilitates face categorization in the 4-month-old brain, and investigate whether this effect depends on visual demand. Scalp EEG was recorded in 2 groups of 4-month-olds while they watched 6-Hz streams of stimuli with faces every 6th stimulus to tag a face-selective response at 1 Hz. In Group 1, we used variable natural stimuli, while stimuli were simplified in Group 2 to reduce perceptual demand. During visual stimulation, infants were alternatively exposed to their mother's vs. a baseline odor. For both groups, we found an occipito-temporal face-selective response, but with a larger amplitude for the simplified stimuli, reflecting less demanding categorization. Importantly, maternal odor enhances the response to natural but not to simplified face stimuli, indicating that maternal odor improves face categorization when it is demanding for the 4-month-old brain. Overall, this study demonstrates that the inverse effectiveness of intersensory facilitation applies to the sense of smell during early perceptual development.

1. Introduction

Humans are exposed to a complex multisensory environment from the very beginning of life. The ability of young infants to form multisensory percepts has long been a matter of debate (e.g., Gibson, 1969; Piaget, 1952), but today much evidence has been obtained showing interactions between the sensory systems at an early age (Bahrick and Lickliter, 2012; Lewkowicz and Bremner, 2020; Murray et al., 2016 for reviews). Newborns already possess the brain architecture to integrate inputs across sensory modalities (Sours et al., 2017) and demonstrate incipient multisensory skills based on correlations between physical cues such as similar intensity (Lewkowicz and Turkewitz, 1980) and temporal occurrence (Lewkowicz et al., 2010). During the first months, multisensory perception develops and allows to bind a large set of multisensory cues insofar as they co-occur in space (Neil et al., 2006) and/or time (e.g., Hyde et al., 2011; Lewkowicz, 1996; Werchan et al., 2018).

An influential view of multisensory development, the intersensory redundancy hypothesis (IRH) proposed by Bahrick & Lickliter (2000), posits principles of multisensory integration in infancy based on the detection of amodal proprieties (e.g., rhythm, intensity, synchrony) across sensory inputs. In particular, the *intersensory facilitation* principle states that at early developmental stages, multisensory stimulations are perceived more efficiently than unisensory stimulations when the latter are not yet easily processed (Bahrick and Lickliter, 2012). As a result, infants can discriminate e.g., tempos at 3 months (Bahrick et al., 2002), rhythms at 5 months (Bahrick and Lickliter, 2000), or prosodies (Bahrick et al., 2019) and emotions (Flom and Bahrick, 2007) at 4 months from temporally synchronized auditory and visual inputs whereas they cannot from unisensory or asynchronous inputs. Interestingly, as the senses mature and develop with age, uni- and multisensory stimulations gradually become equally effective and intersensory facilitation declines. For example, while 3- and 5-month-old infants respectively discriminate the tempo and rhythm of an audiovisual stimulation, they fail when exposed to the sole visual input (Bahrick et al., 2002; Bahrick and Lickliter, 2000). In contrast, at 5 and 8 months of age for tempo and rhythm, respectively, infants demonstrate discrimination abilities in both uni- (visual) and multisensory (audiovisual) conditions with no remaining intersensory facilitation (Bahrick and Lickliter, 2004).

These results suggest that the development of intersensory facilitation follows a well-known principle of multisensory integration evidenced in both animals and humans: *inverse effectiveness* (e.g., Meredith and Stein, 1983; Stevenson et al., 2007). According to this principle, the weakest unisensory responses lead to the strongest multisensory integration. Inverse effectiveness in human adults is generally established by increasing task load (e.g., Santangelo and Spence, 2007) or decreasing the effectiveness of unisensory stimuli to trigger a response, either behavioral (Regenbogen et al., 2016), hemodynamic (Stevenson et al., 2007; Stevenson and James, 2009), or electroencephalographic (EEG) (Stevenson et al., 2012). Likewise, in 5-month-old infants, a study has shown a relation between the effectiveness with which infants discriminate a unisensory stimulation and the strength of intersensory facilitation (Bahrick et al., 2010). By using a tempo discrimination paradigm that 5-month-old infants usually achieve with both visual and audiovisual stimulations and without any sign of intersensory facilitation (Bahrick & Lickliter, 2004), and by increasing the difficulty of the discrimination, the authors have found that intersensory facilitation reappears while unisensory discrimination disappears, as if 5-month-olds were performing like 3-month-olds in the original simpler design. This indicates that intersensory facilitation, in addition to declining as unisensory perception develops with age, depends on unisensory perceptual demand at a given age.

With the notable exception of touch (e.g., Ronga et al., 2021), intersensory facilitation in infancy was almost exclusively investigated using auditory and visual stimulations. Does that mean that this principle does not apply to the chemical senses? In particular, we know that olfaction actively participates in multisensory perception in infants (e.g., Durand et al., 2013; Godard et al., 2016; Jessen, 2020). Using frequency-tagging EEG, recent studies have shown that during a challenging visual task for the infant brain, i.e., the rapid categorization of a variety of naturalistic face stimuli against variable nonface stimuli, adding the mother's body odor boosts face-selective neural activity in 4-month-old infants (Leleu et al., 2020; Rekow et al., 2020). At the same age, maternal odor even initiates a selective EEG response to ambiguous face-like objects (Rekow et al., 2021). Interestingly, in line with the aforementioned studies in the audiovisual domain, intersensory facilitation from the mother's odor gradually declines as rapid face categorization develops between 4 and 12 months (Study 1; Rekow et al., 2023). Moreover, a study in adults found that face-selective EEG activity is not influenced by a concomitant body odor for genuine human faces, which are readily categorized from the sole visual input, but still enhanced for ambiguous face-like objects, which are less effectively categorized (Rekow et al., 2022). This developmental trade-off suggests that olfactory-to-visual facilitation follows the inverse effectiveness principle as it progressively disappears when visual categorization improves and becomes effective on its own.

Here, to directly determine the inverse effectiveness of maternal odor on rapid face categorization in young infants, we used a frequency-tagging EEG approach in two groups of 4-month-olds and built on previous audiovisual studies that manipulated perceptual demand (e.g., Bahrick et al., 2010). The first group (Group 1, natural stimuli) was exposed to a highly variable set of natural face and nonface stimuli as used in previous studies showing a maternal odor effect on rapid face categorization (Leleu et al., 2020; Rekow et al., 2023, 2021, 2020). The second group (Group 2, simplified stimuli) was exposed to a less variable set of edited stimuli to reduce physical variability across face stimuli while keeping high variability between face and nonface stimuli, thus decreasing perceptual demand compared to natural stimuli. In both groups, stimuli were presented as fast streams of 6 stimuli/s (at 6 Hz) with faces inserted every 6th stimulus to tag a face-selective response at 1 Hz and harmonics (i.e., integer multiples) in the EEG spectrum. During visual stimulation, infants were alternatively exposed to a baseline or a maternal odor context. We expected a larger face-selective response in Group 2 (simplified stimuli) than Group 1 (natural stimuli), reflecting less demanding face categorization for the former. We also expected a larger response in the maternal than baseline odor context only for Group 1 (natural stimuli), indicating olfactory-to-visual facilitation when visual perception is not fully effective.

2. Material and methods

2.1 Participants

Forty-eight full-term 4-month-old infants recruited from the local birth registry participated in the study. Before testing, parents were informed about the objectives and methods of the study and signed a written informed consent. None indicated their infants having any sensory (e.g., visual, olfactory), neurological, or psychiatric disorder. Testing was conducted according to the Declaration of Helsinki and approved by the French ethics committee (CPP Sud-Est III - 2016-A02056-45). Data from six infants were excluded on the basis of less than two valid sequences per odor context ($N = 3$), or too noisy EEG data ($N = 3$). The final sample was thus composed of 42 infants who were randomly assigned to one group according to the type of visual stimuli they were exposed to (see section 2.2): 21 infants were exposed to natural stimuli (Group 1, 9 females, mean age ± SD: 132 ± 10 days, range: 119–162 days) and 21 infants to simplified stimuli (Group 2, 9 females, mean age ± SD: 135 ± 13 days, range: 112–168 days). The two groups did not significantly differ in age ($T\,(40) = 0.91$, $p = .37$). We estimated sample size a priori from the maternal odor effect found in Leleu et al. (2020) that we aimed to replicate in Group 1 in the present study. We considered a Cohen's $d = +0.79$ (effect size at right occipito-temporal electrodes), a significance level $\alpha = .05$ (two-tailed), and a high power $1\text{-}\beta = .95$ to optimize our ability to replicate the effect, leading to a sample size $N = 21$. For the sake of simplicity, we made sample sizes equal in both groups.

2.2 *Visual stimuli*

Visual stimuli consisted in pictures of human adult faces and various living and non-living objects (i.e., animals, plants, man-made objects) cropped to a square and resized to 400 × 400 pixels. Two stimulus sets were created (one for each group of infants), each composed of 68 faces (34 females) and 170 objects (85 categories × 2 exemplars; see examples in Figure 2.5A; full stimulus sets in Figure S1, Appendix 2). As in previous studies showing a maternal odor effect on rapid face categorization (Leleu et al., 2020; Rekow et al., 2023, 2021, 2020) the first set (Group 1, natural stimuli) consisted in color natural images in which the item appears at variable locations, under variable lighting conditions, and from variable sizes and viewpoints, together with different facial expressions, external features (e.g., haircut), etc. for faces. Items were embedded in their original background, implying figure-ground segregation. Low- (e.g., luminance, contrast, spatial frequency) and higher-level (e.g., color, curvature) cues are thus highly variable in these natural stimuli, such that inter-stimulus variability is high both within and across face and nonface categories. This avoids the contribution of image-based characteristics to discriminate faces and nonface objects, and to generalize across individual faces, for a measure of rapid face categorization beyond physical cues (de Heering and Rossion, 2015).

The second set (Group 2, simplified stimuli) consisted in color images depicting the same categories as the first set, but items were segmented from their background, which was replaced by a grey background (128/255 in greyscale). In addition, exposure conditions were less variable than in the first set (e.g., constant size, central location). In particular, faces were all depicted from a full-front view with a neutral expression under uniform lighting, and external features such as hair and ears were removed. All faces covered roughly the same surface (about 200-pixel height and 150-pixel width) and were aligned at eye-level. These simplified stimuli were created to reduce physical variability across faces while keeping high variability between faces and nonface objects, thus making rapid face categorization less demanding for the visual system compared to natural stimuli.

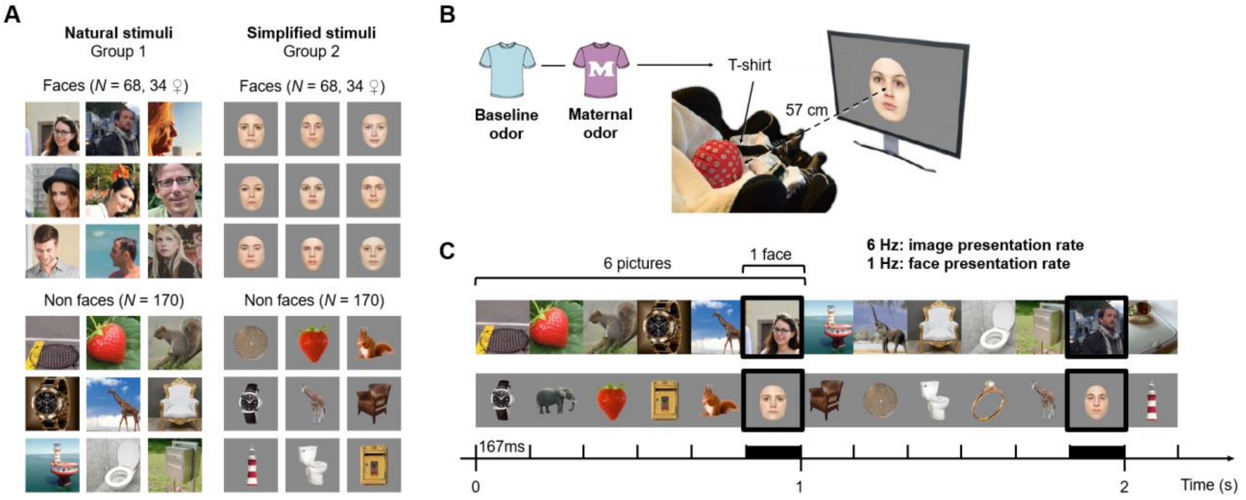

Figure 2.5. A frequency-tagging EEG approach to measure the inverse effectiveness of maternal odor on rapid face categorization. A. Examples of the natural (left) and simplified (right) stimuli respectively presented to Group 1 and Group 2, each depicting human faces (*N* = 68, 34 females) and nonface objects (*N* = 170, 85 categories × 2 exemplars). **B.** Two odor contexts (baseline and maternal odor) were delivered using a t-shirt disposed on the infant's chest during visual stimulation and alternated every 2 sequences. Infants were equipped with an EEG cap and seated at 57 cm in front of the stimulation screen, in which stimuli (item + background) roughly subtended 24° of visual angle. **C.** Excerpt of 2.167 s of fast periodic visual stimulation (from 32-s-long sequences) presenting 6 images/s (i.e., at a 6-Hz rate, stimulus duration: 167 ms) with faces interspersed every 6th stimulus (i.e., at a 1-Hz rate, 1-s interval between two faces).

2.3 Odor stimuli

Infants of both groups were exposed to two odor contexts: the mother's body odor and a baseline odor, which were delivered using white cotton t-shirts as in previous studies (Durand et al., 2013; Leleu et al., 2020; Rekow et al., 2023, 2021, 2020). T-shirts were laundered beforehand with a scentless hypoallergenic powder detergent (Persavon, France) and then stored in a hermetic zip-locked plastic bag. The mother's body odor was collected at home using a clean t-shirt sent to the mother one week before the experiment. Mothers were asked to wear the t-shirt on bare skin during the three consecutive nights preceding the experiment and to refrain from using odorous soap or perfume. During the days of the collection period, they were asked to store the t-shirt in the bag at room temperature, away from any heating device. The baseline odor consisted in the odor of an unworn t-shirt stored in our premises.

2.4 Procedure

For both groups, procedure was identical to that of previous frequency-tagging EEG studies showing a maternal odor effect on rapid face categorization (Leleu et al., 2020; Rekow et al., 2023, 2021, 2020) . After placement of the electrode cap, infants were installed in a baby car seat in front of the stimulation screen (Figure 2.5B) in a light- and sound-attenuated room equipped with an air-extractor located approximately 2 m above the seat and which continuously and silently renewed the air. The room was also aired between experiments and the experimenter did not use or consume any odorous product. During the experiment, infants were placed behind occluding blinds to minimize visual distraction, and continuously monitored through a camera placed on top of the screen. Parents were asked to stay at a minimal 2.5-m distance from their infant and not to interact with her/him except in case of manifest distress.

For odor delivery, the experimenter used dedicated disposable nitrile gloves (Schield Scientific, The Netherlands) to place one t-shirt under the seat belts on the infant's upper chest just before a sequence of visual stimulation (duration: 34.5 s, see below). The t-shirt was folded to optimally expose to axillary, breast, and neck regions. Every two sequences, a break of 1 min at least was introduced during which the experimenter changed the t-shirt (i.e., the odor context). Odor contexts were thus delivered throughout two sequences of visual stimulation and their presentation order was counterbalanced across infants.

Visual stimuli were displayed in the center of a 24-inch LED screen (refresh rate: 60 Hz, resolution: 1920 × 1080 pixels) on a grey background (128/255 in greyscale) at a viewing distance of 57 cm, thus subtending 24 × 24° of visual angle for the natural stimuli (including both the item and its background) and about half this size for the item (no visible background) in the simplified stimuli (Figure 1B). Stimuli were presented through a fast periodic visual stimulation at a rate of 6 Hz (i.e., 6 stimuli per s) without inter-stimulus interval (stimulus duration: 167 ms, i.e., 1 s/6) and faces were inserted as every 6^{th} stimulus, i.e., at a rate of 6 Hz/6^{th} = 1 Hz (1-s interval between two faces, Figure 2.5C). This periodic stimulation resulted in two distinct brain responses tagged at two frequencies in the EEG spectrum: a general visual response recorded at 6 Hz and harmonics (i.e., integer multiples) elicited by all visual cues rapidly changing 6 times per second (common to face and nonface stimuli), and a face-selective response recorded at 1 Hz and harmonics capturing the differential neural activity elicited by faces compared to the nonface categories and generalized across individual faces. The face-selective response is thus a signature of rapid (i.e., single-glance) face categorization (de Heering and Rossion, 2015; Jacques et al., 2016; Rossion et al., 2015).

Each sequence of visual stimulation lasted 34.5 s, starting with a pre-stimulation interval (0.5 s), followed by a fade-in of increasing contrast (0 to 100%, 1.833 s), the full-contrast stimulation (31.167 s), a fade-out of decreasing contrast (100 to 0%, 0.833 s), and a post-stimulation interval (0.167 s). For each group of infants, the set of 68 face stimuli was divided into two subsets of 34 faces (17 females) that were counterbalanced across sequences and odor contexts (all combinations reached after 4 sequences). Therefore, all face stimuli were presented equally across the two consecutive sequences of one odor context and contrasted to the same set of 170 nonface stimuli. When infants looked away from the screen, short sounds (e.g. bike ring or squeak of rubber toys) were used to reorient attention to the screen. Their sporadic and non-periodic appearances minimally contaminated the frequency-tagged EEG responses with auditory-evoked potentials. The number of sequences was not fixed a priori, such that the experiment stopped when the infant manifested disinterest or fatigue, or at parental demand. Infants were included in the final samples if they achieved at least 4 valid sequences (i.e., 2 per odor context). A sequence was considered valid if not aborted prematurely and if it elicited a general visual response (see section 2.5). The 42 included infants achieved between 4 and 16 sequences each (mean ± SD: 9.4 ± 2.8 sequences), for an overall stimulation duration ranging from 2 min 18 s to 9 min 12 s per infant.

2.5 EEG recording and preprocessing

EEG was continuously recorded from a 63 Ag/AgCl electrode cap (Waveguard, ANT Neuro, The Netherlands) according to the 10–10 classification system (acquisition reference: CPz, ground: AFz, initial impedance < 30 kΩ, sampling rate: 1000 Hz) (Figure S2, Appendix 2). EEG data were preprocessed and analyzed using Letswave 6 (http://www.letswave.org/) running on Matlab 2017 (MathWorks, USA).

First, we applied a Butterworth filter (highpass, cutoff: 0.1 Hz, 4th order) to individual datasets. Then, the signal was down-sampled to 200 Hz before being cropped into 36-s-long segments starting from the beginning of the fade-in of each sequence. Resulting segments were cleaned of artifacts using the *Artifact Blocking* algorithm (Fujioka et al., 2011; Mourad et al., 2007) with a threshold of ± 250 µV. Segments were then cropped again, starting from the end of the fade-in (i.e., at the onset of the first stimulus of the full-contrast phase) to the end of the fade-out, resulting in 32-s-long segments. Datasets were re-referenced according to a common average reference.

To increase signal-to-noise ratio, invalid segments were rejected using a data-driven criterion which consisted in identifying segments with no general visual response at first (6 Hz) and second (12 Hz) harmonics (used as a marker of the infant's attention to the stimulation sequence; Leleu et al., 2020; Rekow et al., 2023, 2021, 2020). Baseline-corrected amplitude spectra were extracted for each segment and Z-scores were calculated (see section 2.6) to estimate significance at 4 medial occipital electrodes (POz, Oz, O1, O2) that exhibit the largest response to a 6-Hz stream of complex visual stimuli in the infant brain (e.g., Leleu et al., 2020). Segments were kept for subsequent analyses if at least two *Z*-scores were above 1.64 ($p < .05$, one-tailed, signal > noise). The total number of rejected segments was 45 out of 406 (11%). The remaining average number of segments per infant was (mean ± SD) 8.3 ± 2.7, with no significant difference between groups (Group 1: 9.0 ± 3.4, Group 2: 7.7 ± 1.7, T (40) = 1.63, p = .11). When compared between odor contexts, this mean number of segments was not significantly different for both Group 1 (baseline: 4.4 ± 1.7, maternal: 4.6 ± 1.9, T (20) = 0.91, p = .37) and Group 2 (baseline: 3.8 ± 1.1, maternal: 3.9 ± 0.8, T (20) = 0.77, p = .45). Finally, remaining segments were sorted according to the odor context and averaged in the time domain to obtain a single 32-s-long segment per odor context and infant.

2.6 EEG frequency-domain analysis

First, a fast Fourier transform was applied to the two segments (one per odor context) of each infant and raw amplitude spectra were extracted for all electrodes with a frequency resolution of 1/32 s = 0.03125 Hz. Given the steep power-law function of these spectra, a baseline correction was applied to remove background noise and lead to notional amplitudes of zero in the absence of tagged responses. At each frequency bin, mean noise was estimated from 6 neighboring bins and subtracted out. These bins were selected among the 10 surrounding bins (5 on each side, ± 0.15625 Hz) after the exclusion of the 2 immediately adjacent (one on each side, in case of spectral leakage) and the 2 extreme (minimum and maximum) bins (to avoid signal and potential outliers in noise estimation). Then, we estimated the number of significant harmonics separately for each brain response using *Z*-scores calculated on the average across odor contexts, electrodes, and infants (from both groups). *Z*-scores were defined as the difference between the amplitude at the frequency of interest and the mean amplitude of 20 neighboring bins, divided by their standard deviation (SD). Neighboring bins were selected among 22 surrounding bins beyond those used for baseline correction (11 on each side, from ± 0.1875 Hz to ± 0.5 Hz) after the exclusion of the two extreme bins. Harmonics were included until *Z*-scores were no longer consecutively significant ($Z > 1.64$, $p < .05$, one-tailed, signal > noise). For the general visual response, 4 consecutive harmonics were significant (i.e., from 6 to 24 Hz, Table S1, Appendix 2), and 5 consecutive harmonics were significant for the face-selective response (i.e., from 1 to 5 Hz, Table S1, Appendix 2).

Next, we identified regions of interest (ROIs) for subsequent analyses. To obtain a compiled representation of each brain response, we summed their amplitude across significant harmonics (Retter et al., 2021). Given that both responses are located over posterior brain regions (e.g., de

Heering and Rossion, 2015; Leleu et al., 2020), we then explored which electrodes were significant among the 21 occipital, occipito-temporal, and parietal electrodes (Figure S2, Appendix 2) using *Z*-scores (see above) calculated across odor contexts and infants (from both groups). *Z*-scores were considered significant when $Z > 2.82$ ($p < .05$, one-tailed, signal > noise, Bonferroni-corrected for 21 electrodes). For the general visual response, every electrode was significant (all *Z*s > 17.6, Table S2, Appendix 2). We thus kept the 4 best electrodes, all located over the middle occipital cortex (Oz, O2, O1, POz) and identical to those of previous studies (e.g., Leleu et al., 2020; Rekow et al., 2023, 2021, 2020). For the face-selective response, 15 electrodes were significant (all *Z*s > 2.82, Table S2, Appendix 2). We selected them (except electrode P5 due to the non-significance of its contralateral homologous electrode P6, Figure S2, Appendix 2) to form three ROIs: right (rOT: P8, P10, PO6, PO8, O2) and left (lOT: P7, P9, PO5, PO7, O1) occipito-temporal regions, and a medial occipital region (mO: PO3, PO4, Poz, Oz).

Having defined harmonics and ROIs from the mean responses across odor contexts and infants, we then conducted a two-step analysis pipeline separately on each brain response to compare (1) the two groups of infants (i.e., natural vs. simplified stimuli) irrespective of the odor context; (2) the two odor contexts for each group of infants (i.e., each type of stimuli). For (1), we first averaged the responses across odor contexts and used *Z*-scores to determine how many harmonics were significant for each group of infants. *Z*-scores were also used to estimate the significance of the summed responses for each group and each individual infant within groups. Next, the mean amplitude of the summed brain responses was quantified for each group, and individual amplitudes were finally submitted to a repeated-measures ANOVA using *Group* (Group 1: natural stimuli, Group 2: simplified stimuli) as a between-subject factor. For the face-selective response, *ROI* (rOT, lOT, mO) was also used as a within-subject factor and comparisons between ROIs were performed using *T*-tests. Mauchly's test was used to estimate sphericity violation and the Greenhouse-Geisser correction for degrees of freedom (df) was applied whenever sphericity was violated (adjusted df and the epsilon coefficient (ε) are reported). Significance was fixed at $p < .05$ and effect sizes are reported as partial eta squared (η_p^2) and/or Cohen's *d*.

For (2), the mean amplitude of the summed brain responses was first quantified for each odor context and group, and individual amplitudes were submitted to a repeated-measures ANOVA using the *Group* and *ROI* (for the face-selective response) factors, and adding *Odor* (baseline, maternal) as a within-subject factor. However, since in (1) we found a strong difference between the two groups (i.e., types of stimuli) for each brain response (i.e., larger general and face-selective visual responses to natural (Group 1) and simplified (Group 2) stimuli, respectively, see section 3), the *Odor* effect for the group with the weakest response might be masked by the larger response for the other group in the omnibus ANOVA. To avoid that, we normalized individual data separately for each group before running the ANOVA. We subtracted the mean amplitude across odor contexts (and ROIs for the face-selective response) and divided by its standard deviation, such that, for each group, the resulting mean amplitude and standard deviation across conditions were equal to 0 and 1, respectively (leading to a null main effect of *Group*). Given our aim to delineate the influence of maternal odor, we focused on effects involving the *Odor* factor. Significant interactions were decomposed using contrasts and paired comparisons were performed using *T*-tests. As in (1), the Greenhouse-Geisser correction was applied whenever necessary, significance was fixed at $p < .05$, and effect sizes are reported as η_p^2 and/or Cohen's *d*. To illustrate individual odor effects (maternal minus baseline) for each group, we expressed them as effect sizes by dividing by their standard deviation. Lastly, since the face-selective response to natural stimuli (Group 1) is mainly concentrated on the 1st harmonic whereas the response to simplified stimuli is distributed on 5 harmonics (see section 3), we estimated whether this difference drives the odor effect by analyzing separately the 1st harmonic (1 Hz) and for the sum of the four remaining harmonics (2 to 5 Hz).

3. Results

3.1 General and face-selective visual responses to natural and simplified stimuli in the 4-month-old brain

As expected, a fast 6-Hz train of either natural or simplified visual stimuli elicited a large response at the same frequency in the infants' EEG spectrum (Figure 2.6A). This general neural response to the rapid stimulation stream is significantly distributed until the 4th harmonic (24 Hz) at medial occipital electrodes for both types of visual stimuli (all *Z*s > 9.73, all *p*s < .001, Table S3). The summed response across harmonics (Figure 2.6C) is also highly significant for both natural (Group 1: $Z = 113$, $p < .001$) and simplified (Group 2: $Z = 85.1$, $p < .001$) stimuli. Such a robust response was confirmed by individual infant data (Table S4) as all infants exhibit a significant general response at the medial occipital ROI (all *Z*s > 3.35, all *p*s < .001) except one in Group 2 ($Z = 1.25$, $p = .11$). Interestingly, however, visual inspection also indicates a stronger general visual response to natural than simplified stimuli (Figure 2.6). At electrode Oz where the highest response is recorded for both types of stimuli, amplitude is 123% larger (Cohen's $d = 1.01$) for Group 1 (natural: 4.90 ± 0.84 (SEM) µV) than Group 2 (simplified: 2.20 ± 0.33 µV). This difference is smaller but remains strong (+89%, Cohen's $d = 0.87$) for the mean amplitude across medial occipital electrodes (Group 1: 3.32 ± 0.49 µV, Group 2: 1.76 ± 0.30 µV) and is statistically significant, as revealed by the main effect of *Group* ($F(1, 40) = 7.47$, $p = .009$, $\eta_p^2 = 0.16$).

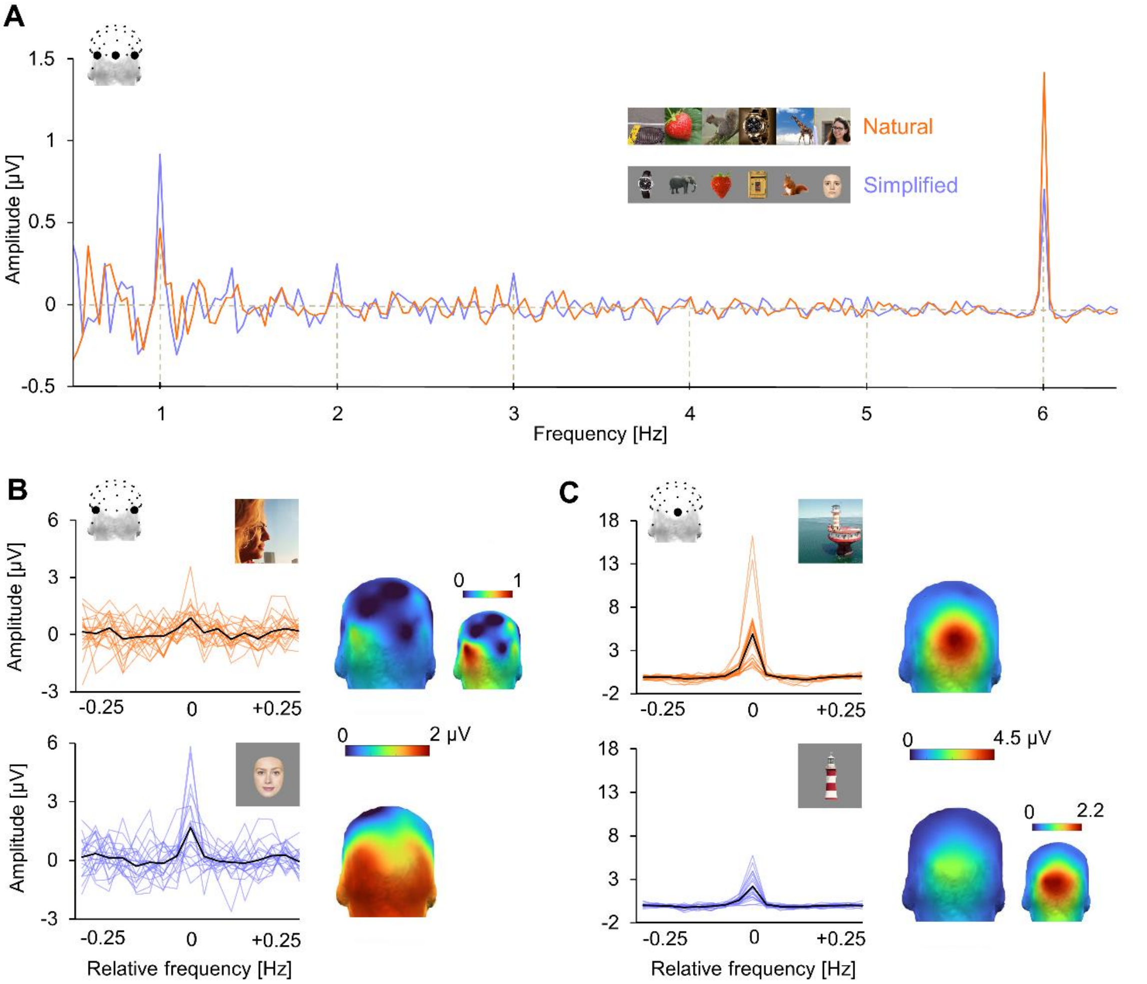

Figure 2.6. General and face-selective visual responses to natural and simplified stimuli. A. Mean amplitude spectrum across two occipito-temporal (PO7, PO8, best at 1 Hz) and one occipital (Oz, best at 6 Hz) electrodes averaged across odor contexts and infants for natural (Group 1, orange) and simplified (Group 2, purple) stimuli. The general visual response is recorded at 6 Hz and harmonics (i.e., integer multiples, not displayed) and the face-selective response at 1 Hz and harmonics (displayed from 2 to 5 Hz). **B.** and **C.** Amplitude of the face-selective (B) and general visual (C) responses (relative frequency = 0 Hz) and their surrounding noise (± 0.25 Hz) summed across 5 (face-selective) and 4 (general) harmonics and averaged across odor contexts for natural (Group 1, orange) and simplified (Group 2, purple) stimuli. The face-selective response is pooled across two occipito-temporal electrodes (PO7, PO8) and the general visual response is displayed at electrode Oz. The black line represents the mean of the group and colored lines represent individual responses. Topographical head maps (posterior view) illustrate the spatial distribution of the responses. Smaller maps illustrate the lowest responses with an adjusted scale (i.e., face-selective response to natural stimuli in B, general visual response to simplified stimuli in C).

Another neural response is visible in the EEG spectrum at the 1-Hz frequency of face presentation and its harmonics (Figure 2.6A). Contrary to the general visual response, the face-selective response appears especially large and distributed on several harmonics for simplified stimuli (Group 2), while lower and mainly visible at the 1st harmonic (1 Hz) for natural stimuli (Group 1). The response to simplified stimuli is indeed significant until the 5th harmonic (5 Hz) at almost every ROI and for the mean across ROIs (Table S5, Appendix 2), with *Z*-scores ranging between *Z* = 2.64 (*p* = .004, 4th harmonic) and *Z* = 9.24 (*p* < .001, 1st harmonic). Summed across harmonics (Figure 2.6B), it is significant at every ROI and for the mean across ROIs (all *Z*s > 8.77, all *p*s < .001). In contrast, the face-selective response to natural stimuli is almost exclusively significant at the left-hemispheric ROI (lOT) for the 1st and 4th harmonics, which are also the only significant harmonics for the mean across ROIs (1st harmonic: $Z = 2.09$, $p = .018$; 4th harmonic: $Z = 2.19$, $p = .014$; other harmonics: all *Z*s < 1.20, all *p*s > .11). The summed response reaches significance only in the left hemisphere (lOT) and for the mean across ROIs (all *Z*s > 2.37, all *p*s < .009), with a marginal response in the right hemisphere (rOT: $Z = 1.38$, $p = .084$) (Table S5, Appendix 2). Despite this difference between groups, individual infant data (Table S6, Appendix 2) indicated that the face-selective response is driven by a large subset of infants in both groups, 20 infants out of 21 (95%) showing at least one significant electrode within the ROIs for simplified stimuli (Group 2), and 16 out of 21 (76%) for natural stimuli (Group 1).

Direct comparison between groups of infants confirmed that the mean face-selective response across ROIs is significantly much stronger (+350%, Cohen's $d = 1.29$) for simplified than natural stimuli, with an amplitude of 1.50 ± 0.28 µV for Group 2 as opposed to 0.33 ± 0.11 µV for Group 1 (main effect of *Group*: $F(1, 40) = 14.9$, $p < .001$, $\eta_p^2 = 0.27$). For both groups, the face-selective response is larger at lOT than mO ($T(40) = 3.17$, $p = .003$, Cohen's $d = 0.49$) and intermediate at rOT (no difference with the other ROIs, both *T*s < 1.57, both *p*s > .12, both *d*s < 0.25), as indicated by a significant main effect of *ROI* ($F(1.5, 61.5) = 3.91$, $\varepsilon = 0.77$, $p = .035$, $\eta_p^2 = 0.09$) that did not interact with *Group* ($F < 1$). Nevertheless, this spatial distribution is particularly marked in Group 1 (natural stimuli), as lOT (0.58 ± 0.20 µV) represents 58% of the overall response across ROIs *vs.* 28% for rOT (0.28 ± 0.12 µV) and only 14% for mO (0.14 ± 0.15 µV). Topography is more balanced in Group 2 (simplified stimuli) with 38% for lOT (1.71 ± 0.30 µV), 34% for rOT (1.52 ± 0.37 µV), and 28% for mO (1.26 ± 0.27 µV).

In sum, a 6-Hz train of natural visual stimuli triggers a larger medal occipital response than a train of simplified stimuli, whereas the appearance of human faces at 1 Hz within such rapid stimulations elicits a weaker occipito-temporal face-selective response to natural than simplified face stimuli, reflecting more demanding visual categorization for the 4-month-old brain.

3.2 Maternal odor selectively improves the more demanding categorization of natural face stimuli

Visual inspection of the face-selective response dissociated between groups and odor contexts suggests that the mother's body odor enhances the response to natural stimuli (Group 1) over the right occipito-temporal cortex while the response to simplified stimuli is less affected in any region (Figure 2.7A). We indeed found a significant *Odor* × *Group* interaction ($F(1, 40) = 5.19$, $p = .028$, $\eta_p^2 = 0.11$) due to a significant *Odor* effect for natural ($F(1, 40) = 7.66$, $p = .009$, $\eta_p^2 = 0.16$) but not simplified ($F < 1$) stimuli. There was also a significant interaction between the *Odor* and *ROI* factors ($F(2, 80) = 3.14$,

$p = .049$, $\eta_p^2 = 0.07$) revealing an *Odor* effect only at rOT ($F (1, 40) = 9.02$, $p = .005$, $\eta_p^2 = 0.18$; two other regions: both *F*s < 1).

Comparison between odor contexts for each group (type of stimuli) and each ROI confirmed that the face-selective response to natural stimuli (Group 1) recorded at the right occipito-temporal region (rOT) is significantly larger in the maternal (0.62 ± 0.16 µV) than baseline (-0.05 ± 0.16 µV) odor context ($T (20) = 2.95$, $p = .008$, Cohen's $d = 0.64$). In contrast, the advantage for the mother's body odor was non-significant at mO (maternal: 0.30 ± 0.22 µV, baseline: -0.02 ± 0.17 µV, $T (20) = 1.16$, $p = .26$, Cohen's $d = 0.25$) and lOT (maternal: 0.61 ± 0.18 µV, baseline: 0.54 ± 0.27 µV, $T < 1$, Cohen's $d = 0.06$). Interestingly, the face-selective response is entirely distributed at lOT in the baseline odor context, whereas the response is spatially more extended in the maternal odor context with 40%, 40%, and 20% of the overall response across ROIs at lOT, rOT, and mO, respectively.

For simplified stimuli (Group 2), there was also a slight increase (+19%) of the face-selective response with the mother's odor over the right hemisphere (rOT: maternal: 1.66 ± 0.37 µV, baseline: 1.39 ± 0.43 µV) together with a decrease (-18%) over the left hemisphere (lOT: maternal: 1.54 ± 0.29 µV, baseline: 1.88 ± 0.38 µV), but both failed to reach significance (both *T*s < 1.05, both *p*s > .30, both *d*s < .23). Though stronger over the middle occipital cortex (mO), the diminution of the response (-24%) with maternal odor (maternal: 1.08 ± 0.28 µV, baseline: 1.43 ± 0.28 µV) was only a trend ($T (20) = 1.99$, $p = .061$, Cohen's $d = 0.43$). As a result, contrary to Group 1, the topographical distribution of the response across ROIs in Group 2 remains quite stable between odor contexts, with 40% at lOT, 30% at rOT, and 30% at mO in the baseline odor context as opposed to 36% at lOT, 39% at rOT, and 25% at mO in the maternal odor context. To illustrate mean and individual odor effects at rOT in both groups of infants (type of stimuli), Figure 2.7B depicts them as effect sizes (Cohen's *d*s, medium effect for natural stimuli, $d = 0.64$, negligible effect for simplified stimuli, $d = 0.19$).

In sum, while the face-selective response to simplified stimuli (Group 2) does not significantly change with maternal odor, the response to natural face stimuli (Group 1) evolves from a focal activity at left occipito-temporal sites in the baseline odor context to a more widespread response, especially in the right hemisphere, when adding the mother's body odor.

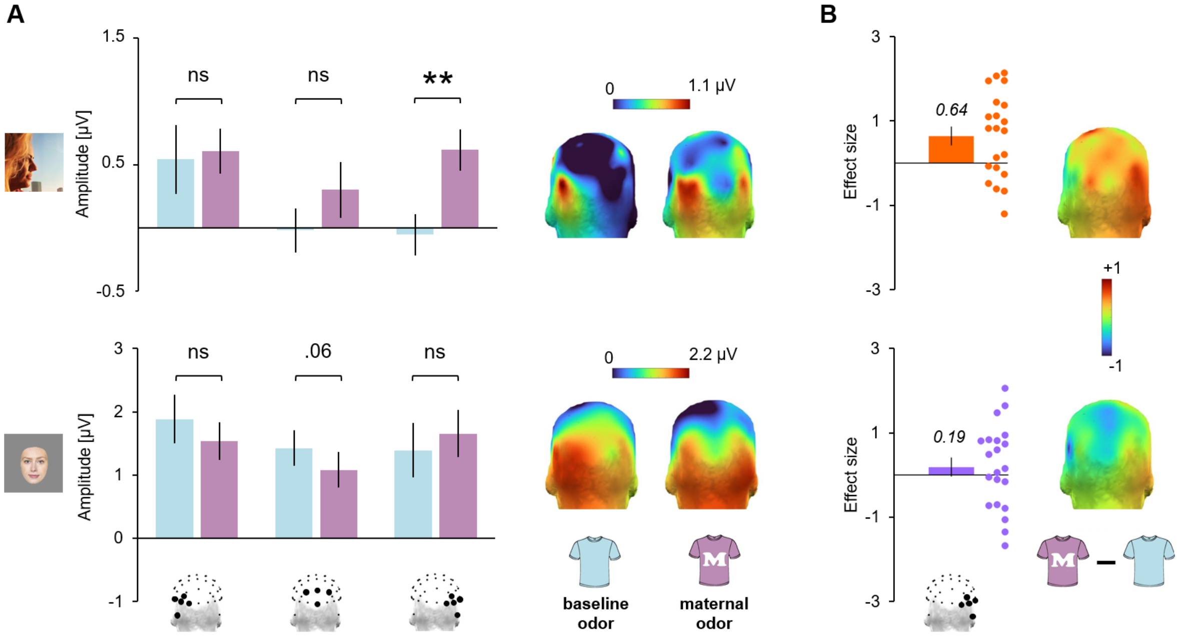

Figure 2.7. Face-selective response to each type of stimuli (group of infants) as a function of the odor context. A. Amplitude of the face-selective response at the left occipito-temporal (lOT: P7, P9, PO5, PO7, O1), medial occipital (mO: POz, PO3, Oz, PO4), and right occipito-temporal (rOT: P8, P10, PO6, PO8, O2) regions for natural (Group 1, top) and simplified (Group 2, bottom) stimuli in the baseline (blue) and maternal (violet) odor contexts. Error bars represent standard errors of the mean (** *p* = .008, ns *p* >. 25, *p* = .06 for mO and simplified stimuli). Topographical head maps (posterior view) illustrate the spatial distribution of the response. **B**. Mean (box) and individual (circles) effect sizes (Cohen's *d*) of the odor effect (maternal – baseline) at rOT. Error bars represent standard errors of the mean and head maps (posterior view) illustrate the topography of the effect size.

Finally, given that the face-selective response to natural stimuli (Group 1) is mainly concentrated on the 1st harmonic (1 Hz) whereas the response to simplified stimuli (Group 2) is distributed on 5 harmonics (from 1 to 5 Hz), we determined whether the odor effect observed at rOT in Group 1 depends on these different frequency representations of the response. When considering only the 1st harmonic (1 Hz, Figure 2.8A), the amplitude of the face-selective response to natural stimuli is still significantly larger in the maternal (0.48 ± 0.15 µV) than baseline (-0.04 ± 0.13 µV) odor context (*T* (20) = 2.38, *p* = .027, Cohen's *d* = 0.52). In contrast, for the summed response across remaining harmonics (from 2 to 5 Hz, Figure 2.8B), we did not find a significant difference between the mother's (0.13 ± 0.12 µV) and the baseline (-0.02 ± 0.09 µV) odors (*T* (20) = 0.92, *p* = .37, Cohen's *d* = 0.20). Similarly, the odor effect on the face-selective response to simplified stimuli is neither significant at 1 Hz (maternal: 1.01 ± 0.29 µV, baseline: 0.84 ± 0.26 µV, *T* (20) = 0.68, *p* = .51, Cohen's *d* = 0.15), nor for the sum from 2 to 5 Hz (maternal: 0.64 ± 0.14 µV, baseline: 0.55 ± 0.22 µV, *T* (20) = 0.48, *p* = .63, Cohen's *d* = 0.11). Hence, the odor effect on the face-selective response to natural stimuli (Group 1) is mainly driven by the 1st harmonic, and no odor effect is masked by harmonic summation for the response to simplified stimuli (Group 2).

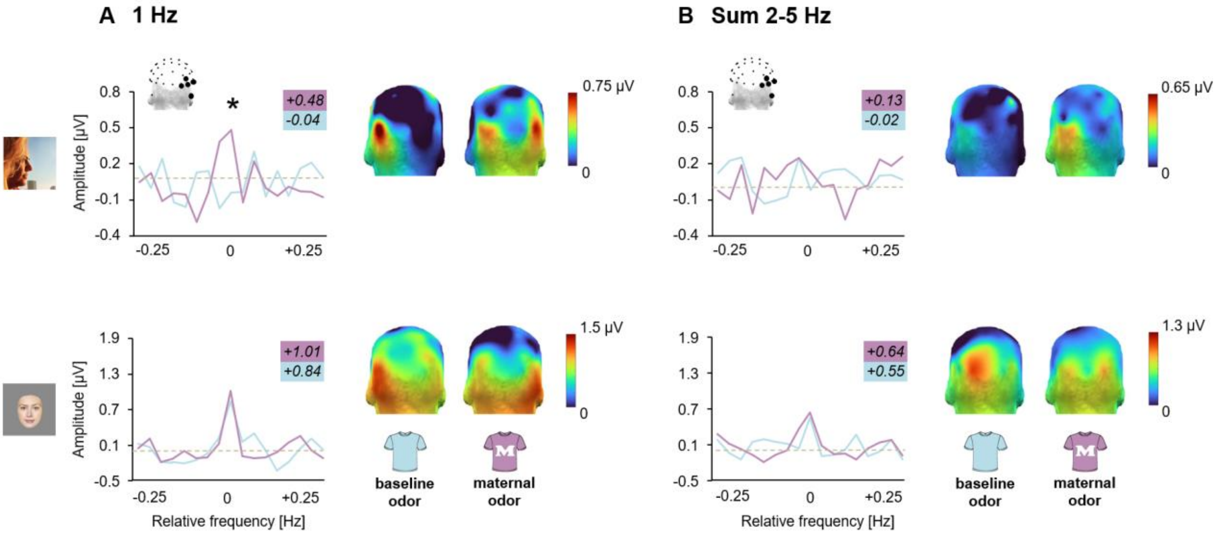

Figure 2.8. First and other harmonics of the face-selective response to each type of stimuli (group of infants) as a function of the odor context. Amplitude of the face-selective response (relative frequency = 0 Hz) and its surrounding noise (± 0.25 Hz) for the 1st (1 Hz, **A**) and for the sum from the 2nd to 5th (2-5 Hz, **B**) harmonics at rOT for natural (Group 1, top) and simplified (Group 2, bottom) stimuli in the baseline (blue) and maternal (violet) odor contexts. The dashed grey line represents 0 µV. Topographical head maps (posterior view) illustrate the spatial distribution of the response. A significant difference between the two odor contexts was found at 1 Hz for natural stimuli (* $p = .027$).

3.3 No odor effect on the general visual response to either type of stimuli

As visible in Figure 2.9, the general visual response to a fast train of natural stimuli (Group 1) is slightly larger with maternal odor while the opposite is apparent for the response to simplified stimuli (Group 2). However, neither the main effect of *Odor* ($F < 1$) nor the *Odor* × *Group* interaction ($F(1, 40) = 1.78$, $p = .19$, $\eta_p^2 = .04$) reached significance.

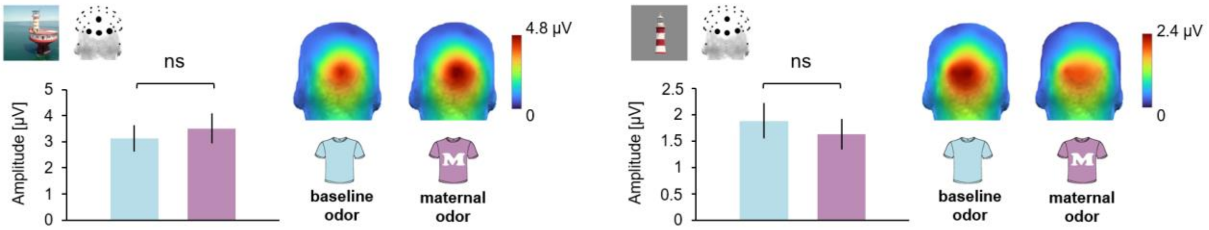

Figure 2.9. General visual response to each type of stimuli (group of infants) as a function of the odor context. Amplitude of the general visual response at the medial occipital region (POz, O1, Oz, O2) for natural (Group 1, left) and simplified (Group 2, right) stimuli in the baseline (blue) and maternal (violet) odor contexts. Error bars represent standard errors of the mean (ns $p > .26$). Topographical head maps (posterior view) show the spatial distribution of the response.

For natural stimuli, the amplitude of the general visual response does not significantly increase in the maternal (3.51 ± 0.58 µV) compared to baseline (3.13 ± 0.51 µV) odor context ($T(20) = 0.80$, $p = .43$, Cohen's $d = 0.18$), and for simplified stimuli, it does not significantly decrease in the maternal (1.63

± 0.29 µV) compared to baseline (1.89 ± 0.34 µV) odor context (*T* (20) = 1.13, *p* = .27, Cohen's *d* = 0.25). Therefore, despite descriptive trends, the general visual response to either type of stimuli remains immune to the presence of the mother's odor.

4. Discussion

By using frequency tagging EEG to measure rapid face categorization in two groups of 4-month-old infants, and by exposing them to their mother's *vs*. a baseline odor, our study provides two major findings. First, the ability to rapidly (i.e., at a glance) categorize a variety of human faces at 4 months depends on the complexity of visual stimuli, improving in simplified (Group 2) compared to natural (Group 1) stimuli. Second, the mother's body odor fosters rapid face categorization only when perceptual demand is high (Group 1, natural stimuli), this effect disappearing when perceptual demand is reduced (Group 2, simplified stimuli). Therefore, our results provide the first evidence that olfactory-to-visual facilitation follows the inverse effectiveness principle in the 4-month-old brain, extending previous behavioral studies that manipulated perceptual demand in audiovisual displays (Bahrick et al., 2010) and generalizing them to olfactory-visual stimulations.

The use of two types of visual stimuli in a frequency-tagging design revealed a clear dissociation between the two tagged brain responses. The general visual response, elicited by the fast 6-Hz stimulation stream, is a large and reliable medial occipital activity recorded for both natural (Group 1) and simplified (Group 2) stimuli. However, it is significantly two times larger for natural than simplified stimuli. This neural activity reflects the mere response to all cues that change 6 times per second, both low- (e.g., contrasts, spatial frequencies) and higher-level (e.g., colors) cues (Norcia et al., 2015). Hence, the high physical heterogeneity across natural stimuli, which depict both an item and its background under variable exposure conditions, triggers a larger general response than the lower physical change across simplified stimuli, which depict items on a uniform grey background and under less variable exposure conditions.

In contrast, the periodic appearance of human faces at 1 Hz within the train of stimuli elicits a clearly (4.5 times) weaker occipito-temporal response to natural than simplified face images, which is mainly left-hemispheric and concentrated on the 1st harmonic for natural stimuli, while more extensively distributed over posterior brain regions and significant for 5 harmonics for simplified stimuli[1]. This face-selective response is a signature of rapid face categorization in the brain – a differential neural activity elicited by the reliable discrimination between the various faces and nonface objects displayed in a sequence (de Heering and Rossion, 2015; Jacques et al., 2016; Rossion et al., 2015). Previous studies using the same approach also found a weak and single-harmonic response to

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[1] Harmonics in the frequency domain represent the complexity (i.e., nonlinearity) of the response in the time domain. A response with several short components in time is represented by several harmonics in the frequency spectrum, whereas a single and slow response is represented by less harmonics (Retter et al., 2021).

natural face stimuli at 4 months (e.g., de Heering and Rossion, 2015; Leleu et al., 2020). Later on, the response to natural faces increases and becomes distributed on more harmonics in older infants (Study 1; Rekow et al., 2023), children (Lochy et al., 2019; Vettori et al., 2019), and adults (Jacques et al., 2016; Rossion et al., 2015), reflecting improved face categorization with maturation and development. Similarly, here, the larger and more complex response to simplified stimuli indicates that edited pictures of faces, all displayed with similar size, viewpoint, expression, background, etc., are more readily categorized than widely variable natural face stimuli. As intended, our simplified stimuli reduced perceptual demand for the 4-month-old brain. In particular, while natural stimuli imply categorization beyond mere physical cues (de Heering and Rossion, 2015), image-based characteristics (e.g., local contrasts) may contribute more to the response to simplified stimuli, as suggested by a greater contribution of the medial occipital region (+14%) compared to natural stimuli.

When dissociating the two odor contexts, the general response to either natural (Group 1) or simplified (Group 2) stimuli remains of similar magnitude, confirming prior evidence that the mother's body odor does not simply enhance attention to the visual stimulation (e.g., Leleu et al., 2020). In contrast, the face-selective response to natural stimuli is only recorded at left occipito-temporal sites in the baseline odor context, and increases in the right hemisphere in the presence of the mother's body odor. This replicates previous studies using the same EEG approach in 4-month-old infants and showing larger right-hemispheric face-selective activity during exposure to maternal odor, either with human faces (Leleu et al., 2020; Rekow et al., 2023) or face-like objects (Rekow et al., 2021). While future studies should delineate which odor cues drive the effect, and whether other body odors can foster face categorization in young infants, as found in adults (e.g., Rekow et al., 2022), this reinforces accumulating evidence that the mother's odor influences face perception in infancy (Durand et al., 2020, 2013; Endevelt-Shapira, 2021; Jessen, 2020).

The mother's body odor is a potent stimulus that promotes a variety of responses from the very beginning of life and often accompanies infants during the first social interactions (Schaal et al., 2020 for review). This could create an intersensory association between maternal odor and (visual) faces from repeated co-exposure, as previously found for faces and voices (e.g., Hyde et al., 2011). At the brain level, this could shape reentrant connectivity between the olfactory system and face-selective regions in the ventral visual stream (Edelman, 1993), as suggested by adult studies showing that the lateral fusiform gyrus, which is part of the face-selective network, responds to body odors (e.g., Zhou and Chen, 2008) and interacts with the primary olfactory cortex ((Zhou et al., 2019). Moreover, the greater contribution of the right hemisphere, dominant for face categorization (Rossion & Lochy, 2021 for review), and more engaged in odor recognition (Brand et al., 2001; Royet, 2004), suggests that the mother's odor triggers a "high-level" response to faces in the right occipito-temporal cortex. This interpretation is also suggested in Group 2 by a trend for a lower contribution of the medial occipital region when simplified face stimuli are perceived in the maternal odor context.

However, and importantly, no maternal odor effect was found for the face-selective response to simplified stimuli (Group 2). This observation remains when the first harmonic is analyzed separately, ensuring that the effect is not masked by the compiled representation of the response across harmonics. Therefore, according to our main hypothesis, olfactory-to-visual facilitation is found only when perceptual demand is high for the 4-month-old brain, i.e., when faces must be rapidly categorized from variable natural stimuli. This extends to olfaction and vision previous audiovisual studies showing that intersensory facilitation depends on unisensory perceptual demand at a given age (e.g., Bahrick et al., 2010). More generally, this accords with the view that intersensory facilitation is mainly observed in young infants, when unisensory perception is not effective by itself, and gradually disappears as unisensory perception develops and improves (Bahrick and Lickliter, 2012), as characterized in the audiovisual domain (e.g., Bahrick and Lickliter, 2004) and recently for olfactory-visual interactions (Study 1; Rekow et al., 2023).

Interestingly, such relative weight of intersensory facilitation along development relates to the inverse effectiveness principle whereby the strength of multisensory integration is a function of the effectiveness of unisensory perception (e.g., Meredith and Stein, 1983; Stevenson et al., 2007)). Indeed, multisensory cues help disambiguate difficult-to-perceive unisensory inputs (Ernst and Bülthoff, 2004). Accordingly, inverse effectiveness is generally evidenced in adults by using ambiguous or degraded stimuli (e.g., Regenbogen et al., 2016; Stevenson et al., 2012). The same has been recently found with olfactory-visual interactions, a body odor facilitating the rapid categorization of ambiguous face-like objects in the adult brain, while the categorization of human faces, which is already effective from the sole visual input, remains immune to the odor effect (Rekow et al., 2022). Hence, by using the reverse approach – making rapid face categorization less demanding – the present study is the first to demonstrate that inverse effectiveness also applies to olfactory-to-visual facilitation in the 4-month-old brain. Future studies should pursue this effort in making face categorization more demanding at an age where no odor effect is observed (e.g., 12 months; Study 1; Rekow et al., 2023), to determine whether olfactory-to-visual facilitation reappears.

In conclusion, we have evidenced the inverse effectiveness of olfactory-to-visual facilitation in the 4-month-old brain using a well-established maternal odor effect on rapid face categorization and making categorization less demanding with simplified stimuli. This generalizes to olfactory-visual interactions previous findings in the audiovisual domain (e.g., Bahrick et al., 2010). Interestingly, this also indicates that the principles subtending how the senses interact apply to olfaction despite dissimilarities with the other senses. In particular, odor perception relies less on spatiotemporal synchrony compared to vision and audition (Sela and Sobel, 2010). This means that contrary to audiovisual perception, which strongly relies on spatiotemporal synchrony in infants (Lewkowicz, 1996; Neil et al., 2006; Werchan et al., 2018), olfactory-visual interactions operate on a broader spatiotemporal relation that does not hamper their association, and may even favor categorization by increasing generalization across variable signals. This should be further investigated by comparing the ability of odors and sounds to improve visual categorization. In sum, our findings indicate that odors participate in the concert of the senses from early on and help young infants to navigate their complex environment when unisensory perception is not effective by itself.

Study 3. When maternal odor impedes visual categorization in the 1-year-old infant brain: A case of sensory overload?

Abstract

Visual face categorization (i.e., discriminating faces from other objects and generalizing this discrimination across individual faces) follows a protracted development and recent evidence shows, this important visual ability is modulated by maternal body odor as a function of age. In line with the principle of inverse effectiveness, it shows that the weak visual response of young 4-month-old (but not 12-month-old- infants) is correlated to the strongest olfactory-visual interaction. However, whether this principle applies at a given age as a function of visual demand and relying on the same stimuli still needs to be addressed. The present study thus aims to test this hypothesis by manipulating visual demand during face categorization in two groups of 12-month-old infants. Relying on frequency-tagging coupled with EEG as in previous studies, one group (Standard condition) was presented with streams of 6 images per second (6-Hz sequences) with faces inserted every 6th stimulus to tag a face-selective response (1000 ms interval between faces); while the other group (Fast condition) was presented with a doubled speed rate (12-Hz sequences) with faces inserted every 9th stimulus (750 ms interval) to increase visual demand. During visual stimulation, infants in both groups were exposed to a T-shirt worn by their mother or to a control T-shirt. Our findings reveal that by raising visual demand in the Fast group, despite a decrease of the visual response, we observed a negative maternal body odor effect. These results are discussed in light of the sensory overload hypothesis.

1. Introduction

Intersensory interactions and multisensory perception set on from an early age in human development. For example, newborns can detect cross-modal relationship between auditory and visual cues basing on their intensity (Lewkowicz & Turkewitz, 1980). Likewise, newborns more easily acquire a sight-sound association when the stimuli are temporally-bound, as well as when they are spatially congruent (Morrongiello et al., 1998). Such spatiotemporal synchronization is in line with the basic principles of multisensory integration (Meredith & Stein, 1986; Meredith et al., 1987): newborn infants can already exploit the fact that the properties of multisensory objects/events are correlated in space and time instead of being arbitrarily spread in the environment.

Such early multisensory binding of distinct sensory cues could be partly understood in the context of the Intersensory Redundancy Hypothesis (IRH) (Bahrick & Lickliter, 2000), with the assumption that infants are capable to detect *amodal* proprieties which are common across several sensory modalities (e.g., synchrony, rhythm, intensity). Bahrick & Lickliter suggest that amodal information is redundantly specified and attracts attention during initial learning when infants bind different object features across the senses into a unified percept. It allows them to detect salient amodal properties in bimodal synchronous stimulation more efficiently than in unimodal ones. For example, 3 month-old infants are able to detect a change in the tempo of tapping only during synchronous bimodal stimulations (video and sound of hammer) compared to the asynchronous, or unimodal conditions (video only) (Bahrick et al., 2002). The same results were observed with prosody (Bahrick et al., 2019) and emotional affect detection of audiovisual speech (Flom & Bahrick, 2007), showing an advantage of synchronous multisensory condition at 4 months. However, intersensory facilitation changes with age and seems to depend on the difficulty of the task: indeed, contrarily to 3-month-olds, Bahrick & Lickliter (2004) found that 5-month-olds efficiently detect a hammer-tapping change during both types of stimulation (i.e., uni- and bimodal) without using intersensory facilitation. Besides developmental improvement, the difficulty of the task at a given age also leads to a shift in intersensory facilitation. Indeed, increasing the visual demand of discriminating the hammer tapping (i.e., decreasing the contrast between the two presented tempos) enforced 5-month-olds to rely on intersensory facilitation in the same way as 3-month-olds did in the easier discrimination task (Bahrick et al., 2010).

Aforementioned results relate to the principle of inverse effectiveness (Meredith & Stein, 1983), implying that sensory systems that become sufficiently effective on their own would to perceive an object no longer need any reliance on cues from the other senses, and hence on multisensory integration, to reach an effective percept. The sense of vision may function according to this principle. The human visual system follows a protracted development over the first year (Braddick & Atkinson, 2011), while the other sensory systems are functional and provide rich information already from the fetal stage (Graven & Browne, 2008; Schaal et al., 2004; Turkewitz & Devenny, 1993). Thus, during the first months after birth, infants' visual cognition might benefit of multisensory tutoring, while this tutoring might decrease by the end of the first year with the improvement of visual processing. To date, this inverse effectiveness principle was mainly investigated in the context of audio-visual integration. Humans do indeed easily bind information from these two senses due to their high attentional potential along both spatial and temporal dimensions. However, not all sensory systems function along the same criteria. For example, olfaction being not as time-locked as vision or audition, and its cuing of spatial coordinates being less accurate than visual/auditory cues, it may induce a more stable perception, less bound by spatiotemporal parameters (Sela & Sobel, 2010). This relative spatiotemporal stability of odors, along with their reassuring effects, make them ideal contextual cues for perceptual learning in infancy, which benefits from long presentation times. Odors, especially familiar odors, do also stabilize the infants emotional state, reducing high-arousal states, favoring indirectly attention mediated by the other senses. Familiar odor cues, as maternal body odor, evoke indeed episodes of eye opening in neonates (Doucet et al., 2007), which may help early multisensory binding in social situations. Accordingly, maternal body odor increases visual preference for faces in 4-month-old infants (Durand et al., 2013) and decreased the neural response to fearful faces in 7 month-olds (Jessen, 2020).

Using frequency-tagging electroencephalography (EEG) and fast stimulus presentation (e.g., 6 images per second to elicit a 6 Hz visual response in the EEG spectrum), other studies reported that maternal odor facilitated the rapid categorization of faces (Leleu et al., 2020) or face-like objects (Rekow et al., 2021), but not of cars in the 4-month-old brain (Rekow et al., 2020) (i.e., discriminating a given category from various exemplars and generalizing across them). But this multisensory interaction seems to be linked with the task difficulty, since the odor effect was decreasing while face-selective response was increasing with age in the 4-12 month range (Study 1; Rekow et al., 2023). Moreover, no odor facilitation was found in adults for which the face-selective response was equally strong in presence or absence of (stranger's) body odor (Rekow et al., 2022); however, when the visual demand was heightened in adults in using ambiguous face-like stimuli, intersensory facilitation (i.e., the odor effect) emerged again (Rekow et al., 2022), probably because the visual cues were not efficient enough. Conversely, in 4 month-old infants whose face-selective response elicited by naturalistic faces was enhanced in the presence of mother's odor (Leleu et al., 2020), this odor effect was suppressed with simplified visual stimuli (i.e., full-front neutral faces cropped from background), leading to a more efficient face categorization than with the sole visual stimulation (Study 2). Overall, the contribution of olfaction appears not always necessary to categorize a visual object, but can help when the visual stimulus is degraded.

However, aforementioned studies exploring olfacto-visual interactions using frequency-tagging EEG have directly manipulated the difficulty of the visual categorization task by changing the types of stimuli: (i.e., faces vs. face-likes, natural vs simplified pictures). The confirmation that, in line with audio-visual interaction studies (Bahrick et al., 2010), olfacto-visual interaction is directly bound to the demand of the visual task is awaited. To do so, the present study evaluated the inverse effectiveness principle was applicable to face categorization tasks in 12-month-old infants presented with maternal odor. Considering that at this age, infants show a reliable face-selective response to streams of 6 Hz images with faces tagged every 6th stimulus, we rendered the visual stimulation more difficult to process in doubling the rate of stimulation (i.e., 12-Hz stream of stimulation). Due to the constraints inherent to infant neuroimaging studies, these sequences were tested in a between-subject paradigm, one group being exposed to Standard 6-Hz sequences while the other is exposed to the Fast 12-Hz sequences (optimally used in adults, Retter et al., 2020; e.g., Rekow et al., 2022). Importantly, we kept the same types of stimuli across Standard or Fast visual sequences, but their presentation time on screen were 167 ms (Standard) or 83 ms (Fast). In addition, faces were inserted at different rates as 6th stimulus for the Standard condition (i.e., face presentation rate: 1 Hz, interval between faces: 1000 ms) and as 9th stimuli for the Fast condition (i.e., face presentation rate: 1.33 Hz, interval between faces: 750 ms). Thus, the Standard condition provides a less demanding face categorization than the Fast condition. Accordingly, we hypothesize that: (1) the face-selective responses in the Fast condition («Fast group») should be lower compared to the Standard condition («Standard group») because of a higher visual demand, and (2) a maternal odor facilitation (positive odor effect) should emerge only in the Fast group demonstrating a trade-off between vision and olfaction.

2. Material and methods

2.1 Participants

Fifty-nine full-term infants aged between 11 and 13 months were recruited through the local birth registry. Interested parents contacted us for information completion on the objectives and methods of the study and, if willing to participate, they were sent the material for collecting the maternal body odor. All parents gave written informed consent, and none reported their infants have any visual, olfactory, neurologic, or psychiatric disorder. Procedure of testing was performed according to the Declaration of Helsinki and approved by a French ethics committee (CPP Sud-Est III - 2016-A02056-45). Data from ten infants were excluded based on their completion of less than two valid sequences per odor context (N = 4) or on too many artifacts in EEG recordings (N = 6). The final sample thus contained of 26 infants for Standard group (7 females, mean ± SD: 378 ± 22 days, range: 339–411 days) and 23 infants for Fast group (11 females, mean ± SD: 381 ± 22 days, range: 346–420 days). Both groups did not significantly differ in terms of age (T (47) = 0.6, $p = .58$).

2.2 Visual stimuli

We used naturalistic photographs of various living and non-living objects (animals, plants, man-made objects: N = 368) and human adult faces (N = 92, 46 females). The images contained a single item embedded in the natural background of the image and present in variable colors, viewpoints and lighting conditions. Images were cropped to a square and resized to 400 × 400 pixels. Each item (objects or faces) was more or less off-centered in the square image, as visible from examples in Figure 2.10A. The distance from the infant's face to the computer screen was set at 57 cm so that images subtended a visual angle: 24 × 24°, which represents a large area of the infants' visual field.

2.3 Odor stimuli

Following maternal odor collection procedure described in previous studies (Durand et al., 2013; Leleu et al., 2020; Rekow et al., 2020, 2021), we sent t-shirts to participating families 10 days before the experiment day to collect maternal odor. During collection period, we asked the mothers 1) to wear the t-shirt on bare skin for three consecutive nights before testing, 2) to refrain from using odorous soap or perfume, and 3) to store the t-shirt in the hermetic bag at room temperature but at distance from any heating device. Before the collection of the maternal odor, the t-shirts were laundered at the laboratory using a scentless hypoallergenic powder detergent (Persavon, France). The same washing procedure was realized for the t-shirts of the baseline odor context. After that, all t-shirts were stored in a hermetic zip-lock plastic bag in our premises. During the experiment, each infant was exposed to two odor contexts: 1) maternal and 2) baseline odor delivered by the worn and unworn white t-shirts (100% cotton), respectively (see Procedure described below).

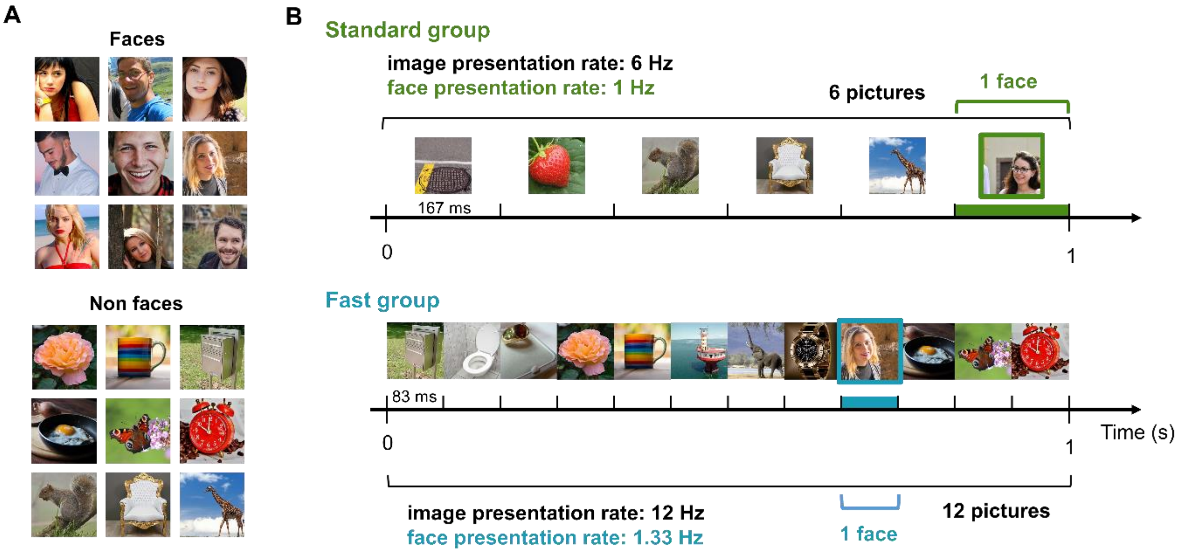

Figure 2.10. Frequency-tagging EEG approach to measure the inverse effectiveness of maternal odor on rapid face categorization. A. Examples of the naturalistic pictures containing human faces (N = 92, 46 females) (left) and nonface base objects (N = 368) (right). **B.** 1-s excerpt of fast periodic visual stimulation (from 30-s-long sequences) showing for the Standard group, 6 images/s (i.e., a 6-Hz base rate; stimulus duration: 167 ms) with faces interspersed as every 6th stimulus (1-Hz face-selective rate; 1000-ms interval between two faces) (top) and 12 images/s (i.e., a 12-Hz base rate; stimulus duration: 83 ms) with faces interspersed as every 9th stimulus (1.33-Hz face-selective rate; 750-ms interval between two faces) in the Fast group (bottom).

2.4 *Procedure*

The same procedure as in previous frequency-tagging EEG studies (Leleu et al., 2020; Rekow et al., 2020, 2021) was used in both experimental groups. After placement of electrode cap, infants were seated on their parent's (99% mothers) lap in front of the screen in a light- and sound-attenuated room with an air-extractor which continuously and silently renewed the air. Parents were provided protection blouse and disposable nitrile gloves (Schield Scientific, The Netherlands) to mask their odor. To reduce the presence of olfactory noise, the room was well aired between testing sessions and experimenters did not use, eat, or drink any odorous product before testing. For delivering the odor contexts, we disposed the T-shirt on the infants' upper chest, just before a sequence began, using dedicated disposable nitrile gloves. Each infant was tested in the two odor contexts alternated every two sequences, interleaved by a minimum interval of 1 min. Odor presentation order was counterbalanced across infants.

Visual stimuli were presented in the center of 24-inch LED screen (refresh rate: 60 Hz, resolution: 1920×1080 pixels, gray background: 128/255 in grayscale) at a viewing distance of 57 cm, thus subtending 24 × 24° of visual angle for the visual stimuli. They were presented at base rate of 6 Hz (6 images per second) or 12 Hz (12 images per second) without inter-stimulus interval with a fixed stimulus duration: 167 ms (i.e., 1 s/6) or 83 ms (i.e., 1 s/12) according to the Standard or Fast group, respectively. Faces were inserted every 6th (rate of 6 images /6 = 1 Hz with 1000 ms between two faces) or 9th stimuli (rate of 12 images/9 = 1.33 Hz with 750 ms between two faces) also according to each condition (Figure 2.10B). Due to this a-priori-defined periodicity of stimulation, we could isolate in the EEG spectrum of each group two distinct brain responses at these two different frequencies: a general visual response at the base frequency of stimulation (i.e., 6 or 12 Hz and harmonics (i.e., integer multiples)) and a face-selective response at the lower frequency (i.e., 1 or 1.33 Hz and harmonics). The general visual response reflects the common visual activity in response to all presented stimuli (e.g., color, shape, texture, etc), while the face-selective response is the differential neural activity elicited by faces among the non-face stimuli and consistently generalized across the face exemplars present within each sequence resulting in a single-glance (i.e., rapid) face categorization (e.g., de Heering & Rossion, 2015; Rossion et al., 2015).

Visual sequences lasted 34.5 s including a fixed pre-stimulation interval (0.5 s), fade-in (2.833 s), stimulation (29.417 s), fade-out (1.25 s) and a fixed post-stimulation interval (0.5 s). For each condition, the set of faces were split into 2 or equal distribution (i.e., Standard group: 34 faces including 17 females; Fast group: 46 faces including 23 females) and were randomly assigned to one sequence during the testing of one odor context. The set of nonface stimuli were used in all sequences of the respective condition. Each set of the nonface images was alternatively assigned with one of the two sets of the face images. During the experiment, the infants were reoriented towards the screen using short sounds (e.g. bike ring or squeak of rubber toys) launched manually if they diverted their gaze from the screen. To estimate the validity of sequences to be included in the analyses, we verified if they elicit a general visual response (see ‘EEG recording and preprocessing’). The 49 included infants performed between 4 and 16 sequences each (mean ± SD: 8 ± 2.6 sequences), for an overall stimulation duration ranging from 2 min 18 s to 9 min 12 s per infant and was not differ between conditions (T (47) = 0.8, p = .45).

2.5 EEG recording and preprocessing

EEG was recorded from a 63 Ag/AgCl electrode cap (Waveguard, ANT Neuro, The Netherlands) according to the 10-10 classification system (acquisition reference: CPz, ground: AFz, initial impedance < 30 kΩ, initial sampling rate: 1000 Hz) (Figure S1, Appendix 3).

EEG analyses were run on Letswave 6 (http://www.letswave.org/) carried out using Matlab 2017 (MathWorks, USA). For the first step we used a Butterworth filter (highpass filter, low cutoff: 0.1 Hz, 4th order) applied to individual datasets. Then we downsampled each one to 200 Hz to reduce file size. Next, we cropped the sequences from the beginning of the fade-in until the end in 34.5-s segments (6900 bins). To correct high-amplitude the artefacts we applied the *Artefact Blocking* algorithm (Fujioka et al., 2011; Mourad et al., 2007) on individual epochs with a threshold of ± 250 µV. Datasets were further screened for remaining artifacts, following visual screening no data required interpolation and using Independent Component Analysis (ICA, computed with a square mixing matrix with algorithm RUNICA and 32 defined IC) we identified eye-blinks in a single IC and removed them in 2 infants. We thus cropped the sequences from the end of fade-in (first image of the full-contrast phase) until the end of the fade-out in 30-s-long epochs (that equivalent to 30 for 1 Hz and 40 for 1.33 Hz cycles of face presentation) and datasets were re-referenced according to a common average reference.

To increase signal-to-noise ratio (SNR), we excluded unusable epochs at individual level using data-driven criteria identifying segments without a general visual response, which is a marker of infant's attention during visual stimulation (Peykarjou, 2022). In this intermediate step, a fast Fourier Transform (FFT) was applied to each individual epoch of each participant, and surrounding noise [estimated from 6 neighboring bins, selected among the 10 surrounding bins (5 on each side, ± 0.167 Hz) after the exclusion of the 2 immediately adjacent and the 2 extreme (minimum and maximum) bins]. Next, we calculated the Z-score as the difference between the amplitude at the frequency of interest and the mean amplitude of 20 neighboring bins (selected among 22 surrounding bins beyond those used for baseline correction (11 on each side, from ± 0.19 Hz to ± 0.5 Hz) after the exclusion of the two extreme bins), divided by their standard deviation (SD). Z-scores were extracted for the medial occipital area (as typically observed over channels: POz, O1, O2, Oz) and for the first (6 or 12 Hz) and the second (12 or 24 Hz) harmonic of the general visual response of the Standard or Fast group, respectively. Individual epochs were retained for further analyses if 2 (out of 8) Z-scores were above 1.64 ($p < 0.05$, one-tailed, signal > noise). For Standard group, the final number of epochs ranged between 2 and 8 epochs, with an overall rejection of 20/229 (i.e. 9 %) and for Fast group, it ranged between 2 and 7 epochs, with an overall rejection of 33/216 (i.e. 15 %). After having identified the epochs to exclude, the data from the previous step (just after the re-reference step) were sorted out individually according to the odor context (baseline or maternal odor), and averaged in the time domain to obtain one single 30-s epoch per context for each infant. The remaining average number of sequences was of 4.1 ± 1.4 in the baseline odor context and 4.0 ± 1.6 in the maternal odor context for the Standard group (and 4.1 ± 1.6 for the baseline odor context and 3.8 ± 1.3 for the maternal odor context for Fast group.

2.6 EEG frequency-domain analysis

For the frequency-domain analysis, we first applied fast Fourier transform (FFT) to the individual datasets and extracted raw amplitude spectra for all electrodes with a frequency resolution of 1/30 s ≈ 0.033 Hz. Next, we subtracted the surrounding noise from 6 neighboring bins (see definition above). Then, we defined the number of harmonics (i.e., integer multiples) required for the evaluation of general visual and face-selective response separately. For this purpose, we calculated Z-scores on the average across odor contexts and across all individual datasets (respective to each group) for the 63 channels pooled together as the difference between the amplitude at the frequency of interest and the mean amplitude of 20 neighboring bins (see definition above), divided by their standard deviation (SD). We considered harmonics until Z-scores were no longer consecutively significant ($Z > 1.64$, $p < .05$, one-tailed, signal > noise) (de Heering & Rossion, 2015). For the general visual response range of significant harmonics amounted until 24 Hz in both groups (i.e., 4 and 2 consecutive significant harmonics in Standard and Fast groups, respectively, Table S4, Appendix 3). However, the face-selective response was distributed on 5 consecutive significant harmonics in the Standard group (i.e., from 1 to 5 Hz) and only on a single significant harmonic in the Fast group (i.e., 1.33 Hz) (Table S1, Appendix 3). We compiled each response by summing significant harmonics according to the highest range across groups to obtain an overall presentation of both brain responses (Retter et al., 2021). Further mentions (6 Hz or 12 Hz and 1 Hz or 1.33 Hz) referred to each sum across their respective number of harmonics. Thus, the general visual response refers to the sum of 4 or 2 harmonics for the Standard or Fast group respectively (i.e., up to 24 Hz in both cases), while the face-selective response will be summed across 5 or 4 harmonics according to the condition to cover a comparable range in the spectrum from 1 to 5 Hz (i.e. 1 Hz * 5 = 5 Hz and 1.33 Hz * 4 = 5.32 Hz).

For the second analytic step, we identified regions of interest (ROIs) to be used in following analyses. Z-score were here calculated (see above) across odor contexts and for posterior channels only (N = 21) (Figure S1) because both brain responses are located over this region (e.g., de Heering & Rossion, 2015; Leleu et al., 2020). *Z*-scores were estimated as significant when $Z > 2.82$ ($p < .05$, one-tailed, signal > noise, Bonferroni-corrected for 21 electrodes). For the face-selective response, 19 (all *Z*s > 3.34) and 13 (all *Z*s > 3.20) electrodes were significant in the Standard and Fast group, respectively. Among them, we selected the 8 best electrodes (all *Z*s > 4.40, Table S2, Appendix 3) common to both groups considering only significant contralateral pairs. It resulted into two ROIs: the right (rOT: P8, P10, PO6, PO8) and the left (lOT: P7, P9, PO5, PO7) occipito-temporal regions. For the general visual response, every electrode was significant in both conditions (all *Z*s > 11.14, Table S2, Appendix 3). We thus kept the 4 best electrodes composing a single ROI: the middle occipital region (mO: POz, O1, Oz, O2) and identical to previous studies (Leleu et al., 2020; Rekow et al., 2020, 2021)

Finally, both brain responses were quantified in a single value expressed in microvolts (µV): the amplitudes were directly extracted for the channels of every ROI, infant and group in each odor context. Repeated-measures ANOVAs on individual amplitudes were calculated separately for the face-selective and the general visual response in two independent analyses. (1) A first analysis aimed to quantify the differences in brain activity between groups (i.e., Standard vs. Fast) irrespective of odor context: for the face-selective response the *Hemisphere* (RH, LH) was used as within-subject factor, and *Group* (Standard, Fast) as a between-subject factor, for the general visual response an ANOVA included only between-subject factor of *Group* as we used a single ROI (mO). All individual amplitudes were averaged across odor contexts. According to the different levels of visual demand in the two visual conditions, we expected that the amplitude of the face-selective and the general visual response might be highly different between the Standard and Fast groups. Thus, the Odor effect might be masked by the largest responses in the omnibus ANOVA for the weak face-selective and general responses in the Fast condition. To avoid that, we have run a repeated-measures ANOVA for the second time but on normalized data by subtracting the mean amplitude across odor contexts from individual datasets (more details about normalization in Study 2) For this purpose from all individual amplitudes we subtracted the group mean of hemispheres and odor contexts and divided it by the group standard deviation. (2) The second analysis sought to evaluate the influence of the odor contexts in each group, respectively: for the face-selective response *Hemisphere* (RH, LH) and *Odor* (baseline, maternal) were used as within-subject factors and for the general visual response only *Odor* (baseline, maternal) as single within-subject factor as we used a single ROI (mO). Significant interactions were further described using orthogonal contrasts. For all ANOVAs, if Mauchly's test yielded sphericity violation, Greenhouse-Geisser corrections for degrees of freedom were applied and reported whenever necessary (ε). Effect sizes are specified with partial eta squared (ηp^2) and tests use a significant threshold of $p < .05$.

To illustrate the differences of brain responses between the two odor contexts, we also calculated the odor effect by subtracting the amplitude in the baseline odor context to the amplitude in the maternal odor context for each infant in each group. Then, Cohen's *d*s were computed to estimate the strength of the odor effect over the occipito-temporal area (OT).To do so, individual odor effects were divided by the standard deviation of the odor effect of each group. In addition, T-tests were performed as paired comparisons. Next, to verify that the odor effect is specific for the face-selective response, we normalized all individual amplitudes and divided them by the group's mean of the general visual response according to the odor context. Computed Cohen's *d*s allowed us to estimate the strength of the odor effect over OT before and after this normalization by general visual response. In the case of a declining effect size after normalization, it would indicate that the odor effect is not specific of the face-selective response and lowers the visual attention of participants to the sequence of stimulation.

3. Results

3.1 The face-selective and general visual responses depend on visual demand in the 12-month-old infant brain

The first analysis aimed to compare the effect of visual demand through the speed of stimulation, across groups. We observed significant face-selective responses in EEG spectra for both visual conditions (Figure 2.11A). Across odor contexts and all channels, the face-selective neural response was significantly distributed at the 1-Hz frequency of face presentation and its subsequent harmonics (i.e., from 2 to 5 Hz) (all *Z*s > 4.80, all *p*s < .001) in the Standard group, while in the Fast group, it was significant only for the 1st harmonic (1.33 Hz) (Z = 5.09, p = .005, one tailed) (Table S1, Appendix 3). Thus, to obtain a compiled representation of the brain response (Retter et al., 2021) while having an even comparison across groups, we summed the face-selective response of each group for the maximum number of significant harmonic across them (i.e., from 1 Hz to 5 Hz, as obtained in the Standard group). Accordingly, the summed response across five and four harmonics for Standard and Fast group (Figure 2.11B), respectively, was also highly significant (Standard: Z = 13.33, p < .001) and (Fast: Z = 7.91, p < .001). Individual data were obtained for both groups: in the Standard, 18 infants presented a significant response (Z > 1.64, p < .05, one tailed) over bilateral occipito-temporal cortex (OT) and another 3 infants over at least one electrode from OT (as Z scores were calculated for OT area and for all electrodes from OT separatally). In other words, 21/26 (i.e., 82%) infants present a significant response to faces. In the Fast group, 15 infants presented a significant response (Z > 1.64, p < .05, one tailed) over OT and another 4 infants over at least one other electrode from OT, resulting in 19/23 (i.e., 82%) infants with a significant face-selective response (Table S3, Appendix 3). No effect of *Hemisphere* was noted (F(1, 47) = 1.65, p = .20, η_p^2 = .03) but, as expected from visual inspection, the face-selective response was stronger in the Standard compared to the Fast group with a mean amplitude of 2.14 ± 0.30 (SEM) µV vs. 0.93 ± 0.18 µV, respectively (Figure 2.11B) as revealed by the main effect of *Group* (F(1, 47) = 10.02, p = .003, η_p^2 = .18).

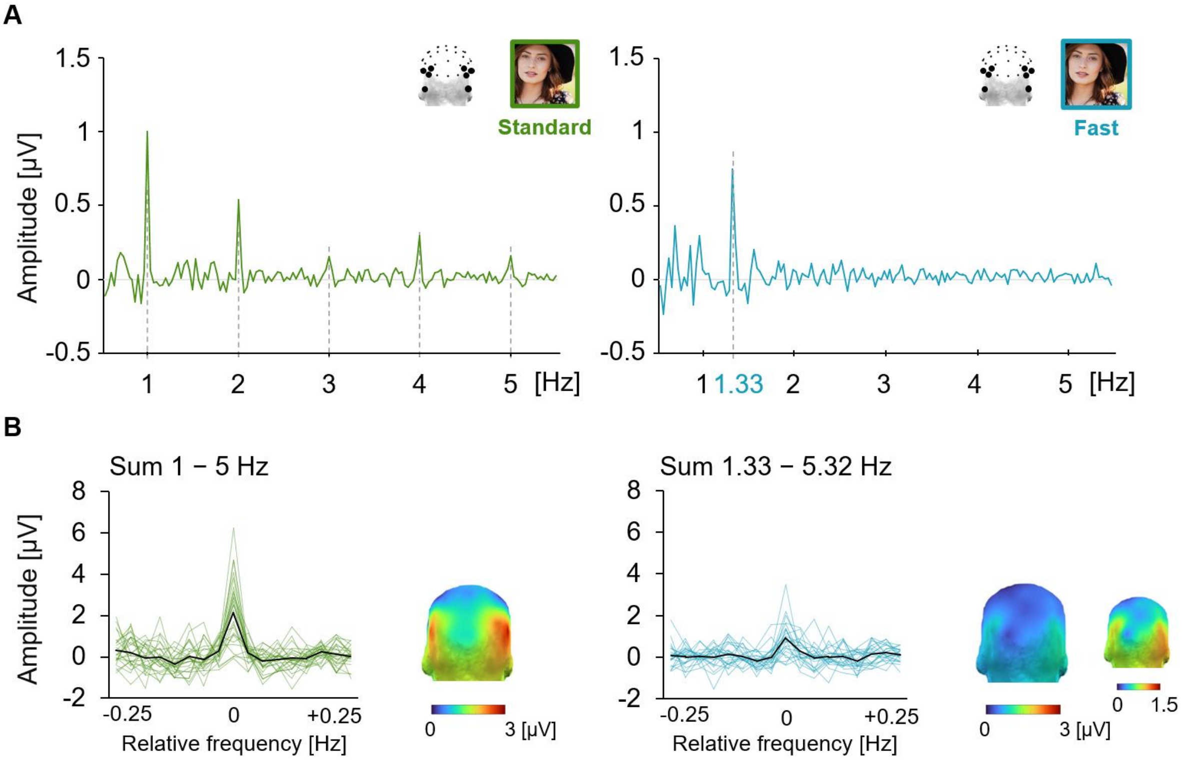

Figure 2.11. Face-selective response in Standard and Fast groups. A. Mean amplitude spectra averaged across odor contexts and infants for Standard Group (left, green) and Fast Group (right, blue) conditions. The amplitude is averaged from the best 8 occipito-temporal electrodes (P7, P9, PO5, PO7, P8, P10, PO6, PO8). In both groups, clear responses (larger than surrounding frequencies) are visible at the predefined frequencies (1-Hz face-selective frequency and its harmonics for Standard, and 1.33 Hz for Fast). **B**. Amplitude spectra summed across harmonics and compared to surrounding frequencies (± 0.25 Hz, amplitude ≈ 0, signal ≈ noise) in the Standard (left, green) and in the Fast (right, blue) groups. The black line represents the mean of the group and colored lines represent individual responses. 3-D topographical head maps demonstrate the spatial distribution of the responses (back view). Smaller maps illustrate the lowest responses with an adjusted scale.

The general visual response is also clearly visible in the EEG spectra (Figure 2.12A). Across all channels and odor contexts, the 6-Hz visual stream in the Standard condition was significantly distributed until the 4th harmonic (i.e. 24 Hz), while the 12-Hz visual stream in the Fast condition, it was significantly distributed until the 2th harmonic that represented the same frequency range: 24 Hz (all *Z*s > 8.71, all *p*s < .001, (Table S4, Appendix 3). Accordingly, summed across these four and two harmonics, the general visual response was highly significant (Standard group: Z = 65.45; Fast group: Z = 63.71, p < .001). Such a robust response was confirmed by individual infant data demonstrating that every single infant has a significant response in both visual conditions (i.e., Z > 1.64, p < .05, one tailed) over the mO electrode (Table S5, Appendix 3). We observed a stronger mean amplitude in the Standard than in the Fast group (2.98 ± 0.35 µV vs 1.29 ± 0.20 µV, respectively) (Figure 2.12B) as revealed by a main effect of *Group* (F(1, 47) = 13.70, p < .001, η_p^2 = 0.23).

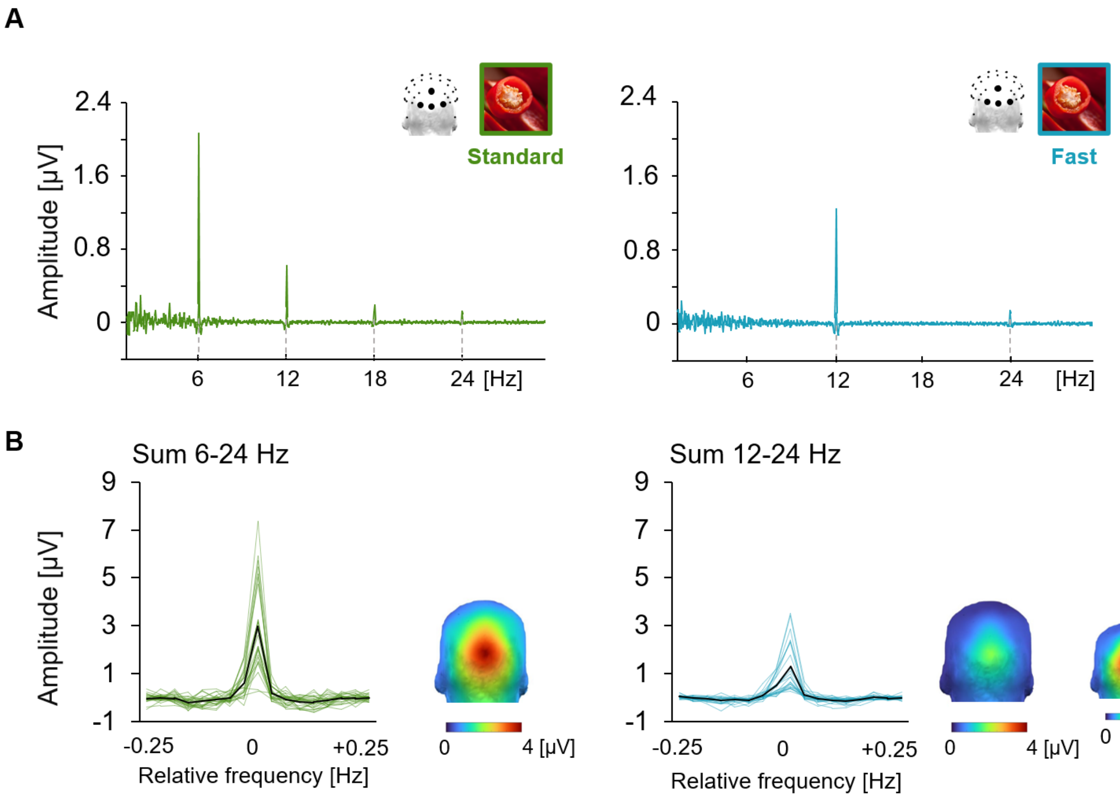

Figure 2.12. General visual response in Standard and Fast groups. A. Mean amplitude spectra averaged across odor contexts and infants for Standard (left, green) and Fast group (right, blue) conditions. The amplitude is averaged across the best 4 middle occipital electrodes (POz, Oz, O1, O2). **B**. In both groups, clear responses (larger than surrounding frequencies) are visible at the predefined frequencies (6-Hz general rate of stimulation and harmonics for Standard and 12 Hz and harmonics for Fast). **B**. Amplitude spectra summed across harmonics and compared to surrounding frequencies (± 0.25 Hz, amplitude ≈ 0, signal ≈ noise) in the Standard (left, green) and in the Fast (right, blue) groups. The black line represents the mean of the group and colored lines represent individual responses. 3-D topographical head maps demonstrate the spatial distribution of the responses (back view). Smaller maps illustrate the lowest responses with an adjusted scale.

3.2 Maternal odor reduces the face-selective and general visual responses under higher visual demand

As we detected a significant difference of Group on the amplitude of both the face-selective and general visual responses, we normalized individual amplitudes (see Material and Methods) before running a repeated-measures ANOVA using the factor of *Odor* (baseline, maternal) to avoid missing the odor effect due to too weak amplitudes in the Fast condition.

First, we investigated the face-selective response and found a significant interaction: *Odor × Group* (F(1, 47) = 5.96, p = .018, ηp^2 = .11 due to a significant *Odor* effect for the Fast (F(1, 47) = 5.68, p = .021), but not for Standard (F(1, 47) = 1.06, p = .31) group. Comparison between odor contexts demonstrated a significant negative difference between amplitudes of the face-selective response in the maternal (0.73 ± 0.21 µV) vs. baseline (1.18 ± 0.20 µV) odor contexts (T = -3.66, p = .001; Cohen's *d* = -0.76) recorded over the bilateral occipito-temporal cortex (OT) in the Fast Group (Figure 2.13B, bottom). Interestingly, we found a significant decrease of face-selective response in maternal odor context by -0.52 ± 0.18 µV (T = -2.94, **p = .008) over left occipito-temporal cortex (lOT) and a marginal decrease of -0.39 ± 0.20 µV (T = -1.95, p = .064) over right occipito-temporal cortex (rOT), however, no effect of *Hemisphere* was detected (F(1, 47) = 1.79, p = .19, η_p^2 = .04) (Figure 2.13A, bottom). In contrast, the face-selective response in the Standard group non-significantly increases over both hemispheres (OT) (T = 0.84, p = .41; Cohen's *d* = +0.16) in the presence of the odor (Figure 2.13B, top) by +0.39 ± 0.43 µV and by +0.23 ± 0.43 µV, (T = 0.90, p = .38 and T = 0.53, p = .60) for lOT and rOT respectively (Figure 2.13A, top).

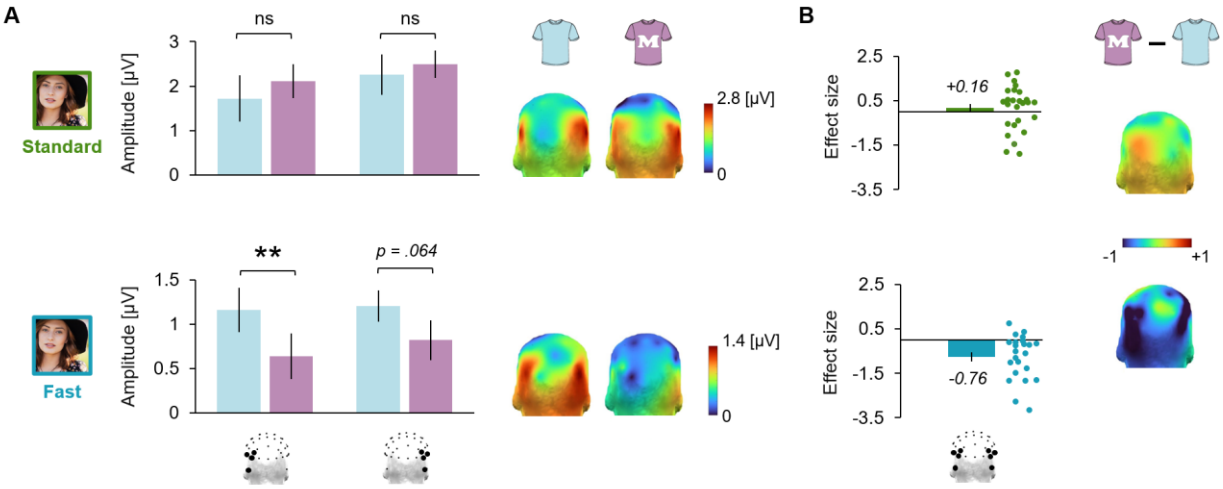

Figure 2.13. Influence of maternal odor on the face-selective response. A. The amplitude of the face-selective response over left occipito-temporal (lOT) and right occipito-temporal (rOT) regions in the Standard (top) and Fast (bottom) groups shows a maternal effect only in the Fast, with a significant decrease over lOT and a marginal reduction of the amplitude over rOT. The 3-D head maps (back view, in adjusted scales) illustrate the spatial distribution of the responses over the scalp. **B**. Mean (box) and individual (circles) effect sizes (Cohen's d) of the odor effect (maternal – baseline) in Standard (*Top*, d = 0.16: negligible) and Fast (*Bottom*, d = 0.76: medium) groups over OT.

Next, we investigated the general response and found a marginal interaction: *Odor × Group* (F(1, 47) = 3.46, p = .069, ηp^2 = 0.07) due to a significant *Odor* effect for the Fast (F(1, 47) = 4.35, p = .042), but not for Standard (F(1, 47) = 0.25, p = .62) group. Comparison between odor contexts demonstrated a marginal (T = -1.90, p = .070; Cohen's *d* = -0.40) negative difference between amplitudes of general visual response in the maternal (+1.20 ± 0.18 µV) vs. baseline (+1.53 ± 0.27 µV) odor contexts over the middle occipital cortex in the Fast group (Figure 2.14, bottom). In the Standard group, the general visual response increased non-significantly over mO by +0.13 ± 0.24 µV in the maternal odor context (T = 0.55, p = .60; Cohen's *d* = +0.11) (Figure 2.14, top).

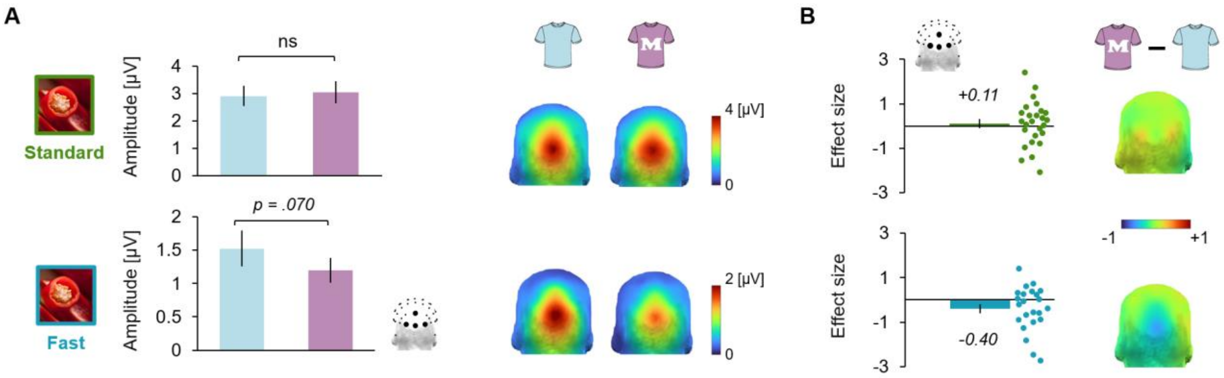

Figure 2.14. Influence of maternal odor on the general visual response. A. The amplitude of the general visual response averaged across middle occipital channels (mO) in Standard (top) and Fast (bottom) groups, showing a marginal negative odor effect (-0.33 ± 0.17 µV, m: p = .070) in the Fast condition. **B**. Mean and individual effect sizes (Cohen's d) of the odor effect in Standard (*Top*, d = 0.11: negligible) and Fast (*Bottom*, d = 0.40: small) groups at mO. Error bars represent standard errors of the mean and head maps (posterior view) illustrate the topography of the effect size.

3.3 The negative maternal odor effect under the higher visual demand

As reported above, the general visual response in the Fast group was marginally reduced in the maternal odor context (T = -1.90, p = .070). The strength of this decline (d = 0.40) (Figure 2.14, bottom) is weaker than for the face-selective response (d = 0.76) (Figure 2.13, bottom) but stronger than the effect size for the general visual response in the Standard group (d = 0.11) (Figure 2.14, top). Visual examination of 3-D topographical head maps (Figure 2.14A, bottom) reveals an unexpected difference between odor contexts, something that was never reported so far in comparable studies (Leleu et al., 2020; Rekow et al., 2021, 2022). For this reason, we further investigated the negative odor effect for face-selective response in the Fast group to disentangle the potential confound of a general effect impacting the general visual response. To test this, we normalized the amplitude of the face-selective response by the general visual response (see Materials and Methods), and calculated the normalized odor effect (maternal – baseline). Cohen's d effect sizes of the face-selective responses were computed for each group. We present below (Figure 2.15) these new normalized data along with the previously reported non-normalized results.

In the Standard group, Cohen's effect size remained negligible after normalization (d = 0.16 vs d = 0.11 before and after normalization, respectively; Figure 2.15A) confirming the absence of influence of maternal odor in this condition. In the Fast group, Cohen's effect size after normalization were reduced by normalization, becoming a small effect (d = 0.33) as compared to being ranked as medium (d = 0.76) before normalization (Figure 2.15B). In sum, this indicates that the statistically marginal reduction of amplitude for the general visual response in presence of the maternal odor in the Fast group is responsible for the significant negative maternal odor effect over the face-selective response.

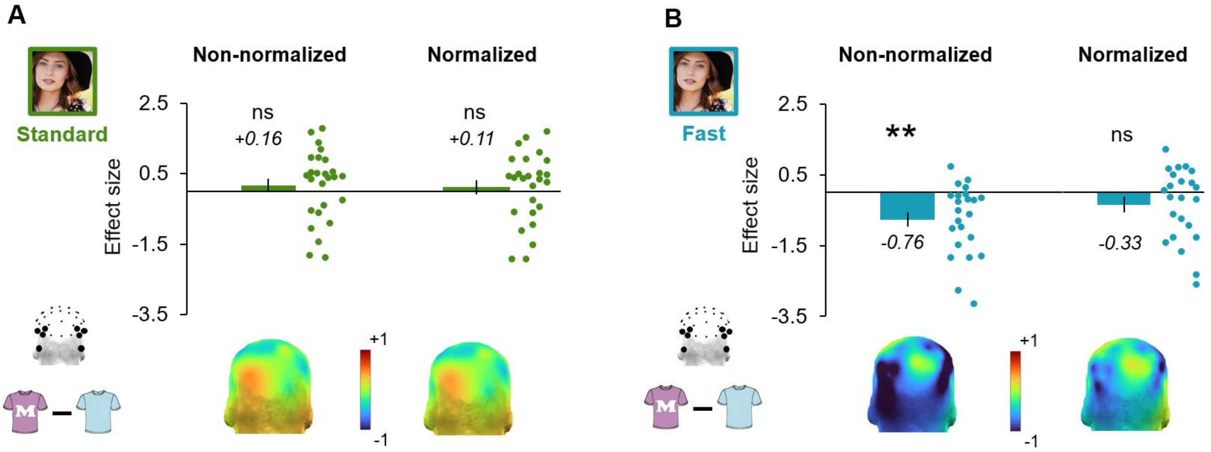

Figure 2.15. Cohen's effect size of the odor effect (maternal – baseline) of the face-selective response before and after normalization. The non-normalized (left) and normalized (right) effect sizes are presented in the Standard (**A**) and Fast (**B**) groups over bilateral OT region. In the Standard group (**A**), the odor effect is negligible (d = 0.16, p = .41 vs d = 0.11, p = .57 before and after normalization respectively) while in the Fast group, the negative odor effect switched from medium (d = 0.76, p = .001) to small (d = 0.33, p = .12) effect size. Group means are depicted by boxes and individual data by circles. Error bars represent standard errors of the mean and head maps (back view) illustrate the topography of the effect size.

4. Discussion

Using frequency-tagging EEG we found a robust occipito-temporal response to faces in Standard and Fast groups, alternatively exposing 12-month-old infants to maternal and baseline odor contexts. In line with our hypotheses, the face-selective response in the Fast group was twice as low due to heightened visual demand. In the Standard group, the face-selective response was robust and did not change in the presence of the mother's odor. This result corroborates previous data (Study 1; Rekow et al., 2023) but in a single group of 12-month-old participants. However, contrary to our hypotheses, in the Fast group, the results did not follow the inverse effectiveness principle: indeed, instead of a higher face-selective response in the maternal odor context, we noted a decreased response, indicating a negative odor effect. In addition, to our knowledge, we are the first to document a trend for a maternal odor influence on the general visual response: while in the Standard group the general visual response was immune to the maternal odor over the middle occipital cortex in both visual conditions as systematically reported in previous studies using similar 6-Hz visual stimulation (Leleu et al., 2020; Rekow et al., 2021), in the 12-Hz Fast group we found a trend for a reduced general visual response in maternal odor context, which would explain the reduction of the face-selective response in the same visual condition. Overall, these results might be interpreted in terms of a sensory overload which was, to date, never described in the context of olfacto-visual interactions.

4.1 Quantitative and qualitative reduction of the face-selective response due to higher visual demand

In both groups, we measured a neural signature of the rapid and automatic face categorization over occipito-temporal cortices, as expected since previous studies reported face-selectivity already in younger infants (de Heering & Rossion, 2015; Leleu et al., 2020; Rekow et al., 2021). However, testing a faster stimulation rate than 6 Hz in infants was unprecedented, with an impressively robust response significance. However, contrary to the strongly right-lateralized responses obtained in 4-month-old infants (de Heering & Rossion, 2015; Leleu et al., 2020; Rekow et al., 2021), at age 12 months, the response seems evenly distributed over bilateral occipito-temporal cortices, which may tend to the bilateral response of 5- (Lochy et al., 2019) and 10-year-old children (Vettori et al., 2019). At the predefined frequencies of 1 Hz and 1.33 Hz and their harmonics (i.e., integer multiples) for the Standard and Fast groups, respectively, we clearly report quantitative (i.e., in amplitude) and qualitative (i.e., in the harmonic distribution) differences depending on the visual condition. Indeed, in the Fast group, the face-selective response is twice as low in amplitude as in the Standard group, which could be explained by the higher visual demand and the constraints put on the visual system to categorize faces, since, at 12-Hz, stimuli are present on screen for only 83 ms (in Fast condition) instead of 167 ms at 6-Hz (in Standard condition). This pattern of a reduced response has already been described in adults, whose 1.33 Hz face-selective response is already at ceiling in streams of 12-Hz stimulation, however, gradual increase of the stimulation rate also leads to an amplitude decrease for the face-selective response (Retter et al., 2020).

This quantitative change is associated with a qualitative change in the face-selective response, as in the Standard group, the response is distributed over more harmonics (i.e., 5 significant harmonics) reflecting integer multiples of stimulation frequency (Retter et al., 2021) compared to a single harmonic in the Fast group. A previous study related the number of harmonics to the visual performance increasing with age (Study 1; Rekow et al., 2023), showing a linear increase of significant harmonics number at an individual level between 4 and 12 months. In addition, studies using similar frequency-tagging EEG in older age groups report a larger number of significant harmonics in 5- (Lochy et al., 2019) and 10-year-old children (Vettori et al., 2019) and even more than a dozen in adults (Rekow et al., 2022; Rossion et al., 2015). Overall, this indicates that progressive brain maturation would be linked with the more complex harmonic distribution of the face-selective response. In the present study, we could link the reduction of harmonics distribution in the Fast group with the increased demand for the visual system due to the more rapid presentation rate of images inducing less time for visual processing and a shorter interval between faces (which could also influence the strength of the response if not enough time is left for the full brain response to unfold, as demonstrated in adults, Retter et al., 2020).

Interestingly, the general visual response which represents the common brain activation for all presented images over the middle occipital region is also quantitatively changed according to the visual condition. As for the face-selective response, the amplitude of the general visual response is twice as low in the Fast compared to the Standard group. However, this reduction is not associated with qualitative changes. Indeed, despite the fact that the actual number of harmonics between condition changes from 4 significant harmonics in the Standard group to only 2 in the Fast group, the general visual response is actually significant for the same frequency range of 24 Hz (i.e., 6 Hz × 4 harmonics and 12 Hz × 2 harmonics for Standard and Fast conditions respectively). These results suggest that the general visual response, which is associated with low-specific visual cues, would be less affected by heightened visual demand.

4.2 The maternal odor effect depends on the visual condition

In the Standard group, rapid face categorization is immune to maternal odor influence. The amplitude of face-selective response is already high in the baseline odor context and remains unchanged in the maternal odor context. This absence of odor effect is likely linked to low demand for the visual system which has become efficient enough to categorize faces presented during 167 ms only, backward and forward masked, in streams of nonface objects. This is in line with a Study 1 which included some participants of this age, where we reported that the odor effect decreased with increasing face-selective response, showing an absence of odor effect towards the end of first year. Altogether these findings are in line with the principle of inverse effectiveness (Stein & Meredith, 1993) which states that the strength of multisensory integration decreases when the strength of unisensory response increases. In the present case, it suggests a developmental trade-off between vision and olfaction and supports the view that visual perception relies on odor cues in the developing infant brain until the sole visual system becomes able to readily achieve categorization. Such trade-off shapes a brain network organization across development minimizing energy costs and keeping only adaptively valuable functional connections between neuronal populations in an economic fashion (Bullmore & Sporns, 2012). Importantly, the general visual response is also immune to the maternal odor influence in the Standard group. The same observations were reported in multiple studies before, at different ages: 4-month-old infants (Leleu et al., 2020; Rekow et al., 2020, 2021), between 4- and 12-month-old infants (Study 1; ; Rekow et al., 2023) and adults (Rekow et al., 2022). This allows to exclude a common stimulating effect of maternal body odor on visual attention and supposes an efficient primary visual processing that is increasingly independent from the odor context.

Surprisingly, but interestingly, in the Fast group, the results contradict our hypothesis. Following previous studies and according to the principle of inverse effectiveness, we predicted that with heightened visual demand at a given age, maternal odor would regain an influence in 12 month-old infants, who otherwise, do not appear to show an odor effect (Study 1; Rekow et al., 2023). However, the face-selective response shows a negative odor effect in this tight visual condition. Surprisingly, we also found a tendency for a reduced general visual response in maternal odor context. The latter results are not significant compared to the significant reduction of the face-selective response, but follow the same pattern. Here, we show that the general visual response can also be modulated by maternal odor. To verify the independence of these observations, we normalized the face-selective response by the amplitude obtained in the general visual response and showed that the significant negative odor effect on the face-selective response certainly also causes the slight reduction of response for the general response, thus suggesting a common influence (i.e., non-independent effect) of maternal odor on visual processing. Thus, probably this olfactory-to-visual interaction seems to be non-specific for face categorization.

In effect, intersensory facilitation (Bahrick & Lickliter, 2000) that we expected to evidence in manipulating the visual demand in 12-month-old infants, reflects one type of multisensory integration called superadditivity or multisensory enhancement (Stein & Stanford, 2008). In this case, the multisensory response is always stronger than the simple sum of two unisensory responses but although we cannot directly measure the response to the olfactory stimuli, the reduction of the response in the multisensory context as compared to the unisensory (baseline odor) context of present study would relate to subadditivity instead (i.e., when multisensory response is weaker then sum of two unisensory responses). This mechanism of multisensory depression (Meredith & Stein, 1983) may be explained by the spatial disparity of stimuli from different modalities, on the basis of their different receptive fields (Meredith & Stein, 1996; Stein & Meredith, 1993): when one of the two stimuli is outside of its receptive field, and thus spatially dissimilar from the other stimulus from this field, the associated neural response to their integration is depressed (Meredith & Stein & Stein, 1986; Wallace et al., 1996). However, while it is tempting to refer to this theory, we can hardly consider the spatial disparity of the olfactory and visual stimuli. However, the multisensory depression phenomenon having been theorized on audio-visual integration, its extrapolation to olfacto-visual interaction requires cautiousness. Another limit to rely on a multisensory depression-related interpretation is that we do not have a direct measure of the unisensory olfactory response. Our paradigm relies indeed on the exact frequency of visual responses in brain activity and how it is modulated by contextual maternal odor.

4.3 When senses overload brain capacity

Taking in account the extremely rapid image presentation rate in the Fast group, we might assume that the negative odor effect is caused by a visual overload. In general, this term refers to an overstimulation from different sensory modalities that leads to difficulties in making sense of incoming inputs in relation with a limited processing capacity (Malhotra, 1984). This phenomenon was indeed documented in psychiatry (Scheydt et al., 2017) and in marketing (Homburg et al., 2012; Jacoby et al., 1974). Sensory overload with olfaction is not simple to interpret: most studies do not report the influence of odors on multisensory perception, contrary to the influence of visual and auditory cues (Doucé & Adams, 2020; Pan et al., 2003). Here, the negative odor effect emerged only in the Fast group with increased visual demand and might be unrelated to the specificity of faces as it also impacts the general visual response. A heightened visual demand engages more brain resources for visual processing and probably, for the production of overlapping responses; but in reducing the time between visual stimuli, in the present scenario, adding an odor cue can render face categorization even less effective because even more neural resources are recruited to process concurrent odor cues. As normalization showed, this negative odor effect seems to be rather general (not only for face-specific responses, but also for low-level visual responses), which may suppose a common impeding role of maternal odor. Due to the hyperacceleration of the image presentation rate, stimulus duration was extremely short and may have overloaded the visual system with overlapping visual responses, impeding concurrent odor processing. Thus, speeding up the visual stimulation to an infant brain seems to induce unforeseen artefactual consequences and is not adapted to test the inverse effectiveness principle.

In sum, the present study sheds some additional light on olfacto-visual interactions in a large group of 11-to-13 month-old infants. In line with a previous study (Study 1; Rekow et al., 2023), it replicated a null odor effect when the visual stimulation allowed to categorize faces on its own. Moreover, infants of this age were able to categorize faces at an extremely fast presentation rate where stimuli are displayed on a screen for 83 ms only. However, although we successfully increased the visual demand for face categorization, intersensory facilitation by maternal body odor did not emerge. On the contrary, adding olfactory cues to a visual task which difficulty is already high seems to induce a sensory overload, pointing out that the visual system may still not be entirely functionally reliable at this age, since such effects where not found in adults using the same designs (Rekow et al., 2022).

General discussion

1. Summary: Inverse effectiveness in the development of face categorization over the first year

Number of studies demonstrated how multisensory integration is advantageous for perceptual learning in early infancy. This was clearly demonstrated for audition and vision (Bahrick & Lickliter, 2000; Lewkowicz, 2010), which are recognized as the dominant senses in human adults and therefore were well investigated compared to the other senses. However, this intersensory facilitation can shift its impact with age, because of better sensory abilities, improved attention formation and enhanced expertise (Bahrick & Lickliter, 2012). This findings follow the principle of inverse effectiveness. However, it is unknown if this principle applies to the other senses, for example, olfaction. Thus, the focus of this dissertation work was directed on the specificities of olfactory system and its role in the visual development in infancy. From the review of literature, we learned that salient olfactory cues conveyed in maternal odor play a facilitatory role in visual processing (Damon et al., 2021) and particularly in face categorization in 4-month-old infants (Leleu et al., 2020). In line with the principle of inverse effectiveness, Rekow et al. (2022) found no intersensory facilitation by body odor on face categorization in adults, but its emergence in the categorization of ambiguous face-like objects. Although encouraging, these results raised some unanswered questions: 1) can we apply the inverse effectiveness principle to odor-driven face categorization in infant development, and 2) how does this principle apply to developmental stages characterized by weak/good visual ability as a function of the more or less demanding visual tasks.

To shed some light to above questions, three studies were run to test the hypothesis that odor-driven face categorization follows the inverse effectiveness principle across development. Specifically, **Study 1** have assessed whether the facilitation effect of maternal odor declines with the improvement of visual abilities over the 1st year in following infants which age is spread between 4 and 12 months. Then, in controlling the assumed visual demand implied by more or less simplified face representations, the inverse effectiveness principle was tested in two studies of 4- and 12-month-old infants. In **Study 2**, we expected that, in 4-month-old infants, the odor effect will decrease while the unisensory face-selective response will increase for a less demanding face categorization task; in **Study 3**, on 12-month-old infants, the odor effect should increase while the unisensory face-selective response decreases for a more demanding face categorization task.

1.1 Main results

Study 1 examines the prediction of a developmental trade-off between vision and olfaction, where the weakest unisensory face-selective response benefits the most from multisensory integration. It came out that the unisensory (visual) face-selective response progressively increases between 4 and 12 months over the bilateral occipitotemporal cortex (OT), while odor effect decreases over the right occipitotemporal cortex (rOT). This confirms the principle of Inverse effectiveness.

Study 2 was performed in two groups of 4-month-olds, one being exposed to the more demanding face categorization task, while the other was exposed to the homologous less demanding task. The more demanding categorization task consisted in presenting naturalistic complex images of faces and objects, while the less demanding task presented simplified images, both visual tasks being run in the mother's odor or baseline odor contexts. In the 1st group exposed to the more demanding face categorization, we found a strong odor effect over the rOT and a weak unisensory face-selective response that replicates a previous study (Leleu et al., 2020). In 2nd group we saw a strong unisensory face-selective response largely distributed over the OT that did not lead to the emergence of the odor effect. Vision was thus maximally effective on its own in this less demanding face categorization task, while olfaction effect, if any, was shadowed or nil. Taking together, results of both groups confirm the Inverse effectiveness principle in 4 month-old infants: the strongest unisensory face-selective response toward less demanding visual stimuli benefits the less from multisensory integration with odor cues, and conversely for the most demanding visual stimuli which are boosted by contextual maternal odor to be reads as faces.

While, **Studies 1** and **2** confirmed our predictions, the results of **Study 3** were surprising, at least in part. As in **Study 2**, we controlled the visual demand of face categorization creating two groups of 12-month-old infants exposed to a more vs. less demanding task. The group of infants exposed to the less demanding task, which reproduced the task design of **Study 1**, exhibited an effective face categorization and the absence of the odor effect. The second group had to face a more demanding task, which consisted in accelerating twice the image presentation rate. In this case, we predicted a decrease of the unisensory (visual) face-selective response and increase of the odor effect. Compared to the less demanding face categorization we found indeed a reduced unisensory face-selective bilateral response to these more demanding stream of images over the OT. However, the expected odor effect did not emerge in the more demanding face categorization task. Moreover, the face-selective response was even significantly weaker in presence of maternal odor compared to the baseline odor. The EEG showed a negative bilateral odor effect over OT, explainable by probable sensory overload or by developmental specificities of the mother-infant interaction at this age (see for the more details section 2.5).

1.2 Additional observations

In addition to these main results, some interesting observations emerged from the studies that might complete and qualify our conclusions. Thus, in next paragraphs, we will detail more the qualitative characteristics of the face-selective visual response, the specificities of the general visual response across different conditions, the right hemispheric dominance in the odor effect, and the null effects of sex and infant feeding method.

1.2.1 Complexity of face-selective response increases with efficiency of face categorization

We analyzed not only the quantitative characteristics of brain response (e.g., amplitude) but also qualitative variables, as the number of harmonics. In the frequency domain, we observe brain response at the stimulation frequency (e.g., 1 Hz) as first harmonic and also at its integer multiples (2 Hz, 3 Hz, 4 Hz etc). The number of harmonics reflects the complexity of brain response distribution. This variable is important to take into account as, according to the number of significant harmonics, we can sum their amplitudes to have final estimate of the brain response (Retter et al., 2021). Previous infant studies proved that the number of harmonics increases with age: the investigated face-selective response in 4-month-old infants was captured at a single harmonic (de Heering & Rossion, 2015; Leleu et al., 2020; Rekow et al., 2020, 2021), while in the 5- (Lochy et al., 2019) and 10-year-old brain (Vettori et al., 2019) it was distributed at few harmonics, to it is found at more than a dozen harmonics in adults (Rekow et al., 2022; Rossion et al., 2015). In Study 1, we also found an increasing number of harmonics between 4 and 12 months (predicted number of 1.62 at 4 months to 2.92 at 12 months) that corroborates the notion of increasing complexity of brain response across early development.

Interestingly, in Studies 2 and 3, we also found a different harmonic distribution of the face-selective response according to the less vs. more demanding categorization task. Both 4- and 12-month-old infants evinced a significant face-selective response distribution at a single harmonic in the more demanding task, while in the less demanding task it was distributed at 5 harmonics. Thus, the number of harmonics distribution relates rather to the efficiency of the face categorization task than only to the brain maturation level. It may be noted that the range of harmonic distribution of the general visual response stayed invariable 1) despite assumed functional improvement of the visual system in Study 1 and 2) despite manipulating visual demand in Studies 2 and 3; which confirms the more protracted development of face categorization compared to the common visual processing.

1.2.2 The general visual brain response across different conditions

The general visual brain response, reflecting common visual activity over the middle occipital cortex (mO), did not differentially react to variations of the olfactory context in previous category-selective studies (Leleu et al., 2020; Rekow et al., 2020, 2021). However, the present doctoral work found some specificities of the level of visual processing. First, the general visual response was dependent on the level of visual demand, as shown by its manipulation in Studies 2 and 3. In Study 2, the graphically simplified stimuli elicited a weaker general visual brain response than the natural stimuli, which relates to the fact that former stimuli conveyed lower quantity of visual information, as all backgrounds of the images were replaced by a single gray level. Thus, a particular reciprocal relationships came out between the general and face-selective responses in each visual condition: while naturalistic complex stimuli elicited weak face-selective and strong general visual responses, the simplified stimuli led to stronger face-selective and weaker general visual responses. In Study 3, which kept the visual complexity constant, but accelerated the rate of stimuli presentation, both the face-selective response and the general visual response were decreased. Thus, different properties of visual stimulation induced different patterns of relationship between both types of brain responses in Studies 2 and 3, which might be explained by a reduced stimuli presentation time and interval between faces in the fast condition of Study 3 that rendered both face-categorization and general visual processing much more demanding.

Moreover, Study 3 found an effect of the olfactory context on the general visual response, which was otherwise stable in our Studies 1 and 2 and also in previous similar studies in infants (Leleu et al., 2020; Rekow et al., 2020, 2021) and adults (Rekow et al., 2022). This decrease of the general visual response in the maternal odor context was only a tangential effect, but this unexpected influence explained the negative odor effect in the Fast group that seems not to be category-selective and explainable by a more general process such as sensory overload (Homburg, 2012; Jacoby et al., 1974).

1.2.3 Right hemispheric dominance in the odor effect

Face processing is right-lateralized, although a possible, but not necessary, involvement of left hemisphere (Grill-Spector et al., 2017; Rossion et al., 2003). In the present experimental paradigm, the face-selective response was observed over the right occipito-temporal cortex in the 4-month-old brain (de Heering & Rossion, 2015; Leleu et al., 2020). At 5 years, this activation becomes a bilateral pattern (Lochy et al., 2019) that is conserved in adults, with nevertheless a right dominance (Rekow et al., 2022; Rossion et al., 2015). Our present Studies 1 and 2 contrarily found a left hemispheric dominance for the face-selective brain response in 4-month-olds in absence of the maternal odor, while Studies 1 and 3 rather confirmed the bilateral activation in older infants. However, despite this lateralization difference in 4-month-olds, the odor effect was always detected in the right hemisphere (see also Leleu et al., 2020). This result might interpreted in the line with the suggestion that the right hemisphere is more engaged in the odor recognition (Brand et al., 2001; Royet, 2004) and therefore is involved in the multisensory olfacto-visual integration, activating the connectivity between different brain regions working on the same semantic field (Mahon & Caramazza, 2011).

1.2.4 Null effects of sex and feeding behavior

Gender differences sometimes play a crucial role in observed phenomena. For example, longer periods of eye opening elicited by mother breast odor were found only in newborn boys (Doucet et al., 2007), however at the same age female infants contrary to males demonstrated a preference for the breast odor of lactating compared to the no parturient women (Makin & Porter, 1989). In childhood, 4-5 years old girls better than boys had identify their classmates (Verron & Gaultier, 1976). At adult age, some studies also showed greater female responsiveness to social scenes including faces (Proverbio et al., 2008). These latter results are in line with higher human empathy in conspecific communication in women. However, it is more difficult to find theoretical bases for gender differences in infants. Indeed, studies based on the influence of maternal odor on face perception was not affected by gender (Durand et al., 2013; Jessen, 2020; Leleu et al., 2020). Our results confirm these findings as no effect of gender was observed across the three experiments.

The breastfeeding status should in theory bring more influence on the odor-driven face categorization task, as breastfeeding mothers spend significantly more time with their infant. Breastfeeding provides obviously longer periods of direct mother-infant contact that impacts on infant emotional development over 1st year of life (Smith & Forrester, 2017). For example, Jessen et al (2020) found that breastfed 7-month-old infants evince no response to fearful faces, while in bottle-fed infants this response was enhanced. On other hand, studies on odor-driven visual preferences for female face over car without particular emotional status showed a null effect of early feeding status (Durand et al., 2013, 2020). Moreover, previous studies on the influence of maternal odor on face (like) categorization also did not report any difference related to early feeding experience (Leleu et al., 2020; Rekow et al., 2021).

All experiments in the present work confirmed these findings. However, in Study 3 on 12-month-old infants, the number of breastfed infants was low. In this case, we computed the correlation between the number of breastfeeding months and the odor effect, with the outcome of no significant links in either the Standard or in Fast visual groups. As the negative odor effect seemed so surprising, we wanted analyze the daily duration of mother-infant interaction, but at the end of first year infants in our sample are particularly seldom kept by their mothers, most of them spend the biggest part of the week with babysitters or in daycares beginning from 4-6 months. Thus, feeding status may be influential for some aspects of visual processing, as for example emotional status of faces, while the generic face categorization may depend less on it. However, the influence of maternal odor without a doubt changes over 1st year due to the progressive distanciation between mother and infant, that is less pronounced for breastfeeding infants and therefore can modify the olfactory impact on them. Anyway, further investigations are needed to settle the issue of the influence of breastfeeding on the multisensory processing of faces.

2. Merging of the senses along development

The benefit from multisensory integration when unisensory response is low seems to be an advantageous developmental mechanism that is functional from early stages. On the other hand, increasing unisensory (e.g., visual) response leads to a relative decrease of multisensory response involving olfaction, and therefore no intersensory facilitation (e.g., odor effect) seems to operate. This developmental trade-off between two sensory systems reflects a minimizing mechanism of energy costs for the developing brain networks (Bullmore & Sporns, 2012). Thus, through our results we confirm the third rule of multisensory integration (Meredith & Stein, 1983) on the principle of inverse effectiveness. But what about the other rules?

2.1 Spatiotemporal coherence and olfaction

Effective multisensory integration of sensory cues from different modalities requires their synchronization in space and time. In other words, sensory events should have the same time onset and space location. All these rules, including the inverse effectiveness principle, were discovered and investigated in audio-visual integration (Meredith & Stein, 1983). Both these senses provide continuously fluctuating streams of information that are perceived with high level of awareness. As a result we are very sensitive to visual and auditory changes in space and time (Sela & Sobel, 2010). Thus, any lack in synchronization between audition and vision can interfere with their multisensory integration. Interestingly, other senses demonstrate different dynamics of attentional capture. For example, human abilities to follow spatial and temporal changes are minimal in olfaction, a property that is thought to explain in part the low olfactory awareness of humans in everyday life (Sela & Sobel, 2010). However, despite this specificity of olfactory attention, odors can modulate visual motion perception at the level of spatial direction (Kuang & Zhang, 2014) and speed (Tsushima et al., 2021).

In our work, we present olfactory and visual cues simultaneous but without exact match in terms of temporal onset and offset. The olfactory stimulus is construed as a context: the source of maternal odor, as the folded t-shirt, is already affixed on the infant's chest before turning on the visual sequence on the screen. Such collocation of odor and visual scenery seems us ecologically relevant and comparable to what occurs in real mother-infant interaction when the odor is perceived rather as a stable context than an exactly timed co-occurring sensory cue (e.g., as lips movements and speech sounds, which are accurately synchronized). Thus, in the case of olfaction integration with other sensory modality, a precise spatiotemporal coherence does not seem necessary. Nevertheless, what is crucial for this process?

2.2 Intersensory learning in the social context

Due to the relative stability of odors in space and time, olfactory information provides an especially adequate context for the engagement of perceptual learning. This stability can be especially important when other quickly changing and potentially confusing, sensory sources intervene. For example, infants learn to perceive faces in the complex and constantly changing visual environment. To build this ability, they can lean on the constant maternal odor, which is highly salient, reinforcing and soothing, and probably helps to pick up faces appearing in the surrounding. Important to note, this association most likely emerges between the maternal face and maternal odor, but it may concerns faces in general as during the first months, infant spend much time in mother's arms perceiving her body odor and, in the same time, the faces of other conspecifics. Thus, maternal odors are relevant sensory cues since birth, favoring associative learning supporting interactions with mothers and other conspecifics (father, siblings, nanny, etc) (Reynolds & Roth, 2018; Schaal et al., 2020). Human faces and maternal body odor are indeed highly congruent in the social semantic field. Studies on olfactory-to-visual interaction in 4-month-old infants show a selective influence of maternal odor that increases looking time toward a face but not toward a car (Durand et al., 2013), and promotes the categorization of face (Leleu et al., 2020) and face-like objects (Rekow et al., 2021), but not of non-social items, such as car pictures (Rekow et al., 2020). Moreover, the general visual response elicited by any type of visual stimuli remained immune to the influence of maternal odor in all previous studies on face (like) categorization (Leleu et al., 2020; Rekow et al., 2021, 2022) and in the present dissertation work.

Semantic congruency seems to be an universal property facilitating auditory-visual integration and associative learning (Bahrick & Lickliter, 2012; Lehmann & Murray, 2005). However, returning to the intersensory redundancy hypothesis of Bahrick and Lickliter, (2000) we find some differences between auditory, visual and olfactory information as conveyors of amodal features. Indeed, some amodal properties, such as synchronization, rhythm or duration, can be detected by infants from a very early age across several sensory modalities, and can constitute a basis for intersensory facilitation. However, the intersensory redundancy hypothesis seems not easily adaptable to the case of olfaction, as its temporal properties are rather fuzzy. One temporal property of olfaction is well functioning in adults, the matching of periodic inhalation with stimulation of the olfactory mucosa, or sniffing. But sniffing is not well functional in the first year of life. Thus, so far, the a/modal characters of stimuli was mainly conceived as pertaining to some psychophysical properties on timing, synchronization and colocation of stimuli. In turn, amodal properties could also concern congruency in semantics or in social affordances of stimuli from different sensory domains (viz., the social context unifying maternal odor and faces), therefore, I propose social saliency might be a basis for intersensory facilitation on a par with redundant amodal characteristics.

2.3 From global to specific categories

In early development, salient amodal properties appear simpler to detect in multimodal stimulations (Bahrick et al., 2002, 2019; Flom & Bahrick, 2007) as compared with non-redundant modal characteristics that are more specific (Bahrick et al., 2004, 2005, 2006). This happens because infant attention is global and very broadly tuned to be focused on highly salient stimuli with vital ecological valence. At this stage, intersensory facilitation plays a crucial role in perception because unimodal stimulation often is not efficient enough due to ambiguity of sensory cues or to low functional level of sensory systems. However, along the first year of life, infant sensory perception changes dramatically. Based on structural and functional sensory improvement coupled with the accumulation of experience and learning, the process of perception becomes more differentiated and rapid (Gibson, 1988; Ruff & Rothbart, 2001). Thus, older infants become capable to detect both amodal and modal characteristics in both uni - and multimodal stimulations without any need of intersensory facilitation (Bahrick et al., 2002; Bahrick & Lickliter, 2004; Bahrick & Newell, 2008). The effective use of only one sensory source to direct behavior economizes indeed attentional costs, allowing to focus from the more global properties to less salient and more specific characteristics. This hierarchical principle of attention was proposed by Gibson (1969) and many studies have since corroborated that older infants evince a shift in detection from general to more detailed information processing (e.g., Bahrick & Newell, 2008; Frick et al., 2000; Oakes & Madole, 2008; Xu et al., 2004). This increased attentional selectivity provides the basis of cognitive development, mediated by category formation.

Figure 3.1 represents a possible model of development of odor-driven face categorization over the first year based on the IRH principle. Younger infants, between 4 and 8 months, are very familiar with their mother’s odor, not only as they spend a lot of time in mother's arms, but also because they met this scent as fetuses in their amniotic fluid and catch it again in the overlapping flavor of colostrum and milk, and in the areolar and skin secretions (Schaal, 2005, 2016, 2023). Thus, at this age range, maternal odor is an overlearned, highly salient sensory cue which becomes rapidly coupled with the frequently-encountered mother’s face. This recurring semantic congruency of the odor and the face of the primary caregiver provides the basis for the intersensory facilitation (i.e., odor effect) of effective face categorization. As vision further ameliorates in functionality, visual inputs become more and more straightforward and dominant in controlling directional behavior: the eyes take then the lead over the nose in directing multisensory attention to the face. Contrarily to younger infants, older infants not only improve visual competence, but they also extend their sensory panel of seen faces. Between 8 and 12 months, infants meet indeed much more conspecifics, often by their own movements, as they spend most part of the day in various socially-rich environments. However, not only do visual experiences become more abundant and diverse with age, those infants also meet a wider palette of social odors, as they distantiate from their mother and approach new interactants. In this context, novel associative pairings between different faces and body odors are engaged (Damon et al., 2021) and their «odor-facescape» gradually narrows down from broadly tuned multisensory perception toward more specific unisensory percepts (Murray et al., 2016). As a consequence, 1) maternal odor may tend to become less salient in a global social context and 2) parallel functional improvements of visual competence provide sufficiently effective face categorization without necessitating anymore the intersensory facilitation of olfaction.

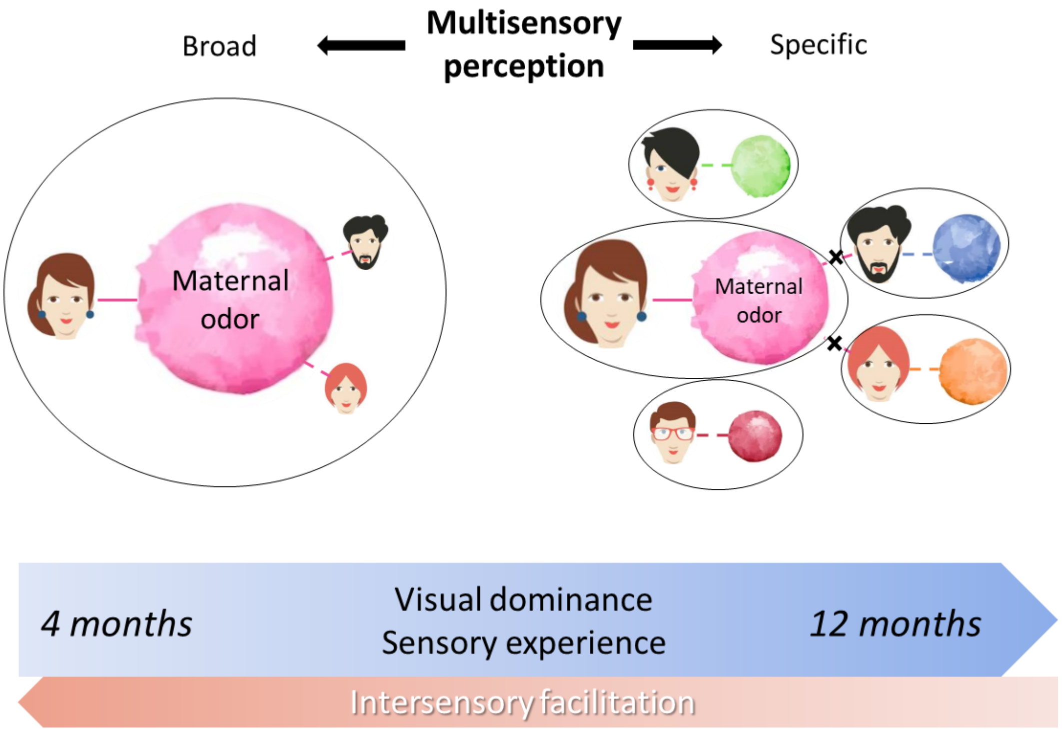

Figure 3.1. Developmental model of odor-driven face-categorization over the first year. At 4 months, face-categorization is based on semantic congruency between maternal odor and face. Maternal odor represents the basic social context engaging discrimination of faces from other objects in complex visual environment, and generalizing them across different exemplars. At this early age stage, vision functional development is far to be completed explaining why infants benefit a lot from this multisensory interaction. During the first year, the visual system improves functionally in combination with increasing sensory experience, and leads to perceptual differentiation of faces. Thus, infants become capable to build finer categories as multisensory perception shifts from broadly tuned to more specific. At this level of visual development infants of 12 months are able to categorize faces without the engagement of olfaction and the intersensory facilitation (i.e., odor effect) declines with age. Probably, maternal odor is then no more involve in generic face categorization because olfactory-visual associations become finer, replacing the global social context of maternal odor.

2.4 Experts vs. novices in categorization

However, after developmental milestones of progressive maturation are achieved in sensory and cognitive abilities, the reliance on intersensory facilitation is far from being lost, turning to multisensory resources when the perceptual demand is occasionally high. Infants, children and adults do indeed acquire new information without discontinuation, becoming more and more experienced in issues that are specific to their stage, learning always finer distinctions between conspecifics, objects or contexts, and, accordingly, classifying them into more and more well-defined categories. Such progressive acquisition of age-adequate expertise, from novice becoming an expert, is characterized by high levels of sensory/cognitive load, which challenges their current level of skill. The process of intersensory facilitation is then, at all life stages, mobilized as a strategy to keep an optimal level of perceptual learning. For example, Bahrick et al. (2010) found that 5-month-old infants cannot discriminate the tempo of a hammer tapping in unisensory visual mode when the conditions of this task become too difficult, requiring finer tempo discrimination. In this case, infants rely on intersensory facilitation, although in previous simpler conditions they were efficient in both uni- and multisensory modes of stimulation (Bahrick & Lickliter, 2004). Other studies applying high sensory loads in motor and cognitive tasks came to the same conclusion in infants (Berger, 2004; Corbetta & Bojczyk, 2002) and adults (Santangelo et al., 2008; Santangelo & Spence, 2007; Spence, 2010).

Previous studies on odor-driven face-categorization described that adults do not (need to) use intersensory facilitation, probably because their visual system and cognition are effective on their own (Rekow et al., 2022). Adults are experts in this type of perceptual tasks, suggesting a developmental trade-off between vision and olfaction in favor of vision. To confirm the principle of inverse effectiveness in adults, these authors replaced the typical faces by ambiguous face-like objects, which could be read as objects or as faces. In this case, imposing an increased perceptual difficulty to categorize the visual stimuli changed the perceptual load of the task, and the adult participants solicited additional olfactory cues (body odor) to solve it: intersensory facilitation worked out. This prior result induced us to manipulate the demand of the visual task in Studies 2 and 3 in infants of different ages to test again the principle of inverse effectiveness that was supported in Study 1.

In Study 2, 4-month-old infants were presented simplified, less-demanding to categorize stimuli for less demanding face categorization. It came out that this less demanding face categorization task induced a stronger unisensory face-selective response and a weak odor effect, showing that intersensory facilitation not occurred. Thus, we fully corroborated the principle of inverse effectiveness in 4-month-old infants for olfactory-to-visual interactions. However, the same manipulation of the visual task difficulty (increasing the speed of the visual stream) was made in 12-month-old infants lead to surprising results. While the standard 6-Hz presentation rate of the visual stimuli used in previous studies (Leleu et al., 2020; Rekow et al., 2020, 2021; present Study 1 and 2) replicated the strong unisensory face-selective response and weak odor effect, a presentation rate speeded twice (12-Hz) induced the expected weaker unisensory face-selective response. But much unexpectedly, this face-selective visual response was also weaker in the maternal odor context. Thus, instead of causing intersensory facilitation in the high-demanding visual task, a detrimental intersensory odor effect was noted. Interestingly, this negative odor effect occurred not only for the face-selective response, but also for the general visual response in 12-month-old infants. Potential explanations for this exception of the inverse effectiveness principle is discussed next.

2.5 A paradoxical odor effect: no inverse effectiveness in 12-month-old infants?

2.5.1 Mother-infant interaction

The absence of an odor effect in the more demanding face categorization task in 12-month-old infants fueled new reflexions on the involvement of maternal odor in multisensory integration involving olfaction across development. On the one hand, the progressive infant-mother distanciation over the infants' first 12 months might strengthen both the mother's odor/face association and the individual differentiation of faces. However, our method to present faces conveying different visual identities mismatched with the infants' own mother's odor may render the infant's ability to integrate own mother's odor with unfamiliar women's faces more problematic, leading to the absence of an odor effect. Accordingly, the results of a previous study on adults (Rekow et al., 2022) might appear contradictory on this point, as their face-like selective response was enhanced in the presence of body odor. But the olfactory cues differed between both studies. While in the adult study, the odor stimulus was a pool made out of the body odors from 8 unfamiliar donors, erasing any odor cue of individuality, in the 12-month-olds faced only the unique body odor of own mother. Thus, in these conditions, the odor stimulus was ecological for the infants at the individual level, while the visual stimuli may be considered ecological at a categorical level, potentially leading to a perceptual conflict in the intersensory categorization task. Thus, to confirm the hypothesis of inverse effectiveness in 12-month-olds, future studies might better use a categorization task in which: 1) various images of *own mother's facial identity* are coupled with *own mother's odor*; 2) the generic face categories with *different women's visual identities* are presented concurrently with a *pool of maternal women's body odors* in which odor identities are abolished.

On the other hand, maternal body odor certainly changes through the infants' first year. Physiological states underlying pregnancy, childbirth and different stages of lactation (colostral, mature milk, weaning period) are somehow reflected in maternal body odor (Schaal & Porter, 1991). Obviously, the odor of colostrum (relative to milk) or milk (relative to formula) is a strongly attractive stimulus to human neonates (Marlier & Schaal, 2005; Klaey-Tassone et al., 2020), but lactation also affects the odor of axillary secretions, and neonates prefer the axillary odor of lactating women (not their mother) over the same odor from non-lactating women (Makin & Porter, 1989). Not surprisingly if one considers these behavioral studies, infants aged 2-9 months show brain activity of higher magnitude to milk than to an arbitrary artificial scent (Gellrich et al., 2021), breastfed 7-month-olds evince reduced brain response for fearful faces in presence of mother's odor (Jessen, 2020). However, in the present work as well as in previous studies (Leleu et al., 2020; Rekow et al., 2020, 2021), the mode of feeding was intriguingly without effect on the odor effect on multisensory categorization. Thus, we cannot be entirely sure that the observed odor effect relates to the own mother's body odor or to a mother's body odor in general, both conveying potentially efficient odor agents for infants. Indeed, the odor of an unrelated, unfamiliar mother's breast can shape the infants' face preference at the same level as own maternal breast odor (Durand et al., 2020) or, in a different task (EEG response to fearful face), it induces weaker effect but following the same tendency (Jessen, 2020). Thus, further studies might collect the body odor of unfamiliar mothers of 4-month-old participants or own mother if collection of the odor may be carried out 8 months before experience day, at a period when women generally still breastfeed, and use it as odor context for a more demanding face categorization task in 12-month-olds. Keeping the odor «stable» (in physiological terms) will allows to affirm our conclusion about role of maternal odor across the 1st year.

2.5.2 Sensory overload

The hypotheses put forward above might explain the absence of odor effect in the more demanding face categorization tasks in the 12-month-olds, but our results found an effect opposite to our prediction: a negative odor effect. Taking in consideration that this phenomenon was evidenced not only for the face-selective response, but also for the general visual response (marginal tendency), we suppose that this decrease of the visual response in presence of maternal odor relates to a more general effect. Moreover, when the face-selective brain response was normalized by the general visual response (see for more details in Study 3) this significant negative odor effect vanished. Thus, adding a second sensory modality while facing a perceptually-challenging task may have been distracting for the visual integration of year-old infants. As the brain capacities to process information is limited, overstimulation by different senses leads to difficulties in sensory processing that is called *sensory overload* (Malhotra, 1984).

This sensory overload phenomenon was mostly studied in adults with psychopathological conditions (Scheydt et al., 2017) and in marketing research (Homburg, 2012; Jacoby et al., 1974). But some related studies were run on the optimization of learning in preschool and school children (Buley, 2017; Goldschagg & Bekker, 2020) or even in premature neonates to find out how to compensate environmental noise (DePaul & Chambers, 1995). Generally, sensory overload supposes distraction from visual or auditory modalities, but these effects may change according to the perceptual balance of each age stage. For example, visual distractors have greater attention cost for older children (6-11 years) (Robinson et al. 2018), while auditory distractors affect more younger children (3-6 years), supporting the idea of a late development of multisensory integration (Burr & Gori, 2012). Anyway, mechanisms of intersensory overload seems to be not enough investigated and even less information is available about role of olfaction in this phenomenon. Despite our suggestion about sensory overload due to the olfaction, some researchers rather do not confirm this conclusion. In a marketing studies with adults Doucé and Adams (2020) noted the advent of sensory overload with auditory and visual cues, but not with odors. Pan et al. (2003) investigating multisensory perception in chamber-experiment, demonstrated that addition of auditory noise during odor exposure gave a masking effect for the latter, while addition of odor did not change the perception of noise. These authors considered vision and audition as «higher senses» capable to induce sensory load effects, as compared to olfaction which is thought to mobilize a low (unconscious: see Köster, 2002) level of attention for change in the environment.

In sum, we suppose that speeding the image presentation rate up to 12 Hz with stimuli duration of 83 ms was not the best methodological option to test the inverse effectiveness in 12-month-olds due to its potential 1) induction of visual overload which probably caused a significant decrease in the face-selective response, and 2) additional sensory overload with the added maternal odor. The sum total of both of these sensory overloads resulted in an intersensory inhibition, actualized in negative odor effect.

3. Perspectives

3.1. *Odor-driven categorization: social context matters?*

Infants in first year are able to engage arbitrary odor-object paring (Schaal & Durand, 2012). We noticed the enhancement of category-selective visual response in the context of congruent odor (e.g., odor of strawberry improves the categorization of strawberry images/object). Rekow et al. (2020) investigated car categorization in 4-month-old infants using non-congruent maternal odor and did not observe intersensory facilitation. The same null effect for car categorization Rekow et al. (2022) found in adults but for this time, authors displayed congruent odor of gasoline, non-congruent body odor and baseline (no odor) context. It seems that adults do not use anymore intersensory facilitation due to the developmental improvement of visual system in line with inverse effectiveness. However, many studies confirm odor priming effect showing that odors increase attention toward congruent objects

(Carrieri et al., 2023; Seigneuric et al., 2010; Seo et al., 2010) or contrary to the non-congruent odor-category pairs providing an «olfactory dominance» effect (Hörberg et al., 2020).

Continuing the axis of social-related sensory cues, we could broaden studied categories to confirm definitively the social role of odor context. Rekow et al. (2021) already investigated categorization of face-like stimuli that do not represent the faces directly, rather giving pattern of facial features to the object (e.g., cup of coffee). Studies on this category demonstrated increasing face-like selective response in the presence of maternal odor in 4-month-old infants and even in adults with the same effect of body odor (Rekow et al., 2022). We hypothesize that body parts or objects of daily life with social meaning (e.g., feeding bottle, cuddly toy) can be categorized as well as faces with intersensory facilitation coming from maternal odor. It is known that 2-to-9-month-old infants already show the ability to distinguish body parts from faces, objects and social scenes (Kosakowski et al., 2022). Moreover, Fausey et al. (2016) found that infants aged 1 month to 2 years demonstrate attentional shift from faces to hands as their visual environment changes due to the increasing locomotion. Thus, future researches could not only confirm social orientation of maternal odor effects but also determine which type of social stimuli is more amenable to the intersensory facilitation across different age stages.

Finally, we would like to broaden range of olfactory cues that we use in our face categorization studies. Currently we are far from understanding which type of chemical compound in maternal odor drives the face processing, however testing different odors during face categorization we could find their similar characteristics. What is paramount? Familiarity of odor in the daily infant life or hormonal smellscape of mother linked with recent birth and lactating status? The odors create an ideal context for association formation and therefore memory due their stability in space and time (Sela & Sobel, 2010). It was confirmed by several studies on the influence of odor context on the memory retrieval on 3 month-old infants (Rubin et al., 1998; Schroers et al., 2007). As face represent the first and more salient visual cue after birth, probably, infant brain can associate it with other often presented odor in the his environment (e.g., father's odor or perfume diffused at home). On the other hand, multisensory face processing was already investigated using the odor of stranger mother that does not suppose the olfactory familiarity. Interestingly, that found effects exactly or in the same line repeated the influence of maternal odor (Durand et al., 2020; Jessen, 2020). It is known that newborns are very sensitive to the milk odor distinguishing the breast odor of lactating women from non-lactating (Makin & Porter, 1989), human milk from formula milk (Marlier & Schaal, 2005) and also recognizing milk from different lactation stages (Klaey-Tassone et al., 2020). In addition, odorous compounds of human milk were well investigated during last decades (Buettner, 2007; Loos et al., 2019), while complex composition of maternal odor still not completely discovered. Thus, we do not have direct evidences for the infant sensitivity to the women hormonal status and future studies will allow us to compare neural signatures of face categorization in context of different women odors (mother, stranger mother, stranger and not stranger nulliparous woman) with parallel chemical analysis of odor compounds.

3.2 Jumping to adults

3.2.1 How does odor-driven face categorization develop in childhood?

Over the first year, Study 1 and 3 shed some light on the qualitative/quantitative development of the face-selective visual response with an apparently declining odor effect. But how do similar processes occur later in infancy and childhood? Many gaps remain in the literature on both the development of recognition of faces and social odors. For example, children of 3-8 years recognize their mother's odor at a significant level (Roberts & Eryaman, 2017; Schaal et al., 1980), and seem to rebound in this ability around adolescence (Weisfeld et al., 2003; Ferdenzi et al., 2010). In addition, the olfactory recognition of siblings (Porter & Moore, 1981) and classmates (Verron & Gaultier, 1976; Mallet & Schaal, 1993) comes to the fore at this developmental stage, and such social odors could could then be used as salient olfactory cuse in future researches. Regarding the development of face detection/recognition/categorization in childhood, this process becomes rapidly efficient on its own (Lochy et al., 2019; Vettori et al., 2019), and we can suppose that, according to the principle of inverse effectiveness, older infants and children will not rely on odor related intersensory facilitation, at least when the conditions of detection/recognition/categorization are not too demanding.

3.2.2 How mature is the infant face-selective response compared to the adults?

As we reviewed over the preceding sections, the visual system takes dramatic changes between first months after birth and the end of first year putting visual abilities on a new qualitative level. Accordingly, some studies argue that 12-month-old infants already demonstrate adult-like patterns in face processing (Conte et al., 2020; Halit et al., 2003). Relating to our data, notably the Studies 1 and 3, we report that amplitudes of the face-selective response (independent on odor context) is on the same level as amplitudes in adult studies (e.g., Rekow et al., 2022). Oldest infant group in Study 1 showed 2.60 ± 0.47 µV (electrodes P7/8, O1/2), infants in the Standard group in Study 3 demonstrated 2.14 ± 0.30 µV (electrodes P7/8, P9/10, PO5/6, PO7/8), while in adults authors observed 2.56 ± 0.21 µV (electrodes P7/8, P9/10, PO7/8; Rekow et al., 2022). Thus, these results suggest that there is no quantitative difference between so distant ages.

However, we remain careful while comparing EEG amplitudes between infant and adults as the background EEG natural activity in infants is usually higher than adults (Bell & Wolfe, 2008) due to the increased cortical shape complexity with age (Kim et al., 2016) and maturation at skull's level as fontanel closes around 14 months (Duc & Largo, 1986). Moreover, comparing only the amplitude does not take into account the complexity of the brain response. For this purpose, we can also compare the range of significant harmonics (integer multiplies) of the face-selective response. In adults this distribution goes up to high frequencies (e.g., until 18.67 Hz that corresponds to the 14th significant harmonics with face presentation rate 1.33 Hz in Rekow et al., 2022), while in Study 3, (Fast group), we have observed only one sole harmonic applying the same stimulation parameters to the group of 11-to-13 month-olds. Interestingly, in latter study we have revealed that there is an increase in visual demand when the rate of image presentation is doubled (i.e., from 6 to 12 images per second), while comparing 2 groups of 11-to-13 month-old infants. However, in adults, a rate of 12 Hz with a 1.33 Hz face presentation frequency have been recommended to optimize testing duration while reaching the optimal interface interval (Retter et al., 2020). Thus, since infants are affected by the speed manipulation but that adults are apparently not, this strongly suggest that the infant generic response to faces is still not as mature as adults.

To tackle this issue directly, we tested a novel group of 27 infants (9 females, mean age ± SD: 394 ± 33.4 days) and 28 adults (18 females, 3 left-handed, mean age ± SD: 22 ± 2.5 years old). In this study, we used the identical visual conditions as in Study 3 (Standard and Fast visual condition, see sections 2.2 and 2.4) however, participants were all exposed to the 2 visual conditions in a within-subjects paradigm and no olfactory stimulation was introduced. Preliminary analyses were carried out on the ROIs defined in adult study of Rekow et al. (2022) which used a similar face categorization design at 1.33 Hz in 12 Hz stimulation sequences (i.e., identical to the Fast group). Based on the maximum range of significant harmonics distribution measured in adults in the Standard group, we summed the amplitudes of the face-selective response for 19 and 14 harmonics for the Standard (until 19 Hz) and Fast (until 18.67 Hz) conditions respectively, similarly for both age groups. Figure 3.2 illustrates the significant decrease *($p = .03$)* of face-selective response over rOT (averaged electrodes P8, P10, PO8) in the Fast group compared to the Standard in infants, while the face-selective response in adults is similar, regardless of the speed of presentation. Despite the fact that the face-selective response in the Standard group yields a higher amplitude response in infants than in adults (due to the neuroanatomical changes explained above), a significant difference is found only in the infants group, in favor of a higher response for the condition with the lower visual demand. Indeed, increasing visual demand in Fast group seems to be impeding face categorization in infants as visual system continue its anatomical and functional development.

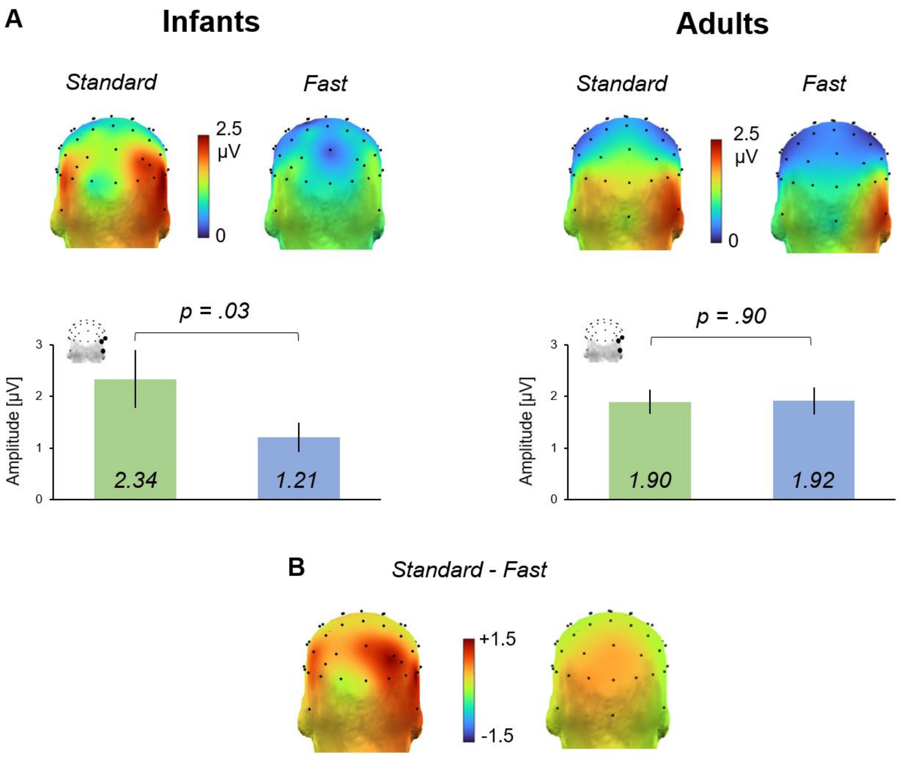

Figure 3.2. Preliminary results for the different patterns of face-selective response according to the visual demand in 12-month-old infants and adults. A. The amplitude of the face-selective response over right occipitotemporal cortex (rOT) (averaged across P8, P10, PO8) in infants (left) and adults (right). In infants the face-selective response in the Fast group (blue) is significantly decreased compared to the Standard group (green) by - 1.13 ± 0.50 µV ($p = .03$), while in adults face-selective response is comparable ($p = .90$). Error bars represent standard errors of the mean. 3-D topographical head maps show the spatial distribution of the responses (back view). **B.** Difference (Standard minus Fast) between Standard and Fast groupsin the face-selective response in infants (left) and adults (right).

These promising preliminary results allows us to better understand effectiveness of visual categorization across different developmental stages. Future studies in the same field will highlight critical points of visual development when contribution of additional sensory cues could be potentially crucial in the context of multisensory integration.

3.3 Olfactory-to-visual strategies as subliminal aids for infants with neurodevelopmental disorders

Autism Spectrum Disorders (ASD) are characterized by early impairments in the social cognition, especially in visual domain (American Psychiatric Association, 2013; Barros & Soares, 2020). Decrease of spontaneous attention to the social stimuli (in 6-month-old infants: Chawarska et al., 2013; in children and adolescents: Riby et al., 2012; Riby & Hancock, 2008, 2009) and especially to the eye region (Ristic et al., 2005; Senju & Johnson, 2009). All together it impacts face processing (Dawson et al., 2005) as emotional (Baron-cohen et al., 1993; Farran et al., 2011; Gross, 2008) and identity recognition (Tang et al., 2015) that leads to the difficulties in social interactions (Chevallier et al., 2012; Senju, 2013). One of genomic disorder hilly associated with ASD (15–50% of cases) is called 22q11.2

deletion syndrome (22q11.2DS) (Ousley et al., 2017). Studies on this syndrome also showed the difficulties in the facial expression discrimination (Leleu et al., 2016, 2019), abnormal eye-gaze within the face exploration (Glaser et al., 2010) and deteriorated socio-emotional behaviors (Jansen et al., 2007).

In view of that olfaction plays important role in emotional processing (Hatfield et al., 1993), this sense can become a bridge for socioemotional information in ASD and 22q11.2DS (Barros & Soares, 2020). Indeed, body odors represent a crucial olfactory cues that mediates social communication (Lübke & Pause, 2015) and taking together with early functioning of olfaction compare to the vision (Lecanuet & Schaal, 1996), we suppose that olfactory-visual interaction can be very promising in the correction of these pathological cases. Moreover, children with ASD demonstrate intact odor detection (Sweigert et al., 2020) that may be used for the forming of familiarity odor context. The positive effect of odor familiarization on food preferences was already investigated in ASD children (Luisier et al., 2019). Considering the important role of maternal odor in social interactions (Schaal et al., 2020), Parma et al. (2013, 2014) showed increasing social imitation and facilitation of action planning in ASD children in the presence of maternal but not stranger body odor.

Several frequency-tagging EEG studies in ASD children between 8 and 12 years old demonstrated impaired individual face discrimination but not rapid face categorization (Vettori et al., 2019, 2020). It seems that at late children age this ability is enough developed, however, in early infancy individuals with ASD and 22q11.2DS probably will have difficulties in rapid face categorization. Unfortunately, most of diagnostics of ASD are realized after 3 years and our paradigm could facilitate early detection of neurodevelopmental disorders linked to the social interactions. Moreover, future studies on the familiarity of odor contexts and its influence on the face processing could open promising avenues to the compensatory mechanisms from very early developmental stages. Thus, confirmed in this doctoral work inverse effectiveness principle seems to be applicable to pathological cases when one sensory modality is not effective on its own and needs contribution of second sense.

4. General conclusion

The present research investigated the principle of inverse effectiveness in olfactory-visual interactions across early development. In particular, we examined the influence of maternal odor on rapid face categorization over first year according different visual demands. We recorded scalp electroencephalograms using a frequency-tagging EEG approach while infants were exposed to their mother's body odor or to a baseline odor. The visual stimulation consisted in a rapid periodic streams of natural (Study 1 to 3) or simplified (Study 2) images at periods of 6 Hz (Study 1 to 3) or 12 Hz (Study 3) with human faces inserted every 6th (Study 1 to 3) or 9th (Study 3) stimulus among other non-face objects to tag a face-selective response at 1 or 1.33 Hz, respectively. On the one hand, the maternal odor effect emerged only in younger infants (Study 1 and 2) and exclusively with natural stimuli that elicited a focal and weak unisensory face-selective response in the baseline odor context, reflecting more demanding face categorization. On the other hand, older infants (Study 1 and 3) showed an enhanced face categorization, probably due to the visual improvements that may explain the absence of odor influence (vision is effective on its own). Reducing the visual demand of the categorization task in younger infants (Study 2) leads to the same effect as in older infants (Study 1 and 3); but this time, we interpret the results not in terms of developmental improvement of vision, but by the fact that the simplified stimuli may have facilitated visual categorization, with a stronger face-selective response and a weaker odor effect. Taken together, these results confirm the inverse effectiveness principle in olfactory-visual interactions in infancy, in that categorization relies more effectively on multisensory cues when unisensory inputs are not fully effective.

These findings contribute further to our understanding of the functional interactions of olfaction and vision at early age. One important outcome is that olfaction is an crucial player in the field of multisensory integration, obeying the inverse effectiveness principle on a par with other senses. We wish these results and approaches can open new avenues for future studies on the integrative mechanisms of different sensory domains in typical, as well as in atypical, human development.

Résumé de thèse

L’efficience inverse de l'influence de l'odeur maternelle sur la catégorisation des visages chez le nourrisson

1. Introduction

Chaque jour, nous recevons une grande quantité d'informations provenant de nos différents sens. En principe, nous gérons ces signaux de manière très efficace, souvent en les fusionnant en des perceptions unifiées (par exemple, la fusion de l’olfaction, de la gustation et des sensations trigéminales dans ce que nous appelons communément « le goût »). L'apparente facilité et automaticité de ce processus de multisensorialisation est toutefois sous-tendue par des mécanismes cérébraux complexes. Si ces mécanismes commencent à être bien connus chez l’adulte, la façon dont la perception multisensorielle émerge au début de la vie et se développe reste très floue. L'interaction entre les capacités prédisposées disponibles dès la naissance et l'expérience acquise joue un rôle clé dans l'apprentissage perceptif (Arterberry et Kellman, 2016), mais les débats restent vifs entre chercheurs sur la capacité des nouveau-nés et très jeunes enfants à fusionner l'information qui vient des différents sens dès la naissance ou si cette capacité n'est pas ou peu fonctionnelle au début de la vie et se développe progressivement au cours de l’enfance. Au cours des dernières décennies, les données s’accumulent en faveur du fait que les nourrissons fusionnent les entrées sensorielles très précocement en une synergie multisensorielle qui se façonne avec l'âge et s'accorde aux besoins du moment (Bahrick et Lickliter, 2012; Lewkowicz et al., 2010).

1.1 Intégration multisensorielle

L’intégration multisensorielle repose sur un ensemble de principes qui ont été mis en évidence dans les réponses comportementales et cérébrales, chez les animaux et les humains. Un premier mécanisme impliqué dans la synthèse des modalités sensorielles est la super-additivité de l'efficience de la combinaison de stimuli issus de différentes modalités par rapport à l'efficience de chaque stimulus isolé (Stein et Stanford, 2008). Par exemple, la réponse neuronale aux informations visuelles et auditives combinées est plus forte que la réponse à un seul de ces stimuli sensoriels. L'intégration multisensorielle repose aussi sur la synchronisation des évènements dans le temps et espace (Meredith & Stein, 1986). Il est intéressant de noter que cette synchronie intersensorielle est détectée très tôt dans le développement. Par exemple, les nouveau-nés et les nourrissons âgés de 4 à 10 mois démontrent une sensibilité à la synchronie audiovisuelle (Lewkowicz et al., 2010). L'intégration multisensorielle suit également le principe de l’efficience inverse (Stein et Meredith, 1993). Selon ce principe, les réponses unisensorielles les plus faibles bénéficient le plus de l'intégration multisensorielle. Le principe d’efficience inverse a été étudié pendant les plusieurs années chez l’animal (Avillac et al., 2007; Foxworthy et al., 2013; Meredith & Stein, 1983; Siemann et al., 2015) et chez l’humain, en particulier chez l’adulte, grâce à différentes méthodes (Regenbogen et al., 2016; Stevenson et al., 2007, 2012; Stevenson & James, 2009; Werner & Noppeney, 2010).

Le principe d’efficience inverse a aussi été démontré au cours du développement perceptif du nourrisson humain. Par exemple, les nourrissons de 3 mois discriminent le tempo d'un marteau qui tape lorsque les informations visuelle et auditive sont disponibles, mais ils n’y arrivent pas dans les conditions unisensorielles où seule une information est disponible (Bahrick et al., 2002). Ce phénomène est appelé « facilitation intersensorielle » (Bahrick & Lickliter, 2000) car deux sources d’information sont plus efficaces qu’une seule. En revanche, à 5 mois, les nourrissons ne bénéficient plus de cette facilitation intersensorielle car ils deviennent capables de discriminer le tempo du marteau aussi bien en situation unisensorielle que multisensorielle (Bahrick & Lickliter, 2004). Dès lors, si l'on augmente la difficulté de la tâche de discrimination, les nourrissons de 5 mois recourent à nouveau à la facilitation intersensorielle, c’est-à-dire qu’ils sont meilleurs pour discriminer le tempo en situation multisensorielle (Bahrick et al., 2010).

Les différents principes d’intégration multisensorielle ont été majoritairement évalués en considérant l'intégration des stimulations visuelles et auditives. En particulier, le principe d'efficience inverse lié à la faciliation intersensorielle chez le nourrisson n’a jamais été testé en situation chimio-sensorielle. Ainsi, l’objectif de notre travail a été de déterminer si ce principe s'applique à une modalité sensorielle telle que l'olfaction chez le nourrisson humain.

1.2 Rôle des odeurs dans la perception des congénères : l’importance de l’odeur maternelle

L'olfaction présente des avantages par rapport à la communication visuelle et auditive (Lübke & Pause, 2015; Schaal & Porter, 1991). Les odeurs sont stables dans l'espace et dans le temps (Sela & Sobel, 2010), efficaces dans des environnements sombres ou bruyants, et restent présentes malgré l’absence physique de l'émetteur. Ces avantages font de l’olfaction un moyen privilégié de communication entre les congénères (voir Pause, 2017), en particulier au tout début de la vie lors des premiers liens sociaux entre mère et enfant.

L'olfaction devient fonctionnelle très tôt, après le toucher et avant le système vestibulaire, et donc bien avant la vision (Lecanuet & Schaal, 1996). Dans le liquide amniotique, le fœtus est exposé à des composés odorants dont l'occurrence est régulée, entre autres facteurs, par l'état biologique de la mère dû au transfert transplacentaire (Schaal et al., 2002). Plus précisément, plusieurs études sur le régim alimentaire des femmes enceintes ont montré que l'olfaction est bien fonctionnelle in utero. En effet, les nouveau-nés expriment des réponses préférentielles ou discriminantes aux arômes ou aux odeurs auxquels ils ont été exposés dans l'environnement intra-utérin en raison du transfert de la mère au fœtus (ail: Hepper et al., 2013; Mennella & Beauchamp, 1993; anis: Schaal et al., 2000; carotte: Mennella, 2001; Ustun et al., 2022 et chou: Ustun et al., 2022).

Les analyses chimiques du liquide amniotique indiquent une certaine ressemblance dans les environnements olfactifs prénatal et postnatal, en particulier par le colostrum et le lait (Schaal, 2005, 2016). L'odeur matérielle est donc un signal olfactif très puissant après la naissance car le nourrisson le connait depuis l'environnement intra-utérin. En effet, les nouveau-nés démontrent une capacité fiable de localisation spatiale des signaux olfactifs de faible intensité qui, pour la plupart, stimulent l'activation sensori-motrice (Rosenblatt, 1983; Schaal, 2006). Par exemple, l'odeur du sein provoque une orientation de la tête ipsilatérale à une odeur préférée et favorise même le rampement vers la source d'odeur (Hym et al., 2021; Varendi et Porter, 2001). De plus, les odeurs du sein de la mère induisent également de plus longues périodes d'ouverture des yeux chez les nouveau-nés de 2 jours (Doucet et al., 2007), privilégiant l'orientation visuelle. Plus tard, chez les nourrissons de 4 mois, Durand et al. (2013) ont constaté que l'odeur maternelle augmente la durée de fixation visuelle des nourrissons sur un visage féminin inconnu plutôt que sur un objet non facial (une voiture). Ces résultats suggèrent que la congruence entre les indices sociaux olfactifs et visuels facilite la perception du visage.

1.3 L'influence de l'odeur maternelle sur la catégorisation des visages

Dans ce travail de thèse, nous nous sommes intéressés à l'influence de l'odeur maternelle sur la catégorisation du visage. La catégorisation est une fonction cognitive fondamentale qui permet de structurer les multiples entrées sensorielles en catégories distinctes, selon leur similitude ou d'autres critères communs. Cette fonction n'est pas évidente pour le cerveau immature, en particulier pour les visages, car les visages sont des stimuli complexes qui véhiculent de nombreuses informations, comme l'espèce, l'ethnie, le sexe, l'âge et l'identité des individus (Klein et al., 2009). Pour catégoriser rapidement les visages, les nourrissons doivent en effet 1) les distinguer des autres objets et 2) les généraliser en une seule une catégorie malgré leurs apparences variables.

Pour évaluer l'influence de l'odeur maternelle sur la catégorisation des visages chez le nourrisson de 4 mois, Leleu et al. (2020) ont utilisé une approche dite d'étiquetage fréquentielle en EEG. Les nourrissons étaient exposés à l'odeur corporelle de leur propre mère ou à une odeur témoin (t-shirt porté par la mère vs. odeur de base du t-shirt) lors d'une stimulation visuelle rapide d'images naturelles variées présentant des visages parmi différents objets. Cette approche permet d'isoler deux réponses cérébrales distinctes à deux fréquences différentes au sein de la même stimulation. Les images étaient présentées à une fréquence de 6 Hz, soit 6 images par seconde. Ainsi, une réponse visuelle générale était mesurée à cette fréquence de base de 6 Hz. Les visages étaient quant à eux insérés tous les 6 stimuli, soit une fréquence de présentation des visages de 1 Hz (c'est-à-dire à 6 Hz / 6 = 1 Hz). Cela permet de mesurer une réponse cérébrale sélective aux visages à cette fréquence dans le spectre de l'EEG. Les résultats ont été les suivants : premièrement, une réponse significative sélective aux visages a été enregistrée en regard du cortex occipito-temporal droit (rOT) quel que soit le contexte olfactif, représentant une signature neurale de la catégorisation des visages dans le cerveau du nourrisson de 4 mois. Deuxièmement, cette réponse sélective aux visages était relativement faible dans le contexte olfactif témoin, alors qu'en présence d'odeur maternelle, elle était significativement amplifiée. La différence d'amplitude de la réponse sélective aux visages entre les contextes d'odeur maternelle et de base a été appelée l'effet d'odeur.

Dans une autre étude, les auteurs ont montré que la présence de l'odeur maternelle n'a pas d'influence sur une réponse cérébrale sélective aux voitures, contrairement aux visages, mettant en évidence l'effet de congruence entre l'odeur et le visage de la mère (Rekow et al., 2020). En revanche, si les voitures sont remplacées par des objets ressemblant à des visages (c'est-à-dire des objets qui induisent la perception d'un visage illusoire chez l'adulte, phénomène appelé paréidolie faciale), les nourrissons du même âge présentent une augmentation significative de la réponse sélective aux visages illusoires en présence de l'odeur maternelle (Rekow et al., 2021). Cette activité cérébrale st est mesurée en regard du cortex occipito-temporal droit (rOT), comme dans l'étude de catégorisation des véritables visages humains. Dans toutes les études, la réponse visuelle générale reflétant la réponse visuelle commune à toutes les images en regard du cortex occipital médial n'était pas sensible à l'odeur maternelle. Ces résultats soutiennent la notion d'une influence spécifique de l'odeur maternelle sur la catégorisation des visages plutôt qu'un effet non spécifique d'augmentation de l'attention visuelle. Dans une dernière étude, les auteurs ont montré que contrairement aux nourrissons de 4 mois, les adultes n'ont d'effet d'une odeur corporelle sur la catégorisation des visages (Rekow et al., 2022). Il semble donc qu'un système visuel mature catégorise efficacement les visages sans aucune aide de l'odeur. Cependant, chez ces mêmes adultes, la réponse cérébrale sélective aux visages illusoires est augmentée en présence d'une odeur corporelle. Cela suggère que l'aptitude d'une odeur corporelle à influencer la catégorisation visuelle des visages est fonction de l'efficacité avec laquelle cette catégorisation s'opère, tel que le propose le principe d'efficience inverse.

2. Hypothèses et méthodologie

La littérature abordée en Introduction suggère que dans le cadre de l'influence d'une odeur corporelle sur la catégorisation des visages, le principe d'efficience inverse s'applique. En effet, nous avons vu que : (1) la réponse sélective aux visages humains, chez l'adulte, n'est pas modulée par un odeur corporelle, contrairement à celle mesurée chez le nourrisson de 4 mois ; (2) la réponse sélective aux visages illusoires est en revanche amplifiée par une odeur corporelle, aussi bien chez l'adulte que le nourrisson de 4 mois. Il semble donc que l'effet de l'odeur, soit la facilitation intersensorielle de l'odeur sur la catégorisation des visages, est fonction du l'efficience de la réponse unisensorielle seule. Autrement dit, la réponse unisensorielle la plus forte bénéficie le moins de l'intégration multisensorielle, tel que le prévoir le principe d'efficience inverse. Cependant, le fait que ce principe s'applique aux interactions odeur-vision au cours du développement perceptif dans la petite enfance doit encore être démontré. Ainsi, notre objectif est de mettre en évidence l'efficience inverse de l'effet de l'odeur de la mère sur la catégorisation des visages chez le nourrisson, avec l'hypothèse principale que **l'effet de l'odeur maternelle sur la catégorisation des visages est fonction du principe d'efficience inverse au cours du développement perceptif précoce**.

Pour tester cette hypothèse nous avons mené trois études incluant différents groupes d'âge :

Dans **l'étude 1**, nous évaluons le développement de l'effet de l'odeur sur la catégorisation des visages au cours de la première année de vie (entre 4 mois et 12 mois). Nous prédisons une réponse sélective aux visages qui croît progressivement entre 4 et 12 mois, reflétant le développement de la catégorisation des visages, et un effet de l'odeur qui décroît en parallèle, à mesure que la vue devient efficace pour catégoriser les visages sans autre information sensorielle.

L'étude 2 se concentre sur les nourrissons de 4 mois qui ont une faible réponse sélective aux visages sensible à l'odeur maternelle. Ici, chez un premier groupe de nourrissons, nous utilisons des stimuli visuels identiques à ceux utilisés précédemment pour démontrer l'effet de l'odeur maternelle (diverses images naturelles difficiles à catégoriser pour le cerveau du nourrisson). Chez un second groupe, nous utilisons des stimuli simplifiés pour faciliter la catégorisation des visages. Nous prédisons ainsi une augmentation de la réponse sélective aux visages chez le second groupe, reflétant une perception visuelle facilitée. Selon le principe d'efficience inverse, nous nous attendons aussi à ce que cette catégorisation visuelle moins exigeante soit moins sensible à l'effet d'odeur maternelle.

L'étude 3 se concentre enfin sur les enfants de 12 mois qui ont une réponse sélective aux visages forte et peu sensible à l'odeur maternelle (étude 1). Chez un premier groupe, nous utilisons le paradigme habituel. Chez un second groupe, nous présentons augmentons la difficulté visuelle en accélérant la vitesse de présentation des images et des visages. Nous nous attendons ainsi à trouver une réponse sélective aux visages diminuée et un effet de l'odeur accentué pour cette catégorisation des visages plus exigeante proposée au second groupe.

La méthode utilisée dans toutes les études présentées consiste en un étiquetage fréquentiel en EEG, une mesure de catégorisation des visages au niveau du cerveau qui est adaptée aux aptitude des nourrissons. L'EEG n'est pas invasif et permet l'évaluation directe de l'activité cérébrale en temps réel. Des électrodes EEG placées sur le cuir chevelu enregistrent une activation synaptique synchronisée dans les neurones corticaux. Grâce à une résolution temporelle élevée, l'EEG permet de suivre les réponses cérébrales à une stimulation externe. Malgré sa résolution spatiale approximative, l'EEG peut engendrer une localisation topographique de la source de cette activité cérébrale (Jackson & Bolger, 2014). L'analyse des réponses électrophysiologiques peut être effectuée non seulement dans le temps, mais également dans le domaine fréquentiel. Lors d'une stimulation périodique, l'activité cérébrale se synchronise à la fréquence de la stimulation (Adrian & Matthews, 1934). Le paradigme de stimulation visuelle périodique rapide (FPVS) que nous utilisons est basé sur la présentation imbriquée de deux types de flux visuels conçus à un rythme rapide. Une catégorie cible (par exemple, les visages) est périodiquement insérée parmi diverses catégories d'objets. Par exemple, les stimuli peuvent être présentés à une fréquence de base F = 6 Hz (soit 6 images par seconde, durée de présentation des stimuli = 1 / F = 1/6 = 167 ms). Les visages (c'est-à-dire la catégorie cible) peuvent être périodiquement insérés tous les n = 6 stimuli, à une fréquence de présentation des visages F/n = 6/6 = 1 Hz (1000 ms entre chaque visage). Ainsi, l'approche d'étiquetage fréquentiel en EEG permet de dissocier deux réponses cérébrales différentes générées par les deux fréquences au sein de la stimulation : 1) la réponse sélective à la catégorie cible (visages) reflète une catégorisation visuelle de haut niveau et 2) la réponse visuelle générale qui correspond au traitement de signaux visuels de bas niveau (par exemple, contraste, luminosité) (Regan, 1966). Enfin, l'approche peut être utilisée pour mesurer la réactivité cérébrale dans des contextes sensoriels distincts. Dans notre cas, la stimulation visuelle est présentée dans des contextes olfactifs contrastés représentés par l'odeur d'un t-shirt imprégné des sécrétions cutanées maternelles contre l'odeur de base d'un t-shirt non porté.

3. Partie expérimentale

3.1 Etude 1. La facilitation intersensorielle (olfactive à visuelle) dans le cerveau du nourrisson diminue progressivement de 4 à 12 mois

Jusqu'à présent, les principes sous-tendant le développement multisensoriel ont été plus souvent étudiés avec des stimuli auditifs et visuels. Cependant, des influences intersensorielles au début de l'enfance peuvent également se produire pour un sens comme l'olfaction. Par exemple, les nourrissons de 3 mois regardent plus longtemps un visage souriant associé à une odeur agréable plutôt que désagréable (Godard et al., 2016). À 4 mois, l'exposition à l'odeur corporelle de la mère augmente la durée de regard sur un visage par rapport à une voiture (Durand et al., 2013), et au visage de la mère par rapport au visage d'une étrangère (Durand et al., 2020). Au même âge, l'odeur maternelle facilite la catégorisation des visages, telle qu'indexée par une plus forte réponse EEG sélective aux visages au niveau du cortex occipito-temporal droit (Leleu et al., 2020; Rekow et al., 2020). De même, lorsque des objets ressemblant à des visages (provoquant une paréidolie faciale chez les adultes) sont rapidement présentés parmi d’autres objets non faciaux appartenant aux mêmes catégories, l'odeur corporelle de la mère déclenche une réponse EEG sélective identique à celle observée pour un visage chez les nourrissons de 4 mois (Rekow et al., 2021).

Ces études indiquent que les odeurs sont susceptibles d'influencer la perception visuelle chez les nourrissons. Ici, nous cherchons à savoir si l'effet de l'odeur maternelle observé sur la catégorisation des visage à 4 mois (Leleu et al., 2020; Rekow et al., 2020, 2021) suit le principe d'efficience inverse appliqué au développement perceptif, c'est-à-dire que la facilitation intersensorielle diminue à mesure que la perception unisensorielle se développe, comme montré avec des stimulations audiovisuelles. En effet, les études mentionnées utilisaient un mode rapide de stimulation visuelle associé à une variété de stimuli naturels, ce qui rendait la catégorisation des visages difficile pour le cerveau de 4 mois. Chez les adultes, qui catégorisent efficacement les visages humains, il n'y a pas une telle amélioration avec une odeur corporelle, à l'exception de la catégorisation moins efficace des objets ambigus ressemblant à des visages (Rekow et al., 2022). Par conséquent, ces résultats suggèrent que l'impact d'une odeur corporelle pourrait s'estomper progressivement à mesure que la capacité à catégoriser les visages se développe.

Pour évaluer ce phénomène, nous avons testé 50 nourrissons, âgés de 4 à 12 mois, alors qu'ils étaient exposés à des flux rapides d'images présentées à 6 Hz (6 images/s), avec des visages humains insérés toutes les 6 images pour mesurer une réponse neurale sélective aux visages à 1 Hz et ses harmoniques (multiples entiers) dans le spectre EEG. Lors de la stimulation visuelle, les nourrissons étaient alternativement exposés à un contexte d'odeur maternelle ou témoin. Dans une première série d'analyses, nous avons examiné le développement de la réponse sélective aux visages mesurée dans le contexte olfactif témoin pour déterminer si la catégorisation des visages devient plus efficace avec l'âge. Dans un deuxième temps, nous avons analysé l'évolution de l'effet d'odeur maternel sur la catégorisation des visages en fonction de l'âge, en émettant l'hypothèse d'un effet de l'odeur chez les nourrissons les plus jeunes qui disparaît progressivement chez les nourrissons les plus âgés. Enfin, nous avons mené les mêmes analyses sur la réponse visuelle générale (6 Hz et harmoniques) pour évaluer si le déclin de l'effet odeur avec l'âge est sélectif aux visages.

Nous avons identifié une réponse neuronale sélective aux visages enregistrée sur le cortex occipito-temporal et se développant en fonction de l'âge, à la fois quantitativement (amplitude plus grande) et qualitativement (distribué sur plus d'harmoniques dans le spectre EEG). Nous avons aussi retrouvé une réponse sélective aux visages plus forte sur l'hémisphère droit en présence de l'odeur de la mère pour les plus jeunes nourrissons (Leleu et al., 2020; Rekow et al., 2021). Enfin, nous avons démontré que cet effet de l'odeur maternelle diminue progressivement à mesure que la catégorisation des visages se développe (avec l'âge). La réponse visuelle générale enregistrée sur le cortex occipital médial est quant à elle insensible à la présence d'odeur maternelle, excluant une simple influence sur l'attention visuelle ou l'éveil général. Dans l'ensemble, nos résultats indiquent que pendant le développement perceptif précoce, la facilitation intersensorielle entre l'olfaction et la vision diminue à mesure que la perception visuelle se développe, prolongeant les résultats antérieurs avec des stimulations audiovisuelles (Bahrick et al., 2004) et les généralisant aux interactions olfaction-vision.

3.2 Etude 2. L'efficience inverse de la facilitation intersensorielle (olfactive à visuelle) dans le cerveau de 4 mois

Le principe de facilitation intersensorielle stipule qu'aux premiers stades du développement, les stimulations multisensorielles sont perçues plus efficacement que les stimulations unisensorielles lorsque ces dernières ne sont pas encore facilement traitées (Bahrick & Lickliter, 2012). Ensuite, cette facilitation intersensorielle diminue au cours du développement, en lien avec le principe d'efficience inverse (Meredith et Stein, 1983; Stevenson et al., 2007). L'étude 1 a montré que la facilitation intersensorielle de l'odeur de la mère diminue progressivement à mesure que la catégorisation des visages se développe entre 4 et 12 mois. De plus, une étude chez l'adulte a révélé que l'activité EEG sélective aux visages n'est pas influencée par une odeur corporelle pour les visages humains, qui sont facilement catégorisés, mais encore renforcée pour les objets ambigus ressemblant aux visages, qui sont moins efficacement catégorisés (Rekow et al., 2022). Ce compromis développemental suggère bien que la facilitation de l'odeur sur la vision suit le principe d'efficience inverse car elle disparaît progressivement lorsque la catégorisation visuelle s'améliore et devient efficace.

Ici, pour déterminer directement l'efficience inverse de l'odeur maternelle sur la catégorisation des visages chez les jeunes nourrissons, nous avons manipulé la difficulté perceptive chez deux groupes d'enfants de 4 mois. Le premier groupe (groupe 1, stimuli naturels) a été exposé à un ensemble très variable de stimuli naturels utilisés dans les études antérieures montrant un effet de l'odeur maternelle sur la catégorisation des visages (Leleu et al., 2020; Rekow et al., 2021, 2020) et dans notre étude 1. Le deuxième groupe (Groupe 2, stimuli simplifiés) a été exposé à un ensemble moins variable de stimuli modifiés pour réduire la variabilité physique entre les stimuli faciaux tout en maintenant une variabilité élevée entre les stimuli faciaux et les objets, diminuant ainsi la difficulté perceptive visuelle par rapport aux stimuli naturels. Dans les deux groupes, les stimuli ont été présentés sous forme de flux rapides de 6 stimuli/s (à 6 Hz) avec des visages insérés tous les 6 stimuli pour mesurer la réponse sélective aux visages à 1 Hz et harmoniques dans le spectre EEG. Au cours de la stimulation visuelle, les nourrissons ont été alternativement exposés aux deux mêmes contextes olfactifs que dans l'étude 1. Nous nous attendions à une réponse sélective aux visages plus forte dans le groupe 2 (stimuli simplifiés) que dans le groupe 1 (stimuli naturels), reflétant une catégorisation des visages moins exigeante pour le premier. Nous nous attendions également à une réponse plus forte dans le contexte de l'odeur la mère que dans le contexte olfactif témoin uniquement pour le groupe 1 (stimuli naturels), indiquant une facilitation intersensorielle lorsque la perception visuelle n'est pas assez efficace.

Ainsi, premièrement, nous avons confirmé que la capacité à catégoriser une variété de visages humains à 4 mois dépend de la complexité des stimuli visuels, s'améliorant pour les stimuli simplifiés (groupe 2) par rapport aux stimuli naturels (groupe 1). Deuxièmement, l'odeur corporelle de la mère favorise une catégorisation des visages uniquement lorsque la difficulté perceptive est élevée (groupe 1, stimuli naturels), cet effet disparaissant lorsqu'elle est réduite (Groupe 2, stimuli simplifiés). Par conséquent, nos résultats fournissent la preuve que la facilitation de l'odeur sur la vision suit le principe d'efficience inverse dans le cerveau du nourrisson de 4 mois, prolongeant les études antérieures ayant utilisé une stimulation audiovisuelle (Bahrick et al., 2010).

3.3 Etude 3. Quand l'odeur maternelle entrave la catégorisation visuelle dans le cerveau du nourrisson d'un an : un cas de surcharge sensorielle ?

Nous savons que l'odeur maternelle facilite la catégorisation des visages (Leleu et al., 2020) ou des objets ressemblant à des visages (Rekow et al., 2021), mais pas des voitures dans le cerveau de 4 mois (Rekow et al., 2020). Cette interaction multisensorielle est liée à la difficulté de la tâche, car l'effet diminue tandis que la réponse sélective aux visages augmente entre 4 et 12 mois (étude 1). De plus, aucune facilitation des odeurs n'est trouvée chez les adultes pour lesquels la réponse sélective aux visages est forte en présence ou en l'absence d'odeur corporelle (Rekow et al., 2022), sauf lorsque la difficulté visuelle est accrue en utilisant des stimuli ambigus qui ressemblent à un visage (Rekow et al., 2022). Inversement, chez les nourrissons de 4 mois dont la réponse sélective aux visages naturels non édités est renforcée par l'odeur de la mère (Leleu et al., 2020), l'effet de l'odeur est supprimé avec des stimuli visuels simplifiés, permettant une catégorisation des visages efficace même avec la seule stimulation visuelle (étude 2). Globalement, la contribution de l'olfaction pour catégoriser un objet visuel semble importante lorsque le stimulus visuel est ambigu ou dégradé.

Cependant, les études précédentes ne permettent pas de savoir si l'interaction olfaction-vision et son lien à la difficulté de la catégorisation visuelle peuvent être observés sans changer le type de stimuli visuels utilisé. Par ailleurs, elles questionnent le fait que ce principe d'efficience inverse est présent tout au long du développement, en particulier chez les nourrissons de 12 mois chez qui l'effet de l'odeur maternelle disparaît (étude 1). La présente étude a donc évalué si le principe d'efficience inverse était observé chez les nourrissons de 12 mois. Considérant qu'à cet âge, les nourrissons montrent une réponse sélective aux visages assez forte dans un flux d'images à 6 Hz avec des visages insérés tous les 6 stimuli, nous avons rendu la stimulation visuelle plus difficile en doublant la vitesse de stimulation (soit un flux de stimulation à 12 Hz). Un premier groupe de nourrissons a été exposé à des séquences Standard à 6 Hz tandis qu'un autre a été exposé à des séquences Rapides à 12 Hz (utilisées de manière optimale chez l'adulte, Retter et al., 2020; Rekow et al., 2022). Nous avons conservé les mêmes types de stimuli dans les séquences visuelles Standard ou Rapides, mais leur durée de présentation à l'écran était de 167 ms (Standard) ou 83 ms (Rapide). De plus, les visages ont été insérés à des rythmes différents : en tant que 6ème stimulus pour la condition Standard, soit une fréquence de présentation des visages de 1 Hz (intervalle entre les visages: 1000 ms) ; en tant que 9ème stimulus pour la condition Rapide, soit une fréquence de présentation des visages de 1,33 Hz (intervalle entre les visages: 750 ms). Ainsi, la condition Standard est perceptivement moins difficile que la condition Rapide. Nous émettons l'hypothèse que: (1) la réponse sélective aux visages devrait être plus faible dans la condition Rapide par rapport à la condition Standard en raison d'une difficulté visuelle plus élevée, et (2) une facilitation intersensorielle (effet de l'odeur positif) ne devrait émerger que dans le groupe Rapide, démontrant ainsi l’efficience inverse de la facilitation de l'olfaction sur la vision.

Conformément à nos hypothèses, la réponse sélective aux visages sur le cortex occipito-temporal dans le groupe Rapide était deux fois plus faible en raison d'une demande visuelle elevée. De plus, dans le groupe Standard, la réponse sélective aux visages ne changeait pas en présence de l'odeur de la mère. Ce résultat corrobore les données précédentes (étude 1) mais dans un seul groupe de participants âgés de 12 mois. Cependant, contrairement à nos hypothèses, dans le groupe Rapide, les résultats n'ont pas suivi le principe d'efficience inverse : au lieu d'une réponse sélective aux visages plus élevée dans le contexte olfactif maternel, nous avons noté une réponse diminuée, indiquant un effet de l’odeur délétère. De plus, nous avons observé un effet de l’odeur tendanciel sur la réponse visuelle générale: alors que dans le groupe Standard, elle était insensible à l'odeur maternelle comme systématiquement rapporté dans les études précédentes utilisant une stimulation visuelle similaire à 6 Hz (Leleu et al., 2020; Rekow et al., 2021), dans le groupe Rapide à 12 Hz, nous avons trouvé une tendance à ce que la réponse soit réduite dans le contexte de l’odeur maternelle, ce qui expliquerait la réduction de la réponse sélective aux visages dans la même condition visuelle. Globalement, ces résultats peuvent être interprétés en termes de surcharge sensorielle.

4. Discussion

Un certain nombre d'études ont démontré à quel point l'intégration multisensorielle est avantageuse pour l'apprentissage perceptive dans la petite enfance. Cela a été clairement démontré pour l'audition et la vision (Bahrick et Lickliter, 2000; Lewkowicz, 2010), qui sont reconnus comme les sens dominants chez les adultes humains et ont donc été bien étudiés par rapport aux autres sens. Cependant, cette facilitation intersensorielle change avec l'âge, en raison de meilleures capacités sensorielles, d'une meilleure formation de l'attention et d'une expertise accrue (Bahrick et Lickliter, 2012). Ces résultats suivent le principe de l'efficience inverse. On ignore toutefois si ce principe s'applique aux autres sens, par exemple l'olfaction. Ainsi, l'objectif de ce travail de thèse, en s'appuyant sur les spécificités du système olfactif et son rôle dans le développement visuel du nourrisson, était de déterminer si l'efficience inverse s'applique aux interactions olfaction-vision. De la revue de la littérature, nous avons appris que les signaux olfactifs saillants comme l'odeur maternelle jouent un rôle facilitateur dans le traitement visuel (Damon et al., 2021), en particulier dans la catégorisation des visages chez les nourrissons de 4 mois (Leleu et al., 2020). Conformément au principe de l'efficience inverse, Rekow et al. (2022) n'ont trouvé aucune facilitation intersensorielle par l'odeur corporelle sur la catégorisation des visages chez les adultes, seulement sur la catégorisation des objets ambigus ressemblant à des visages. Ces résultats ont soulevé les questions principales de ce travail : 1) peut-on appliquer le principe d'efficience inverse à la catégorisation des visages basée sur les odeurs dans le développement du nourrisson ? 2) Comment ce principe s'applique-t-il aux stades de développement caractérisés par une capacité visuelle faible/bonne face à des tâches visuelles plus ou moins difficiles ?

Pour répondre à ces questions, trois études ont été menées pour tester l'hypothèse selon laquelle la catégorisation des visages basée sur les odeurs suit le principe d'efficience inverse tout au long du développement.

4.1 Synthèse des résultats principaux

L'étude 1 a examiné la prédiction d'un compromis développemental entre la vision et l'olfaction, où la réponse sélective aux visages la plus faible bénéficie le plus de l'intégration multisensorielle. Il est apparu que la réponse sélective aux visages augmente progressivement entre 4 et 12 mois au niveau du cortex occipito-temporal bilatéral (OT), tandis que l'effet de l'odeur diminue sur le cortex occipito-temporal droit (rOT). Cela va dans le sens du principe d'efficience inverse.

L'étude 2 s'est intéressée à l'impact de la difficulté de la catégorisation visuelle sur l'effet de l'odeur à 4 mois, avec l'hypothèse que cet effet n'est présent que si la difficulté visuelle est élevée. Dans le 1er groupe exposé à la catégorisation des visages plus difficile, nous avons trouvé un fort effet d'odeur et une faible réponse sélective aux visages. Dans le 2ème groupe, nous avons observé une forte réponse sélective aux visages et l'absence de l'effet de l'odeur. Les résultats de ces deux groupes confirment le principe d'efficience inverse chez les nourrissons de 4 mois.

Alors que les études 1 et 2 ont confirmé nos prédictions, les résultats de **l'étude 3** étaient surprenants, du moins en partie. Comme dans l'étude 2, nous avons manipulé la difficulté visuelle de la catégorisation des visages chez deux groupes de nourrissons de 12 mois. Le groupe de nourrissons exposés à la tâche la moins exigeante, qui reproduisait les résultats de l'étude 1, présentait une catégorisation efficace du visage et l'absence de l'effet d'odeur. Le deuxième groupe, confronté à une tâche plus exigeante qui consistait à accélérer deux fois la vitesse de présentation des images, a bien présenté une catégorisation des visages plus difficile. Cependant, l'effet d'odeur attendu n'est pas apparu. La réponse sélective aux visages était même significativement plus faible en présence de l'odeur maternelle par rapport à l'odeur témoin. Ces résultats n'ont pas confirmé le principe d'efficience inverse, mais plutôt une surcharge sensorielle.

4.2 Apprentissage intersensoriel dans le contexte social : des catégories globales aux catégories spécifiques

Au début du développement, les propriétés amodales qui sont communs pour plusieurs systèmes sensorielles (par exemple, synchronie, rythme, complexité) semblent plus simples à détecter dans les stimulations multimodales (Bahrick et al., 2002, 2019; Flom et Bahrick , 2007) par rapport aux caractéristiques modales non redondantes qui sont plus spécifiques (Bahrick et al., 2004, 2005, 2006). Cela se produit parce que l'attention du nourrisson est globale et réglée très large pour se concentrer sur des stimuli très saillants avec une valence écologique vitale. À ce stade, la facilitation intersensorielle joue un rôle crucial dans la perception car la stimulation unimodale n'est souvent pas assez efficace en raison de l'ambiguïté des signaux sensoriels ou du faible niveau de la maturation des sens. Cependant, au cours de la première année de vie, la perception sensorielle du nourrisson change radicalement. Basé sur l'amélioration sensorielle anatomique et fonctionnelle associée à l'accumulation d'expérience et d'apprentissage, le processus de perception devient plus différencié et plus rapide (Gibson, 1988; Ruff et Rothbart, 2001). Ainsi, les nourrissons plus âgés deviennent capables de détecter à la fois les caractéristiques amodales et modales dans les stimulations uni - et multimodales sans avoir besoin de facilitation intersensorielle (Bahrick et al., 2002; Bahrick et Lickliter, 2004; Bahrick et Newell, 2008).

En conséquence, nous pouvons proposer une modèle possible de développement de la catégorisation des visages basée sur les odeurs au cours de la première année. Les nourrissons plus jeunes, entre 4 et 8 mois, connaissent très bien l'odeur de leur mère, non seulement parce qu'ils passent beaucoup de temps dans ses bras, mais aussi parce qu'ils ont rencontré cette odeur en tant que fœtus dans le liquide amniotique et à nouveau à la naissance dans la saveur du colostrum et du lait, et dans les sécrétions aréolaires et cutanées (Schaal, 2005, 2016, 2023). Ainsi, à cette tranche d'âge, l'odeur maternelle est un signal sensoriel surappris et très saillant qui se couple rapidement avec le visage de la mère fréquemment rencontré. Cette congruence sémantique récurrente de l'odeur et du visage constitue la base de la facilitation intersensorielle (c'est-à-dire l'effet d'odeur) pour une catégorisation efficace des visages. Au fur et à mesure que la vision se développe, les nourrissons plus âgés améliorent non seulement leur compétence visuelle, mais ils élargissent également leur panel de visages vus. Entre 8 et 12 mois, les nourrissons rencontrent en effet beaucoup plus de congénères, car ils passent la majeure partie de la journée dans divers environnements socialement riches. Cependant, non seulement les expériences visuelles deviennent plus abondantes et diversifiées avec l'âge, mais ces nourrissons rencontrent également une palette plus large d'odeurs sociales, à mesure qu'ils s'éloignent de leur mère et développement de nouvelles interactions. Dans ce contexte, de nouveaux appariements associatifs entre différents visages et odeurs corporelles sont engagés (Damon et al., 2021) et leur « paysage olfactif » se rétrécit progressivement de la perception multisensorielle large vers des percepts unisensoriels plus spécifiques (Murray et al., 2016). En conséquence, 1) l'odeur maternelle peut avoir tendance à devenir moins saillante dans un contexte social global et 2) des améliorations fonctionnelles en parallèles avec la compétence visuelle permettent une catégorisation des visages suffisamment efficace sans la facilitation intersensorielle.

4.3 Perspectives

Les nourrissons durant la première année sont capables d'effectuer des paires arbitraire odeur-objet (Schaal et Durand, 2012). Nous pourrions donc investiguer l'amélioration des réponses visuelles sélectives à d’autres catégories dans le contexte d'une odeur congruente (par exemple, l'odeur de fraise améliore la catégorisation des images/objets de fraise). Rekow et coll. (2020) ont étudié la catégorisation des voitures chez les nourrissons de 4 mois en utilisant une odeur maternelle non congruente et n'ont pas observé de facilitation intersensorielle. Le même effet nul pour la catégorisation des voitures a été trouvé chez les adultes mais cette fois, les auteurs ont utilisé une odeur congruente d'essence, une odeur corporelle non congruente et un contexte de base (sans odeur). Il semble donc que les adultes n'utilisent plus la facilitation intersensorielle en raison de leur système visuel développé, comme le suggère le principe d'efficience inverse. Néanmoins, de nombreuses études montrent par exemple un effet d'amorçage des odeurs sur l'attention portée aux objets congruents (Carrieri et al., 2023; Seigneuric et coll., 2010; Seo et autres., 2010). La généralisation de l’effet de l’odeur à diverses catégories mérite d’être évaluée.

En ce qui concerne la nature sociale de l’effet de l’odeur maternelle, nous pourrions élargir les catégories étudiées pour confirmer définitivement le rôle social du contexte olfactif. Rekow et al. (2021) ont déjà étudié la catégorisation des stimuli ressemblant à des visages qui ne représentent pas directement des visages. Des études sur cette catégorie ont démontré une augmentation de la réponse cérébrale sélective aux objets semblables aux visage en présence d'odeur maternelle chez les nourrissons de 4 mois et même chez les adultes ayant le même effet d'odeur corporelle (Rekow et al., 2022). Nous pourrions donc déterminer si la catégorisation des parties du corps ou des objets de la vie quotidienne ayant une signification sociale (par exemple, biberon, peluche) bénéficie de la facilitation intersensorielle provenant de l'odeur maternelle.

Enfin, nous aimerions élargir la gamme des indices olfactifs que nous utilisons dans nos études de catégorisation des visages. Actuellement, nous sommes loin de comprendre quel type de composé chimique dans l'odeur maternelle facilite la perception du visage. En testant différentes odeurs lors de la catégorisation, nous pourrions trouver quelles caractéristiques sont primordiales. Est-ce la familiarité de l'odeur dans la vie quotidienne du nourrisson ou la signature olfactive spécifique d'une jeune mère (par ex. liée à la naissance récente et au statut d'allaitement) ? Les odeurs créent un contexte idéal pour la formation d'associations et donc la mémoire en raison de leur stabilité dans l'espace et le temps (Sela & Sobel, 2010). Cela a été montré par plusieurs études sur l'influence du contexte olfactif sur la récupération en mémoire chez les nourrissons de 3 mois (Rubin et al., 1998; Schroers et al., 2007). Comme le visage représente le premier et le plus important signal visuel après la naissance, le cerveau du nourrisson peut probablement l'associer à d'autres odeurs souvent présentes dans son environnement (par exemple, l'odeur du père ou le parfum diffusé à la maison). D'autre part, le perception multisensoriel des visages a déjà été étudié en utilisant l'odeur d'une mère étrangère qui ne suppose pas la familiarité olfactive (Durand et al., 2020; Jessen, 2020). De plus, les composés odorants du lait maternel ont été bien étudiés au cours des dernières décennies (Buettner, 2007; Loos et al., 2019), alors que la composition complexe de l'odeur maternelle n'est toujours pas complètement connue. Ainsi, nous n'avons pas de preuves directes de la sensibilité du nourrisson aux différents indices olfactifs émis par la mère et de futures études devront nous permettre de comparer les signatures neurales de la catégorisation des visages dans le contexte de différentes odeurs féminines (mère, mère étrangère, femme nullipare étrangère et non étrangère) avec une analyse chimique parallèle des composés odorants.

4.4 Conclusion générale

La présente recherche a examiné le principe de l'efficience inverse dans les interactions olfaction-vision au cours du développement précoce. En particulier, nous avons examiné l'influence de l'odeur maternelle sur la catégorisation des visages au cours de la première année selon différentes demandes visuelles. Nous avons enregistré l'EEG en utilisant une approche d'étiquetage fréquentielle en EEG pendant que les nourrissons étaient exposés à l'odeur corporelle de leur mère ou à une odeur témoin. La stimulation visuelle consistait en un flux périodique rapide d'images naturelles (Étude 1 à 3) ou simplifiées (Étude 2) à des périodes de 6 Hz (Étude 1 à 3) ou 12 Hz (Étude 3) avec des visages humains insérés tous les 6ème (Étude 1 à 3) ou 9ème (Étude 3) stimulus parmi d'autres objets non faciaux pour mesurer une réponse sélective aux visages à 1 ou 1,33 Hz, respectivement. D'une part, l'effet d'odeur maternelle n'est apparu que chez les nourrissons les plus jeunes (études 1 et 2) et exclusivement avec des stimuli naturels qui impliquent une catégorisation du visage plus difficile. D'autre part, les nourrissons plus âgés (études 1 et 3) ont montré une catégorisation des visages plus efficace, probablement en raison du développement visuel, qui pourrait expliquer l'absence d'influence des odeurs (la vision est efficace seule). La baisse de la difficulté visuelle pour la tâche de catégorisation chez les nourrissons plus jeunes (étude 2) n’a pas donné d’effet comme chez les nourrissons plus âgés (études 1 et 3); en lien avec le fait que les stimuli simplifiés facilite la catégorisation visuelle.

Ces résultats contribuent davantage à notre compréhension des interactions fonctionnelles de l'olfaction et de la vision à un âge précoce. Un résultat important est que l'olfaction est un acteur crucial dans le domaine de l'intégration multisensorielle, obéissant au principe d'efficience inverse au même titre que les autres sens. Nous souhaitons que ces résultats puissent ouvrir de nouvelles voies pour de futures études sur les mécanismes intégratifs de différents domaines sensoriels dans le développement humain typique, ainsi qu'atypique.

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Appendices

Appendix 1: Supporting information of Study 1

From Rekow, D., Baudouin, J.-Y., Kiseleva, A., Rossion, B., Durand, K., Schaal, B., & Leleu, A. (2023). Olfactory-to-visual facilitation in the infant brain declines gradually from 4 to 12 months. *BioRxiv, 556823*. https://doi.org/10.1101/2023.09.08.556823

Supplementary data

Supplementary method: EEG preprocessing (references are appended at the end of the document)

EEG data were filtered using a Butterworth filter (highpass filter, cutoff: 0.1 Hz, 4th order) and resampled to 200 Hz. Next, sequences were cropped from the beginning of the fade-in into 36-s segments (i.e., adding 2 s after the end of the sequence). The *Artifact Blocking* algorithm (Fujioka et al., 2011; Mourad et al., 2007) was applied to individual epochs with a correction threshold of ± 250 µV. Epochs were then segmented again from the end of the fade-in (i.e., from 1.833 s, corresponding to the first image of the full-contrast segment) until the end of the fade-out, i.e., in 32-s-long segments, and datasets were re-referenced according to a common average reference.

Following previous frequency-tagging EEG studies in infants (e.g., Leleu et al., 2020; Rekow et al., 2021, 2020), data were screened using two data-driven criteria to remove unusable epochs at an individual level and increase signal-to-noise ratio. The first criterion consisted in identifying epochs with no general visual response at 6 Hz and its second harmonic (12 Hz), used as a marker of the infant's attention to the stimulation. Baseline-corrected amplitude spectra were extracted for individual epochs and *Z*-scores were calculated (see Frequency-domain analysis) for medial occipital electrodes (POz, Oz, O1, O2) that typically exhibit the largest general visual response to a rapid stream of natural images (Leleu et al., 2020). Epochs failing to present a significant ($Z > 1.64$, $p < .05$, one-tailed, signal > noise) general visual response for 2 electrodes, at least, were removed. The second criterion consisted in identifying atypical epochs according to the scalp-wide power of the response at 1 Hz. For each epoch, the root mean square (RMS) amplitude across electrodes was calculated. Epochs were rejected if their RMS amplitude was ±2 SDs of the mean of all epochs.

Table S1. Harmonic significance for the general visual response and the face-selective response. For both responses, harmonic significance was estimated using *Z*-scores calculated on the average of all electrodes, participants and odor conditions. Harmonics were considered significant if their *Z*-score was > 1.64 ($p < .05$, one-tailed, signal > noise). For the face-selective response, the 6th harmonic was not considered as it corresponds to the 1st harmonic of the general visual response. Asterisks indicate significance (* $p < .05$, *** $p < .001$).

	General visual response		**Face-selective response**	
Harmonic	**Frequency (Hz)**	***Z*-score**	**Frequency (Hz)**	***Z*-score**
1	6	148***	1	6.62***
2	12	167***	2	5.35***
3	18	80.8***	3	3.66***
4	24	49.8***	4	3.67***
5	30	8.97***	5	6.22***
6	36	5.07***		
7	42	0.56	7	2.15*
8	48	-0.06	8	-1.04

Table S2. Electrode significance for the general visual response and the face-selective response. For both responses, electrode significance was estimated using *Z*-scores calculated on responses summed across significant harmonics and averaged across participants and odor conditions. Electrodes were considered significant if their *Z*-score was > 2.93 ($p < .05$, one-tailed, signal > noise, Bonferroni-corrected for 30 electrodes). *Z*-scores are presented in decreasing order and asterisks indicate significance (* $p < .05$, ** $p < .01$, *** $p < .001$). Electrodes highlighted in grey were used for further analyses.

	General visual response		Face-selective response	
Rank	**Electrode**	***Z*-score**	**Electrode**	***Z*-score**
1	**Oz**	**168*****	**P8**	**19.5*****
2	**O2**	**133*****	**P7**	**13.1*****
3	**POz**	**122*****	Oz	6.16***
4	**O1**	**102*****	POz	5.32***
5	P3	71.1***	**O1**	**5.31*****
6	CP6	61.0***	**O2**	**4.38*****
7	FC2	46.9***	CP2	4.25***
8	CP5	45.1***	P3	3.45**
9	P4	43.1***	P4	3.38*
10	P7	39.6***	F7	3.27*
11	CP2	33.4***	T7	3.21*
12	FC1	32.4***	FC6	2.70
13	Fz	31.6***	FC1	2.63
14	T8	29.6***	CP5	2.60
15	CP1	28.9***	FC2	2.55
16	Pz	28.9***	Pz	2.51
17	FC5	28.7***	CP1	2.39
18	F3	27.7***	F8	2.07
19	F4	26.9***	F4	2.05
20	P8	26.8***	Cz	1.92
21	C3	26.7***	T8	1.81
22	Fp2	26.5***	CP6	1.77
23	F7	26.0***	F3	1.76
24	FC6	25.9***	FC5	1.71
25	Cz	25.1***	C3	1.61
26	C4	24.3***	Fz	1.19
27	F8	21.4***	C4	1.07
28	Fpz	20.5***	Fpz	0.65
29	T7	20.3***	Fp2	0.53
30	Fp1	17.7***	Fp1	-0.13

Table S3. ANCOVA on the amplitude of the face-selective response in the baseline odor context. A first analysis was conducted in the baseline odor context to determine the effect of AGE and its interactions with the other factors. Significant effects are reported in red. Greenhouse-Geisser epsilon (ε) and corresponding adjusted *p*-values are reported when sphericity was violated (as estimated by Mauchly's test, unreported). The significant HARM × AGE interaction is decomposed in the effect of AGE for each harmonic separately. Another ANCOVA was run on the response summed across the two first harmonics (Harmonics 1 + 2). HARM: Harmonic, ELEC: Electrode, SS: sum of square, Df: degree of freedom, MS: mean square, GG: Greenhouse-Geisser, Adj: adjusted.

	SS	Df	MS	*F*	*p*	η_p^2	GG ε	GG Adj *p*
AGE	21.79	1	21.79	8.41	.006	.149		
Error	124.43	48	2.59					
HARM*AGE	39.18	5	7.84	5.54	.000	.104	.38	.006
Error	339.28	240	1.41					
ELEC*AGE	6.42	3	2.14	2.08	.106	.041	.80	.121
Error	148.31	144	1.03					
HARM*ELEC*AGE	10.17	15	0.68	0.79	.686	.016	.25	.523
Error	614.90	720	0.85					
Harmonic 1								
AGE	38.85	1	38.85	6.03	.018	.112		
Error	309.33	48	6.44					
Harmonic 2								
AGE	19.93	1	19.93	12.01	.001	.200		
Error	79.63	48	1.66					
Harmonic 3								
AGE	0.62	1	0.62	1.83	.182	.037		
Error	16.12	48	0.34					
Harmonic 4								
AGE	0.09	1	0.09	0.22	.638	.005		
Error	19.94	48	0.42					
Harmonic 5								
AGE	1.49	1	1.49	2.17	.148	.043		
Error	32.89	48	0.69					
Harmonic 7								
AGE	0.00	1	0.00	0.00	.996	.000		
Error	5.80	48	0.12					
Harmonics 1 + 2								
AGE	114.42	1	114.42	11.17	.002	.189		
Error	491.80	48	10.25					
ELEC*AGE	20.36	3	6.79	1.51	.215	.030	.78	.224
Error	648.71	144	4.50					

Table S4. ANCOVA on the amplitude of the face-selective response in both odor contexts. A second analysis was conducted to determine the effect of ODOR, its interaction with AGE and their interactions with the other factors. Significant effects are reported in red (one effect is reported in orange because significance did not survive the Greenhouse-Geisser correction). Greenhouse-Geisser epsilon (ε) and corresponding adjusted *p*-values are reported when sphericity was violated (as estimated by Mauchly's test, unreported). The significant HARM × ODOR × ELEC × AGE interaction is decomposed in the effects involving these factors for each harmonic separately. HARM: Harmonic, ELEC: Electrode, SS: sum of square, Df: degree of freedom, MS: mean square, GG: Greenhouse-Geisser, Adj: adjusted.

	SS	Df	MS	*F*	*p*	η_p^2	GG ε	GG Adj *p*
ODOR	1.40	1	1.40	1.48	.233	.029		
ODOR*AGE	0.77	1	0.77	0.80	.376	.016		
Error	46.01	48	0.96					
HARM*ODOR	12.49	5	2.50	2.22	.053	.044	.46	.105
HARM*ODOR*AGE	14.89	5	2.98	2.65	.025	.052	.46	.067
Error	269.43	240	1.12					
ODOR*ELEC	2.65	3	0.88	1.26	.290	.026		
ODOR*ELEC*AGE	2.05	3	0.68	0.98	.406	.020		
Error	100.88	144	0.70					
HARM*ODOR*ELEC	33.76	15	2.25	3.58	.000	.069	.34	.004
HARM*ODOR*ELEC*AGE	40.38	15	2.69	4.28	.000	.082	.34	.001
Error	452.41	720	0.63					
Harmonic 1								
ODOR	7.74	1	7.74	2.05	.159	.041		
ODOR*AGE	4.90	1	4.90	1.30	.260	.026		
Error	181.27	48	3.78					
ODOR*ELEC	32.48	3	10.83	4.32	.006	.083		
ODOR*ELEC*AGE	37.68	3	12.56	5.01	.002	.095		
Error	361.01	144	2.51					
Harmonic 2								
ODOR	4.77	1	4.77	3.52	.067	.068		
ODOR*AGE	8.30	1	8.30	6.12	.017	.113		
Error	65.05	48	1.36					
ODOR*ELEC	1.02	3	0.34	0.57	.637	.012	.76	.592
ODOR*ELEC*AGE	1.35	3	0.45	0.75	.522	.015	.76	.490
Error	86.25	144	0.60					
Harmonic 3								
ODOR	0.25	1	0.25	0.52	.474	.011		
ODOR*AGE	0.67	1	0.67	1.37	.248	.028		
Error	22.34	48	0.49					
ODOR*ELEC	1.61	3	0.54	2.14	.097	.043	.84	.108
ODOR*ELEC*AGE	1.81	3	0.60	2.40	.070	.048	.84	.082
Error	36.14	144	0.25					
Harmonic 4								
ODOR	0.11	1	0.11	0.32	.572	.007		
ODOR*AGE	0.33	1	0.67	1.01	.319	.021		
Error	15.69	48	0.33					
ODOR*ELEC	0.89	3	0.30	1.06	.369	.022		

ODOR*ELEC*AGE	1.19	3	0.40	1.42	.239	.029		
Error	40.26	144	0.28					
Harmonic 5	SS	Df	MS	F	p	η_p^2	GG ε	GG Adj p
ODOR	0.95	1	0.95	1.85	.180	.037		
ODOR*AGE	1.28	1	1.28	2.49	.121	.049		
Error	24.72	48	0.52					
ODOR*ELEC	0.18	3	0.06	0.38	.770	.008	.83	.732
ODOR*ELEC*AGE	0.11	3	0.04	0.23	.873	.005	.83	.838
Error	22.47	144	0.16					
Harmonic 7								
ODOR	0.07	1	0.07	0.62	.434	.013		
ODOR*AGE	0.18	1	0.18	1.60	.211	.032		
Error	5.37	48	0.11					
ODOR*ELEC	0.23	3	0.08	1.53	.208	.031		
ODOR*ELEC*AGE	0.29	3	0.10	1.92	.129	.038		
Error	7.17	144	0.05					
Harmonics 1 + 2								
ODOR	24.65	1	24.65	5.15	.028	.097		
ODOR*AGE	25.95	1	25.95	5.43	.024	.102		
Error	229.57	48	4.78					
ODOR*ELEC	27.58	3	9.19	3.15	.027	.061		
ODOR*ELEC*AGE	29.40	3	9.80	3.35	.021	.065		
Error	420.95	144	2.92					
Electrode O2								
ODOR	48.43	1	48.43	21.56	.000	.310		
ODOR*AGE	49.05	1	49.05	21.83	.000	.313		
Error	107.84	48	2.25					
Electrode P8								
ODOR	1.27	1	1.27	0.29	.596	.006		
ODOR*AGE	0.00	1	0.00	0.00	.999	.000		
Error	213.12	48	4.44					
Electrode O1								
ODOR	2.46	1	2.46	0.68	.413	.014		
ODOR*AGE	5.65	1	5.65	1.57	.216	.032		
Error	172.45	48	3.59					
Electrode P7								
ODOR	0.08	1	0.08	0.02	.879	.000		
ODOR*AGE	0.65	1	0.65	0.20	.658	.004		
Error	157.11	48	3.27					

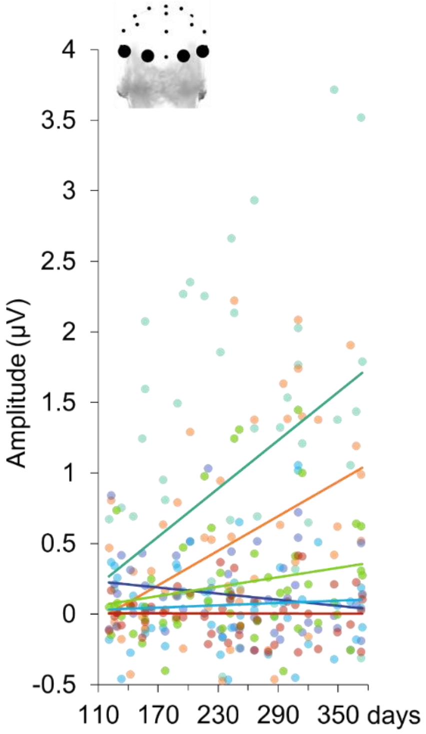

Figure S1. Individual amplitudes of the face-selective response recorded in the baseline odor context over the occipital temporal electrodes for each harmonic separately (see Tables S3 for color codes) as a function of age. Each dot represents an infant and each line represents the linear regression for a harmonic. The effect of *Age* is significant for the two first harmonics (dark green and orange).

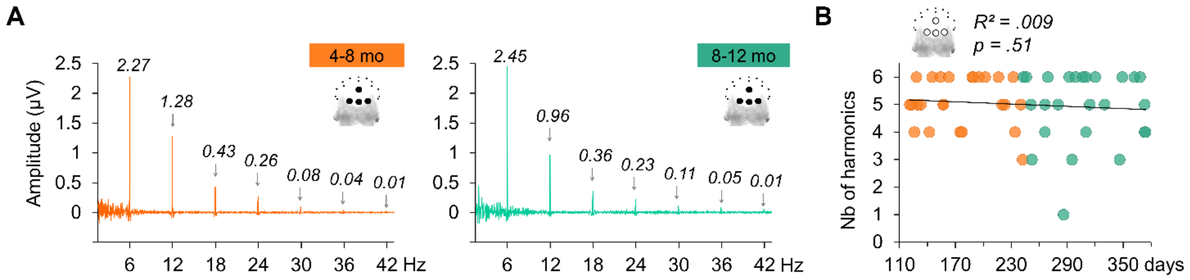

Figure S2. The development of the general visual response with age. A. Amplitude spectra recorded in the baseline odor context for the youngest (4-8 months, orange) and the oldest (8-12 months, green) infants averaged for the 4 middle occipital electrodes (POz, Oz, O1, O2). **B.** Maximum number of significant harmonics recorded among the 4 middle occipital electrodes as a function of age. Each color circle represents an individual infant data depending on its subgroup (orange: 4-8 months, green: 8-12 months).

Table S5. ANCOVAs on the amplitude of the general visual response. A first analysis was conducted in the baseline odor context to determine the effect of AGE and its interactions with the other factors. A second analysis was conducted to determine the effect of ODOR, its interaction with AGE and their interactions with the other factors. This analysis was also conducted after removing one infant who had an outlying odor effect. Greenhouse-Geisser epsilon (ε) and corresponding adjusted *p*-values are reported when sphericity was violated (as estimated by Mauchly's test, unreported). HARM: Harmonic, ELEC: Electrode, SS: sum of square, Df: degree of freedom, MS: mean sum, GG: Greenhouse Geiser, Adj: adjusted.

Baseline odor context	SS	Df	MS	*F*	*p*	η_p^2	*GG* ε	GG Adj *p*
AGE	1.97	1	1.97	0.32	.575	.007		
Error	297.19	48	6.19					
HARM*AGE	14.62	5	2.92	0.94	.454	.019	.23	.348
Error	743.98	240	3.10					
ELEC*AGE	4.71	3	1.57	1.89	.134	.038	.61	.160
Error	119.50	144	0.83					
HARM*ELEC*AGE	5.32	15	0.35	1.03	.419	.021	.14	.362
Error	247.35	720	0.34					
Both odor contexts								
ODOR	0.40	1	0.40	0.27	.606	.006		
ODOR*AGE	0.11	1	0.11	0.07	.791	.001		
Error	72.10	48	1.50					
HARM*ODOR	0.33	5	0.07	0.11	.991	.002	.23	.786
HARM*ODOR*AGE	0.09	5	0.02	0.03	.999	.001	.23	.897
Error	147.54	240	0.61					
ODOR*ELEC	0.13	3	0.04	0.28	.842	.006	.78	.792
ODOR*ELEC*AGE	0.16	3	0.05	0.35	.790	.007	.78	.739
Error	21.59	144	0.15					
HARM*ODOR*ELEC	0.16	15	0.01	0.14	.999	.003	.19	.928
HARM*ODOR*ELEC*AGE	0.51	15	0.03	0.45	.962	.009	.19	.708
Error	54.31	720	0.08					
Both odor contexts without 1 outlier								
ODOR	0.62	1	0.62	0.97	.329	.020		
ODOR*AGE	0.61	1	0.61	0.96	.333	.020		
Error	30.13	47	0.64					
HARM*ODOR	0.59	5	0.12	0.40	.848	.008	.27	.591
HARM*ODOR*AGE	0.53	5	0.11	0.36	.875	.008	.27	.615
Error	68.70	235	0.29					
ODOR*ELEC	0.13	3	0.04	0.30	.828	.006	.74	.768
ODOR*ELEC*AGE	0.13	3	0.04	0.30	.827	.006	.74	.767
Error	20.23	141	0.14					
HARM*ODOR*ELEC	0.16	15	0.01	0.15	.999	.003	.18	.918
HARM*ODOR*ELEC*AGE	0.46	15	0.03	0.42	.974	.008	.18	.722
Error	51.86	705	0.07					

Table S6. ANCOVA on the amplitude of the face-selective response at electrode O2 including the SEX and FEEDING factors. An analysis was conducted to determine whether the ODOR effect and the interaction ODOR × AGE observed at O2 in the main analysis remain when the between-subject categorical factors SEX (26 females *vs.* 24 males) and FEEDING (17 breastfed *vs.* 33 bottle-fed infants) are added. Both effects remained significant (reported in red). In addition, the AGE × SEX, AGE × FEEDING, ODOR × AGE × SEX, and ODOR × AGE × FEEDING interactions were not significant, indicating that sex and feeding status were not significantly different as a function of age (young infants were not significantly more (fe)males or more breastfed than older infants) and did not contribute to the maternal odor effect observed for the youngest infants. SS: sum of square, Df: degree of freedom, MS: mean square.

Electrode O2	SS	Df	MS	*F*	*p*	η_p^2
ODOR	49.33	1	49.33	21.26	.000	.316
ODOR*AGE	48.74	1	48.74	21.01	.000	.314
ODOR*AGE*SEX	0.66	1	0.66	0.28	.597	.006
ODOR*AGE*FEEDING	0.23	1	0.23	0.10	.753	.002
Error	106.73	46	2.32			
AGE*SEX	0.05	1	0.05	0.01	.914	.000
AGE*FEEDING	0.47	1	0.47	0.11	.745	.002
Error	200.90	46	4.37			

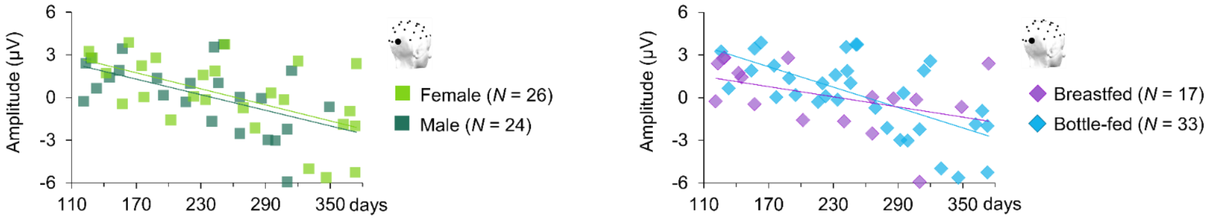

Figure S3. Maternal odor effect at electrode O2 as a function of age and sex (left) or feeding status (right). Each square or diamond represents the odor effect (amplitude of the face-selective response in the maternal minus the baseline odor context) for an individual infant depending on their sex (light green: female, *N* = 26; dark green: male, *N* = 24) or feeding status (purple: breastfed, *N* = 17; blue: bottle-fed, *N* = 33).

Supplementary references

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Appendix 2: Supporting information of Study 2

From Kiseleva, A., Rekow, D., Schaal, B., & Leleu, A. (Submitted). The inverse effectiveness of olfactory-to-visual facilitation in the 4-month-old brain.

Supplementary Material

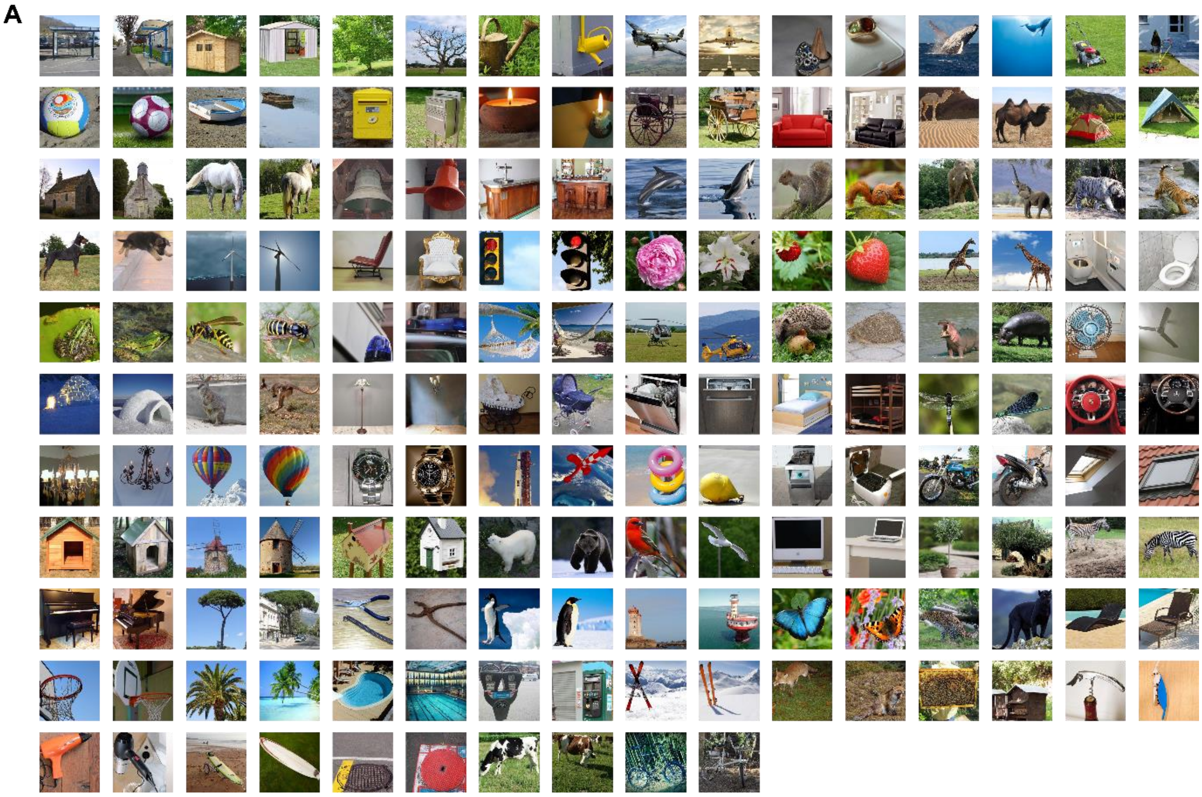

Figure S1. Natural (Group 1; A and C) and Simplified (Group 2; B and D) stimuli. The two visual stimulus sets comprised pictures of 170 living and non-living objects (85 categories × 2 exemplars; A and B) and 68 faces (34 females; C and D).

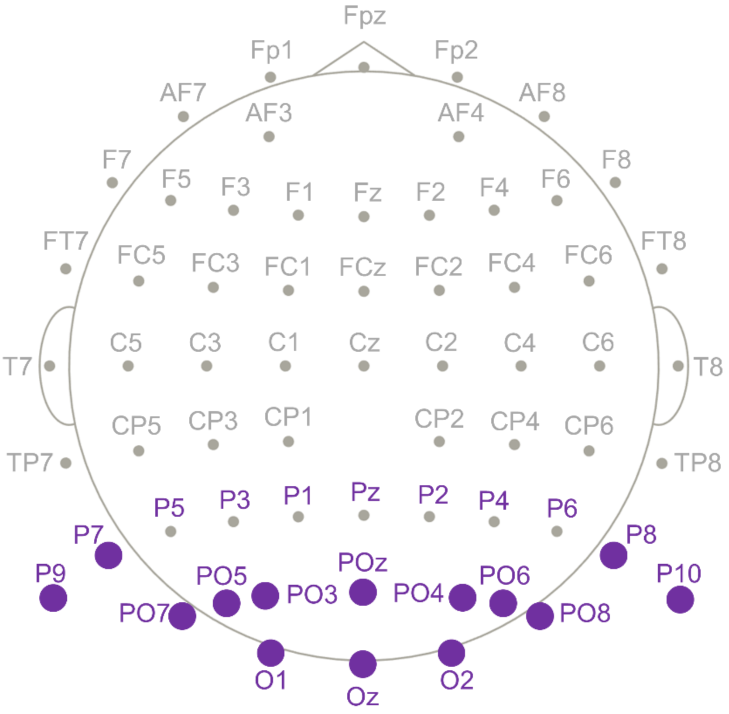

Figure S2. Sixty-three-channel montage of EEG acquisition and electrodes considered for analysis. EEG was acquired from a 63-channel head-cap configured according to the 10-10 classification system. Frequency-domain analysis was conducted on 21 posterior electrodes (labels colored in purple). For the face-selective response, 14 electrodes (identified by purple disks) were selected to define regions of interest (ROIs).

Table S1. Harmonic significance for the general and face-selective visual responses. For each response, harmonic significance was estimated using *Z*-scores calculated on the average of all electrodes, odor contexts and infants. Harmonics were considered significant according to a threshold of $Z > 1.64$ ($p < .05$, one-tailed, signal > noise). For the face-selective response, the 6th harmonic was not considered as it corresponds to the 1st harmonic of the general visual response. Asterisks indicate significance (* $p < .05$, ** $p < .01$, *** $p < .001$).

	General visual response		**Face-selective response**	
Harmonic	**Frequency (Hz)**	***Z*-score**	**Frequency (Hz)**	***Z*-score**
1	6	70.5***	1	7.07***
2	12	71.2***	2	3.66***
3	18	37.4***	3	5.91***
4	24	11.7***	4	2.60**
5	30	1.06	5	1.65*
6	36	-0.35		
7	42	0.25	7	1.27
8	48	-0.84	8	0.71

Table S2. Electrode significance for the general and face-selective visual responses. For each response, electrode significance was estimated for 21 posterior electrodes (Figure S2) using *Z*-scores calculated on responses summed across significant harmonics and averaged across odor contexts and infants. Electrodes were considered significant according to a threshold of *Z* > 2.82 (*p* < .05, one-tailed, signal > noise, Bonferroni-corrected for 21 electrodes). *Z*-scores are presented in decreasing order and asterisks indicate significance (* *p* < .05, *** *p* < .001). Electrodes highlighted in color were used to define ROIs (grey: medial occipital, blue: left occipito-temporal, orange: right occipito-temporal).

	General visual response		**Face-selective response**	
Rank	**Electrode**	***Z*-score**	**Electrode**	***Z*-score**
1	Oz	106***	P9	9.05***
2	O2	101***	PO7	8.69***
3	O1	92.2***	P10	6.95***
4	POz	73.2***	PO8	6.56***
5	PO3	68.5***	O1	6.52***
6	PO5	68.0***	PO4	5.34***
7	PO4	63.4***	P7	5.20***
8	PO6	59.9***	PO5	5.06***
9	PO7	41.2***	P5	4.50***
10	PO8	40.6***	P8	4.05***
11	P8	37.8***	PO6	3.99***
12	P6	32.1***	Oz	3.13*
13	P3	26.9***	PO3	3.12*
14	P1	25.1***	POz	3.05*
15	P5	24.4***	O2	2.83*
16	Pz	23.2***	P6	2.78
17	P7	21.9***	P4	2.04
18	P9	19.9***	P2	1.50
19	P10	18.5***	P3	1.46
20	P4	17.8***	P1	1.14
21	P2	17.6***	Pz	0.77

Table S3. Significance of the general visual response at the medial occipital ROI for each group of infants (i.e., type of stimuli). Significance was estimated for each harmonic and for the summed response across harmonics using *Z*-scores calculated on the average across electrodes within the ROI, odor contexts and infants within groups. Significance was fixed at *Z* > 1.64 (*p* < .05, one-tailed, signal > noise). Asterisks indicate significance (*** *p* < .001).

		Group 1 Natural stimuli	**Group 2 Simplified stimuli**
Harmonic	**Frequency (Hz)**	***Z*-score**	***Z*-score**
1	6	88.3***	56.9***
2	12	117***	76.4***
3	18	39.5***	36.7***
4	24	26.4***	9.74***
Sum	6 to 24	113***	85.1***

Table S4. Significance of the general visual response at the medial occipital ROI for each individual infant within each group. Significance was estimated for the summed response of each infant, at each electrode within the ROI and for the mean response across electrodes, using *Z*-scores calculated on the average across odor contexts. *Z*-scores in bold indicate significance (*Z* > 1.64, *p* < .05, one-tailed, signal > noise).

Group 1: Natural stimuli

Infant	**POz**	**O1**	**Oz**	**O2**	**mO**
#01	**9.32**	**16.93**	**14.02**	**12.44**	**22.90**
#02	**27.15**	**16.30**	**22.12**	**24.15**	**32.51**
#03	**34.61**	**54.31**	**44.92**	**44.89**	**53.23**
#04	**11.57**	**45.94**	**58.31**	**42.89**	**60.01**
#05	**8.77**	**29.49**	**32.00**	**25.70**	**35.95**
#06	**3.57**	**17.81**	**47.94**	**33.11**	**38.12**
#07	**27.10**	**27.23**	**26.64**	**25.23**	**32.75**
#08	**24.50**	**24.63**	**30.45**	**26.31**	**43.79**
#09	**12.72**	**17.78**	**40.11**	**47.40**	**50.65**
#10	**3.98**	**15.32**	**37.33**	**43.06**	**44.54**
#11	**10.01**	**29.29**	**39.02**	**25.74**	**34.17**
#12	**19.01**	**15.39**	**22.31**	**17.10**	**34.45**
#13	**9.67**	**17.06**	**14.29**	**7.42**	**19.26**
#14	-0.20	**3.92**	**4.25**	**6.10**	**5.37**
#15	**1.66**	**4.78**	**14.02**	**10.22**	**9.88**
#16	**12.99**	**31.01**	**72.01**	**44.66**	**57.97**
#17	**11.75**	**18.36**	**23.15**	**13.35**	**32.78**
#18	**32.40**	**18.20**	**77.36**	**55.56**	**82.36**
#19	0.71	**10.95**	**9.39**	**5.38**	**14.09**
#20	**3.62**	**2.20**	**7.88**	**7.30**	**7.81**
#21	**12.10**	**5.94**	**9.54**	**10.19**	**19.87**

Group 2: Simplified stimuli

Infant	**POz**	**O1**	**Oz**	**O2**	**mO**
#01	**22.55**	**12.11**	**27.59**	**27.17**	**43.45**
#02	0.92	**2.72**	0.72	**5.22**	**3.98**
#03	**5.40**	**4.44**	**9.70**	**9.82**	**11.35**
#04	**5.11**	**12.21**	**10.58**	**5.00**	**17.08**
#05	**6.07**	**8.73**	**17.67**	**7.68**	**13.42**
#06	-1.05	1.64	**3.60**	**4.06**	**3.36**
#07	**5.81**	**6.53**	**3.63**	-2.24	**5.88**
#08	**2.17**	**33.92**	**28.37**	**8.22**	**31.00**
#09	**2.69**	**9.24**	**11.70**	**15.61**	**11.98**
#10	**7.37**	**10.88**	**6.11**	**3.23**	**12.85**
#11	**5.85**	**4.01**	**6.86**	**16.71**	**10.64**
#12	0.42	**5.14**	**5.89**	**2.62**	**5.39**
#13	0.37	1.53	0.70	-0.50	1.25
#14	**51.65**	**44.70**	**51.27**	**21.10**	**52.73**
#15	**2.82**	**21.01**	**35.35**	**28.19**	**30.70**
#16	**11.66**	**8.86**	**15.16**	**6.95**	**15.48**
#17	**11.63**	**29.93**	**17.64**	**7.50**	**27.75**
#18	**4.70**	**27.48**	**22.38**	**14.33**	**34.35**
#19	0.31	0.61	**3.13**	**4.55**	**3.74**
#20	**6.32**	**14.59**	**43.74**	**26.76**	**46.55**
#21	**11.09**	**17.61**	**26.09**	**31.07**	**29.54**

Table S5. Significance of the face-selective response at each ROI and for each group of infants (i.e., type of stimuli). Significance was estimated for each harmonic and for the summed response across harmonics using *Z*-scores calculated on the average across electrodes within the ROIs, odor contexts and infants within the group. Significance was fixed at *Z* > 1.64 (*p* < .05, one-tailed, signal > noise). Asterisks indicate significance (* *p* < .05, ** *p* < .01, *** *p* < .001). (lOT: left occipito-temporal ROI, mO: medial occipital ROI, rOT: right occipito-temporal ROI, 3ROIs: mean of the three ROIs).

		Group 1: Natural stimuli				**Group 2: Simplified stimuli**			
Harmonic	**Frequency (Hz)**	**lOT**	**mO**	**rOT**	**3ROIs**	**lOT**	**mO**	**rOT**	**3ROIs**
1	1	3.45***	0.27	1.81*	2.09*	8.52***	5.41***	7.99***	9.24***
2	2	1.50	0.80	0.06	1.20	6.14***	4.99***	4.68***	9.19***
3	3	-0.34	-0.78	-1.37	-0.89	5.01***	3.89***	6.77***	8.15***
4	4	2.59**	0.85	1.05	2.19*	2.93***	3.04**	0.54	2.64**
5	5	-0.09	-0.45	-0.84	-0.64	3.28***	6.69***	2.17*	5.42***
Sum	1 to 5	3.64***	0.23	1.38	2.38**	11.1***	9.51***	8.78***	14.7***

Table S6. Significance of the face-selective response at each electrode of the ROIs for each individual infant within each group. Significance was estimated for the summed response of each infant and at each electrode within the ROIs using *Z*-scores calculated on the average across odor contexts. *Z*-scores in bold indicate significance (*Z* > 1.64, *p* < .05, one-tailed, signal > noise). (lOT: left occipito-temporal ROI, mO: medial occipital ROI, rOT: right occipito-temporal ROI).

Group 1: Natural stimuli

	lOT					**mO**				**rOT**				
Infant	**P9**	**P7**	**PO7**	**PO5**	**O1**	**PO3**	**POz**	**PO4**	**Oz**	**P10**	**P8**	**PO8**	**PO6**	**O2**
#01	-1.36	-1.13	-1.32	-0.37	-0.10	-0.52	0.01	0.21	-0.97	**1.90**	**1.79**	**1.98**	0.61	0.30
#02	-0.62	-0.55	-0.46	-0.21	-0.18	0.22	-0.67	0.38	0.84	0.63	0.15	0.31	0.71	0.48
#03	1.25	**2.19**	0.95	-0.64	0.63	-0.90	0.63	0.10	0.43	-0.44	0.03	-0.20	-0.11	-1.03
#04	0.30	0.63	-0.12	1.01	0.77	**2.55**	**4.36**	-0.43	-0.02	0.63	0.81	-0.32	-1.47	-1.65
#05	-0.20	-0.36	0.23	-1.20	-0.27	-0.66	-1.03	-1.17	-0.47	0.55	0.64	0.41	-0.98	-0.87
#06	-0.03	0.25	**1.81**	-1.20	1.55	-0.80	-0.87	0.05	0.69	-0.30	0.52	-1.01	0.97	-1.12
#07	**3.10**	0.69	**3.69**	**2.26**	**3.65**	**2.02**	1.03	**2.20**	**2.90**	**4.08**	**4.44**	**2.59**	**2.84**	**1.70**
#08	0.04	0.17	**3.01**	-0.11	1.33	-0.72	-0.72	0.93	0.76	0.53	0.57	-0.15	-0.20	0.52
#09	-2.37	-0.35	1.27	1.11	**2.25**	0.37	0.31	1.58	**2.04**	0.66	**1.94**	**4.19**	**3.71**	**2.74**
#10	0.73	0.80	**2.68**	**3.92**	1.22	**3.91**	0.99	-2.15	-0.29	**1.86**	1.01	-1.98	-2.13	-3.31
#11	-0.56	-0.23	**1.98**	0.40	-2.02	0.02	1.21	0.13	0.15	-0.03	0.80	0.18	1.07	-1.43
#12	**2.23**	1.11	1.36	1.51	1.33	-1.38	-0.53	0.01	**1.71**	0.70	0.27	-1.57	-1.45	-1.34
#13	1.05	0.42	0.45	-0.28	0.41	-1.05	0.00	0.90	0.25	0.77	-1.10	**2.50**	0.35	-0.81
#14	**2.30**	-0.92	-0.49	-0.70	-0.97	-0.73	1.23	-0.49	-1.92	0.95	-0.08	1.44	-1.67	-2.74
#15	**4.03**	**2.18**	**6.36**	**3.35**	**3.44**	**3.09**	0.24	0.85	**1.85**	-0.75	0.08	-0.23	-0.18	1.47
#16	**1.73**	-0.79	0.76	0.61	0.24	0.58	-0.03	0.02	1.39	-0.58	-0.94	0.65	0.08	1.19
#17	-1.01	-2.05	1.20	-2.59	**3.02**	-0.40	0.18	-0.76	0.88	-3.56	-1.65	0.96	1.07	**2.24**
#18	1.54	0.80	1.15	1.02	1.12	1.04	0.39	0.95	-0.54	1.32	1.26	1.13	1.15	0.00
#19	0.60	0.08	0.37	-0.51	1.08	-2.02	-1.35	**1.84**	0.44	1.08	0.03	-0.01	-0.68	-0.83
#20	-1.05	-1.64	1.07	-0.16	0.94	-1.60	-0.92	-0.15	-2.24	0.51	0.26	1.08	0.44	-0.93
#21	-0.22	1.64	0.54	0.30	-0.69	-0.39	-1.92	-0.04	-3.31	-1.42	-0.79	0.69	-1.16	0.58

Group 2: Simplified stimuli

	lOT					mO				rOT				
Infant	**P9**	**P7**	**PO7**	**PO5**	**O1**	**PO3**	**POz**	**PO4**	**Oz**	**P10**	**P8**	**PO8**	**PO6**	**O2**
#01	1.62	-0.14	1.25	1.41	1.52	**2.15**	0.49	0.48	**1.98**	**4.86**	**6.71**	**2.25**	**1.72**	**2.40**
#02	-1.21	-0.36	-0.59	-0.70	0.73	0.47	-0.09	-0.24	0.96	-0.30	-0.68	-0.42	**2.20**	-0.57
#03	1.06	-0.48	0.04	0.13	-0.92	0.02	0.36	1.36	-0.52	**2.83**	**3.83**	1.21	1.38	-0.19
#04	**2.06**	-0.18	1.28	**2.23**	-1.01	1.33	-1.11	0.93	-1.68	0.31	-2.69	-1.34	-0.48	-0.81
#05	**2.36**	**2.02**	**3.52**	**3.18**	**3.94**	**4.93**	0.83	0.10	**1.85**	0.97	**2.04**	-0.09	-0.24	-1.63
#06	1.57	**3.13**	**1.87**	**2.86**	**2.50**	**2.98**	0.71	1.59	**3.03**	1.35	**3.46**	**2.73**	**2.28**	**1.99**
#07	-1.19	0.57	0.53	0.26	0.16	1.22	0.12	**3.18**	0.01	0.96	0.50	**2.89**	**2.92**	1.36
#08	0.98	-0.69	1.09	0.75	**1.71**	-1.23	-0.12	0.05	1.25	0.80	0.87	-1.31	-1.59	1.32
#09	1.54	0.99	0.14	0.43	-0.08	1.26	1.12	-0.21	-0.14	0.17	-0.08	0.66	1.03	-0.27
#10	**3.98**	1.06	0.38	**1.74**	**1.92**	1.05	0.76	**1.92**	**1.89**	0.05	-0.45	-0.24	1.29	**2.12**
#11	1.33	0.26	-1.34	1.02	0.48	**3.21**	**2.22**	**3.87**	0.11	1.11	**3.76**	**3.11**	**3.54**	0.20
#12	**4.93**	**2.45**	-0.99	0.74	-0.72	0.96	-0.76	-0.47	**2.07**	1.46	**2.27**	-0.28	-0.30	1.14
#13	**3.22**	0.07	-0.55	0.00	0.80	-0.07	-1.19	0.34	-0.70	-1.58	-2.00	-3.10	0.23	-0.96
#14	0.75	0.04	1.23	1.32	0.39	-0.06	1.49	0.58	0.42	1.57	1.13	**2.41**	1.56	1.40
#15	1.52	0.54	**5.65**	**4.78**	**12.85**	**3.61**	**4.11**	**10.85**	**9.73**	**3.46**	**3.80**	**11.62**	**12.49**	**10.90**
#16	**4.76**	**5.25**	**4.87**	**4.57**	**2.06**	**4.45**	1.25	**1.71**	**2.49**	**8.16**	**2.07**	**5.58**	1.44	**3.59**
#17	**4.63**	1.15	**3.26**	**5.19**	1.22	**3.31**	1.45	**2.27**	1.69	**5.35**	-0.30	**1.94**	**2.27**	**2.30**
#18	**6.91**	**6.66**	**4.13**	0.63	**6.25**	0.02	1.04	**2.26**	**2.42**	**2.62**	0.38	1.09	0.30	**2.56**
#19	0.88	1.53	1.10	-0.11	**3.41**	-0.09	1.09	-1.75	-0.63	**2.14**	-1.47	1.51	-1.05	0.38
#20	0.59	0.42	**2.18**	**1.97**	-0.06	1.33	0.71	0.30	-0.95	0.13	-0.93	-0.89	-0.89	-1.52
#21	**5.26**	**4.69**	**6.05**	**6.96**	**3.27**	**3.92**	**2.14**	**1.82**	**4.03**	**18.66**	**6.88**	**11.15**	**2.35**	0.90

Appendix 3: Supporting information of Study

Supplementary Material

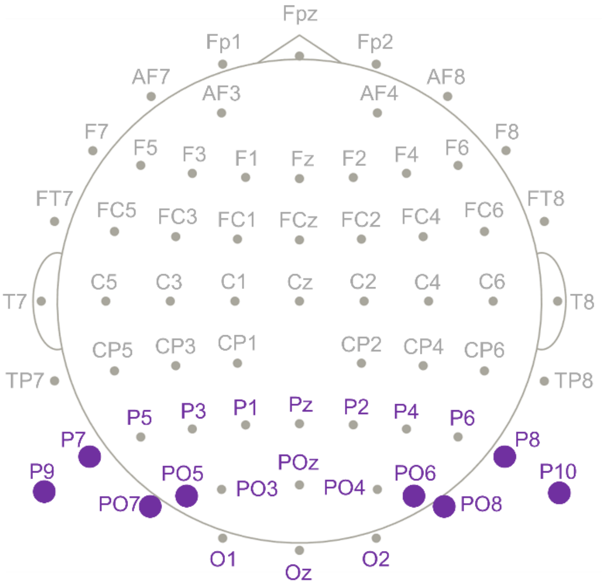

Figure S1. Sixty-three-channel montage of EEG acquisition and electrodes considered for analysis. EEG was acquired from a 63-channel head-cap configured according to the 10-10 classification system. Frequency-domain analysis was conducted on 21 posterior electrodes (labels colored in purple). For the face-selective response, 8 electrodes (identified by purple disks) were selected to define regions of interest (ROIs).

Table S1. Harmonic significance for the face-selective response. For each response, harmonic significance was estimated using *Z*-scores calculated on the average of all electrodes, odor contexts and separately for each group. Harmonics were considered significant according to a threshold of $Z > 1.64$ ($p < .05$, one-tailed, signal > noise). *Z*-scores in bold indicate significance.

		Group 1		**Group 2**
		Standard condition		**Fast condition**
Harmonic	**Frequency (Hz)**	***Z*-score**	**Frequency (Hz)**	***Z*-score**
1	6	**9.62**	1.33	**5.09**
2	12	**8.44**	2.66	1.57
3	18	**5.25**	3.99	1.46
4	24	**9.60**	5.32	2.08*
5	5	**4.80**	6.65	-0.21
Sum	1 to 5	**13.33**	1.33 to 5.32	**7.91**

Table S2. Common to both conditions significant electrodes for the general and face-selective visual responses. For each response, electrode significance was estimated for 21 posterior electrodes (Figure S1) using *Z*-scores calculated on responses summed across significant harmonics and averaged across odor contexts and infants separately for each group. Electrodes were considered significant according to a threshold of $Z > 2.82$ ($p < .05$, one-tailed, signal > noise, Bonferroni-corrected for 21 electrodes).

General visual response			**Face-selective response**		
Electrode	***Z*-score Standard**	***Z*-score Fast**	**Electrode**	***Z*-score Standard**	***Z*-score Fast**
Oz	102.88	68.94	PO5	9.68	10.22
O1	69.33	56.65	PO6	10.99	5.59
O2	66.00	49.60	PO7	8.91	6.19
POz	59.44	44.79	PO8	13.12	7.53
			P7	11.15	7.49
			P8	8.11	4.40
			P9	9.91	8.85
			P10	9.28	8.44

Table S3. Significance of the face-selective response at the occipito-temporal ROI for each individual infant in the Standard (a) and Fast (b) groups. Significance was estimated for the summed response of each infant and at each electrode within the ROI using *Z*-scores calculated on the average across odor contexts. *Z*-scores in bold indicate significance ($Z > 1.64$, $p < .05$, one-tailed, signal > noise). (OT: occipito-temporal ROI).

a) Standard group

Infant	**P9**	**P7**	**PO7**	**PO5**	**P8**	**P10**	**PO6**	**PO8**	**OT**
#01	0.13	1.07	-2.61	-2.62	**2.98**	**2.10**	**5.18**	**5.18**	**3.16**
#02	**6.07**	**6.38**	**3.17**	**3.06**	**6.52**	**4.55**	**2.68**	**2.71**	**8.30**
#03	1.08	1.50	0.03	0.02	1.45	-2.36	0.50	0.44	0.58
#04	-0.96	-0.87	-0.88	-1.08	0.41	-0.06	0.71	1.03	-0.32
#05	0.31	**2.79**	-1.00	-1.16	**3.01**	0.95	**3.16**	**3.17**	1.61
#06	1.39	0.36	1.16	0.23	0.38	0.44	0.36	-0.28	0.96
#07	1.30	**7.34**	**3.98**	**3.79**	**5.17**	0.78	**4.23**	**5.01**	**9.06**
#08	**1.93**	**2.22**	**3.30**	**3.24**	**1.97**	**8.20**	**5.00**	**4.91**	**9.52**
#09	0.92	0.46	0.09	0.06	-1.00	-0.04	-0.37	0.01	-0.04
#10	**5.49**	**5.88**	**2.09**	**2.09**	**9.62**	**14.80**	**3.65**	**3.61**	**8.70**
#11	1.48	**2.92**	**3.99**	**3.65**	1.08	**1.72**	1.26	1.13	**4.15**
#12	**2.27**	**4.47**	**4.14**	**4.16**	0.16	**4.86**	0.97	0.85	**4.75**
#13	**2.09**	**5.93**	0.16	0.01	**3.77**	1.10	1.29	0.88	**4.38**
#14	**6.69**	**4.20**	**3.13**	**2.30**	**6.24**	**13.68**	**2.30**	**2.59**	**7.15**
#15	1.23	-1.59	0.08	-0.18	**2.94**	0.24	**2.01**	**2.11**	1.35
#16	0.65	0.63	-0.02	-0.05	0.43	-0.58	-0.56	-0.29	-0.04
#17	**1.88**	**4.47**	**1.93**	**2.67**	**4.70**	**7.40**	**3.16**	**2.86**	**5.37**
#18	**2.08**	1.22	**2.85**	0.71	**4.26**	-1.19	**4.23**	**4.48**	**5.55**
#19	**2.90**	**2.34**	**2.20**	**2.24**	1.22	1.54	1.49	1.56	**2.72**
#20	-0.40	**1.83**	**3.32**	**2.74**	0.01	0.30	1.52	**1.79**	**2.56**
#21	0.29	0.22	0.20	**3.03**	0.10	0.76	1.61	-0.46	**1.77**
#22	**3.26**	**7.88**	**4.28**	**4.25**	**1.91**	**3.12**	0.50	0.55	**6.30**
#23	-1.24	0.09	-0.76	-1.75	0.52	0.01	-0.16	**1.84**	-0.30
#24	**6.75**	**6.47**	**1.96**	**2.41**	**4.97**	**2.20**	**3.97**	**3.92**	**8.04**
#25	1.14	**1.74**	**1.98**	**3.25**	**6.21**	**3.20**	**7.49**	**6.01**	**15.26**
#26	**4.41**	**7.18**	**2.69**	**2.56**	**1.66**	0.01	**4.77**	**5.76**	**7.45**

b) Fast group

Infant	P9	P7	PO7	PO5	P8	P10	PO6	PO8	OT
#01	1.49	1.28	-1.55	-1.54	-0.20	**4.00**	**3.86**	**3.46**	**1.91**
#02	-0.75	0.76	0.44	0.35	1.20	**4.69**	**1.76**	**2.16**	1.41
#03	**3.63**	**2.80**	**2.34**	**2.46**	**7.03**	**5.37**	**3.50**	**2.94**	**5.95**
#04	**2.14**	0.66	0.67	1.57	**2.72**	**3.57**	**2.01**	1.35	**2.26**
#05	**4.26**	**2.53**	0.75	0.74	**4.65**	**4.15**	**4.66**	**4.55**	**5.23**
#06	**2.11**	**1.65**	-0.95	-0.99	0.13	1.18	0.95	0.69	0.70
#07	0.98	-0.62	0.59	0.54	-0.06	**2.11**	-0.45	-0.38	1.49
#08	0.12	-0.18	0.15	0.55	-0.95	-2.77	-1.17	0.05	-1.05
#09	0.80	-0.18	**5.11**	**5.29**	-0.32	**3.81**	**1.98**	**1.65**	**3.51**
#10	**2.17**	-0.40	1.20	1.20	**3.77**	**3.34**	**3.50**	**3.73**	**4.05**
#11	0.82	**1.88**	**1.92**	**2.49**	**6.62**	1.07	-2.51	-3.00	**2.76**
#12	-0.99	1.25	**3.68**	**4.01**	0.17	**1.67**	-0.29	-0.33	**1.72**
#13	**2.92**	0.61	0.73	0.36	0.13	**1.78**	1.32	1.34	**2.86**
#14	**4.34**	**3.22**	**2.49**	**2.45**	**2.65**	**2.28**	**3.02**	**5.64**	**5.80**
#15	0.01	1.13	-0.77	-0.84	-0.13	-2.53	0.31	0.22	-0.92
#16	**2.05**	**2.17**	**2.17**	**2.44**	0.01	-0.44	**1.94**	**1.82**	**3.40**
#17	0.50	**2.38**	-1.53	-1.33	0.30	-0.42	-0.29	-0.21	-0.26
#18	-4.97	-1.37	-1.15	-0.03	0.77	**4.69**	-1.04	-0.82	-1.78
#19	1.59	**1.86**	**3.75**	0.53	0.93	1.58	**3.07**	**2.04**	**4.92**
#20	**3.87**	-1.52	-2.45	**2.06**	-2.31	0.52	1.21	-1.51	-0.47
#21	0.86	0.09	**2.52**	**2.56**	1.31	**2.11**	1.22	1.24	**3.35**
#22	**2.67**	**4.84**	**4.19**	**4.36**	**1.94**	**1.71**	1.51	1.02	**5.55**
#23	**2.69**	**3.53**	**3.24**	**5.37**	**4.16**	**6.80**	**2.20**	**7.13**	**7.59**

Table S4. Harmonic significance for the general visual response. For each response, harmonic significance was estimated using *Z*-scores calculated on the average of all electrodes, odor contexts and separately for each group. Harmonics were considered significant according to a threshold of $Z > 1.64$ ($p < .05$, one-tailed, signal > noise). *Z*-scores in bold indicate significance.

		Group 1		**Group 2**
		Standard condition		**Fast condition**
Harmonic	**Frequency (Hz)**	***Z*-score**	**Frequency (Hz)**	***Z*-score**
1	6	**67.85**	12	**73.57**
2	12	**40.64**	24	**15.21**
3	18	**15.57**	36	0.51
4	24	**8.71**	48	1.09
Sum	6 to 24	**65.4**	12 to 24	**63.71**

Table S5. Significance of the general visual response at the medial occipital ROI for each individual infant in the Standard (a) and Fast (b) groups. Significance was estimated for the summed response of each infant, at each electrode within the ROI and for the mean response across electrodes, using *Z*-scores calculated on the average across odor contexts. *Z*-scores in bold indicate significance ($Z > 1.64$, $p < .05$, one-tailed, signal > noise). (mO: medial occipital ROI).

a) Standard group

Infant	POz	O1	Oz	O2	mO
#01	**11.41**	**12.07**	**9.47**	**14.39**	**13.87**
#02	**27.33**	**34.04**	**67.21**	**43.60**	**56.73**
#03	**4.53**	**10.91**	**10.85**	**4.83**	**8.59**
#04	**5.99**	**4.65**	**9.63**	**18.33**	**18.94**
#05	**2.82**	**10.84**	**7.76**	**4.96**	**10.16**
#06	**3.92**	**1.77**	-0.45	-0.14	**4.10**
#07	**41.90**	**66.24**	**65.65**	**31.55**	**76.04**
#08	**2.23**	**14.24**	**15.81**	**14.94**	**15.20**
#09	**4.05**	**3.17**	**7.49**	**6.50**	**14.93**
#10	**5.21**	**12.84**	**37.66**	**10.86**	**26.81**
#11	**3.35**	**6.30**	**9.79**	**16.59**	**13.16**
#12	**10.77**	**6.51**	**17.05**	**14.30**	**16.51**
#13	**15.47**	**7.12**	**28.63**	**46.01**	**34.02**
#14	**9.41**	**14.99**	**11.55**	**13.09**	**18.07**
#15	**5.52**	**3.97**	**7.79**	**10.51**	**13.49**
#16	**23.53**	**26.25**	**27.91**	**14.22**	**32.04**
#17	**39.07**	**18.09**	**36.33**	**27.37**	**42.57**
#18	**30.24**	**28.21**	**30.32**	**14.60**	**59.65**
#19	**18.01**	**25.22**	**44.07**	**20.67**	**53.91**
#20	0.33	0.63	**5.83**	0.11	**2.69**
#21	**11.64**	**9.54**	**12.37**	**3.41**	**12.22**
#22	0.06	**12.22**	**22.47**	**12.68**	**15.97**
#23	**6.69**	**6.13**	**9.63**	**8.44**	**11.85**
#24	**6.57**	**3.76**	**18.94**	**5.39**	**13.46**
#25	**38.11**	**49.57**	**34.25**	**46.21**	**67.86**
#26	**10.55**	**9.19**	**7.03**	**7.49**	**14.23**

b) Fast group

Infant	POz	O1	Oz	O2	mO
#01	**2.20**	**-0.14**	**6.09**	**3.55**	**5.66**
#02	**13.86**	**59.57**	**55.46**	**22.31**	**79.18**
#03	**12.36**	**3.80**	**19.27**	**13.33**	**27.84**
#04	**4.07**	**0.02**	**6.72**	**9.16**	**5.85**
#05	**38.62**	**32.30**	**50.00**	**30.44**	**50.09**
#06	**4.79**	**3.99**	**5.97**	**4.51**	**10.33**
#07	**3.55**	**2.99**	**3.96**	**4.16**	**5.93**
#08	**13.84**	**11.36**	**9.69**	**10.11**	**16.72**
#09	**4.12**	**1.68**	**4.90**	**1.97**	**5.27**
#10	**5.01**	**14.22**	**13.27**	**7.62**	**12.53**
#11	**13.53**	**32.58**	**19.86**	**20.39**	**30.78**
#12	**15.23**	**12.75**	**12.53**	**8.02**	**18.20**
#13	**12.16**	**16.62**	**22.70**	**17.97**	**22.60**
#14	**31.56**	**10.35**	**48.25**	**38.12**	**46.01**
#15	**27.79**	**24.76**	**32.01**	**28.12**	**38.64**
#16	-0.17	**5.12**	**6.47**	**7.96**	**8.36**
#17	0.64	**4.96**	**4.49**	**4.36**	**6.13**
#18	**36.62**	**20.20**	**38.44**	**27.11**	**49.07**
#19	**16.92**	**12.52**	**17.04**	**29.39**	**34.99**
#20	**6.00**	**5.60**	**6.65**	**6.81**	**13.76**
#21	**2.53**	**1.28**	**15.80**	**13.42**	**13.64**
#22	**4.16**	**4.89**	**11.60**	**3.87**	**13.12**
#23	0.22	**5.14**	**2.26**	**8.18**	**5.64**

Curriculum vitae

Publications

2023 Rekow, D., Baudouin, J.-Y., **Kiseleva, A.,** Rossion, B., Durand, K., Schaal, B., & Leleu, A. (2023). Olfactory-to-visual facilitation in the infant brain declines gradually from 4 to 12 months. *bioRxiv, 556823*. https://doi.org/10.1101/2023.09.08.556823

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Calce, R. P., Rekow D., Barbero, F. M., **Kiseleva A**., Talwar, S., Leleu A., & Collignon, O. (Under review). Voice categorization in the 4-month-old human brain. *Current Biology*

Communications

Talks

2023 **Kiseleva,** A., Rekow, D., Schaal, B., Leleu, A. The inverse effectiveness of maternal odor on rapid face categorization in the 4-month-old infant brain. International *Multisensory Research Forum (26th, IMRF 2023), Brussels, BE.*

Kiseleva A. The inverse effectiveness of the influence of maternal odor on rapid face categorization in the infant brain*. Symposium of Young Researchers in Neuroscience, Brain Awareness Week, Dijon, FR.*

2022 **Kiseleva A.** The selective influence of maternal odor on demanding face categorization in the infant brain. *Annual meeting of the national Research Grouping Odorant Odeur Olfaction (O3), Paris, FR.*

Kiseleva, A., Schaal, B., Rekow, D. & Leleu, A. The selective influence of maternal odor on demanding face categorization in the infant brain. *27th Young Researcher Forum, Dijon, FR*

Kiseleva, A., Schaal, B., Rekow, D. & Leleu, A. The selective influence of maternal odor on demanding face categorization in the infant brain. *PhD students ' day in Centre for Smell, Taste and Feeding Behavior (CSGA), Dijon, FR.*

Rekow, D., Baudouin, J.-Y., **Kiseleva, A.**, Rossion, B., Durand, K., Schaal, B. & Leleu, A. Maternal odor facilitation of rapid face categorization progressively declines in the developing infant brain. *Annual meeting of the national Research Grouping Neurosciences Cognitives du Développement, GDR babylabs, Paris, FR.*

Rekow, D., Baudouin, J.-Y., **Kiseleva, A.**, Rossion, B., Durand, K., Schaal, B. & Leleu, A. Maternal odor tutors neural face categorization in younger, but not older, infants. *Symposium: Delineating the early development of perceptual categorization with EEG* *frequency-tagging (Chair: A. Leleu). International Congress of Infant Studies (23th, ICIS 2022), Ottawa, CA*

Rekow, D., Baudouin, J.-Y., **Kiseleva, A.**, Rossion, B., Durand, K., Schaal, B. & Leleu, A. The facilitating effect of maternal odor on rapid face categorization in the infant brain: A progressive decline over the first year. *European Society for Cognitive and Affective Neuroscience (ESCAN 2022), Vienna, AT.*

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Calce, R. P., Rekow, D., Barbero, F. M., **Kiseleva, A.**, Talwar, S., Leleu, A., & Collignon, O. Selective brain response to voices at four months of age. *Symposium: Delineating the early development of perceptual categorization with EEG frequency-tagging (Chair: A. Leleu) International Congress of Infant Studies (ICIS 2022), Ottawa, CA.*

2021 **Kiseleva, A.** How odors help the development of face categorization in the human infant brain. *PhD students ' day in Centre for Smell, Taste and Feeding Behavior (CSGA), Dijon, FR.*

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2022 **Kiseleva, A.,** Schaal, B., Rekow, D. & Leleu, A. (2022) Maternal odor influence on rapid neural face categorization in natural vs. edited images at 4 months of age. *International Conference of Infant Studies (23th, ICIS 2022), Ottawa, CA.*

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2021 **Kiseleva A.,** Schaal, B., Rekow, D. & Leleu, A. (2021) The development of rapid face categorization in the human infant brain. *NeuroCog, Louvain-la-Neuve, BE.*

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Kiseleva A., Schaal, B., Rekow, D. & Leleu, A. (2021) Maternal body odor helps the development of rapid face categorization in the human infant brain. *Chemical Signals in Vertebrates (15th, CSiV 2021), Online.*

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Teaching activities and tutoring

2021-2023 Teaching assistant – Psychology Department – Université de Bourgogne – Statistics (BSc 3rd year) – 128 hours

Scientific dissemination

2023 19th European Researchers Night: Future, Speed-Searching, *Dijon, FR.*

Young Researchers Festival of Expé: *Le Mans, FR.*

2022 Biology Day: lab tour and EEG workshop for highschool Biology professors, *Dijon, FR.*

Brain Awareness Week: OpenLabs of the Université de Bourgogne, *Dijon, FR.*

18th European Researchers Night: Unexpected, Sensory tent, *Dijon, FR.*

2021 Science festival: Live EEG Demo for an 8-to-88 year-old audience *Dijon, FR.*

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