How does paternal odor influence emotion perception in infancy?

Antonia Düfeld & Sarah Jessen

Institute of Medical Psychology
Center of Brain, Behavior, and Metabolism
University of Lübeck

antonia.duefeld@uni-luebeck.de; sarah.jessen@uni-luebeck.de

ORCiD: 0009-0002-3868-6178

Data Availability Statement
The data that support the findings of this study will be made available on OSF after publication.

Funding Statement
This work was supported by funding of the German Research Foundation (DFG, grant-number: JE 781/3-1 and JE 781/4-1).

Conflict of Interest Disclosure
The authors declare that they have no competing financial interests.

Ethics Approval Statement
The study was conducted according to the Declaration of Helsinki and approved by the ethics committee at the University of Luebeck. Written informed consent was obtained from the guardians of the infant prior to data collection.

Acknowledgements
We thank all the families for participating.

Research Highlights

- 7-month-old infants show an enhanced Nc response to fearful compared to happy male faces when smelling their own father.
- 7-month-old infants showed a differential processing of male but not female emotional faces irrespective of the presence of paternal odor at occipital electrodes.
- Infants' neural processing of emotional male faces differs from that of emotional female faces.
- The father's odor influences early socioemotional processing in infancy, as had previously only been shown for maternal odor.

Abstract

Social odor plays an important role for various facets of early development, including communication and social processing. Previous research focusing on maternal odor has shown that smelling the mother can influence face processing in general as well as emotion processing more specifically. However, it is unclear to what extent these effects are specific to maternal odor or can also be found for other familiar social odors. To address this question, we investigated the impact of the father's odor on emotional face processing in 7-month-old infants. We recorded the infants' EEG response to female and male happy and fearful faces while infants were exposed to either their father's odor or the odor of a different infant's father. Analysis of the frontocentral Nc amplitude revealed an enhanced response to fearful compared to happy male faces only when infants smelled their own father but not when they smelled an unfamiliar father. In contrast, emotion processing at the occipital N290 was not affected by the presence of paternal odor, suggesting an impact of social odor on attention allocation rather than structural face processing. Interestingly, all effects were specific to male faces, pointing to a gender-specific impact of social odor. Our findings therefore provide first evidence for an influence of the father's odor on face processing, specifically male faces, in infancy.

Keywords: social odor, face processing, emotion, EEG, infancy, development

Introduction

Infants are born into a social environment and quickly learn to use social cues to gather information about their environment. While numerous studies have investigated infants' processing of facial and vocal information, only in recent years, researchers have started to study olfaction as a source of social information in infancy.

These first studies show that maternal odor appears to have a specific impact on the processing of social stimuli, in particular faces, during infancy. It increases infants' attention to faces (Durand et al., 2013) and specifically facilitates neural categorization of faces (Leleu et al., 2020) and face-like objects (Rekow et al., 2021), while neither was the case for objects (Rekow et al., 2020). Furthermore, when exposed to their mother's odor, infants showed a reduced response to fearful faces (Jessen, 2020), suggesting that maternal odor also impacts the processing of emotional information. Evidence regarding the specificity of the reported effects to the infants' own mother are mixed. While Durand et al. (2020) found an impact of both, odor from the infant's own as well as a different infant's mother, on attention allocation to faces, Jessen (2020) found no impact of the odor of a different infant's mother on emotion processing.

In sum, initial evidence suggests an impact of maternal odor on various aspects of face processing during infancy, and different aspects might be differently susceptible to the familiarity of the maternal odor (see Düfeld et al., 2025, in press, for a discussion of the potential distinct mechanisms giving rise to these differences). However, while all studies so far have investigated the role of *maternal* odor, most infants are raised also by other caregivers than the mother, among them often the father. The question therefore arises whether we can observe similar effects as previously reported for maternal odor also for paternal odor.

On the one hand, infants have more exposure to their mother's than to their father's odor. This is true for all infants since odor processing already develops prenatally, and after birth, infants show a preference for odor they were exposed to in the womb (Schaal, 1988; Schaal et al., 1998, 2020; Tristão et al., 2021). Furthermore, for many infants this increased exposure to maternal odor continues after birth, as many infants are breastfed, an activity strongly influenced by olfactory processes (Porter & Winberg, 1999; Varendi et al., 1997) and necessarily linked to the mother. But even apart from breastfeeding, in many cultures, the mother is often the primary caregiver, spending on average more time with the infant than the father (Baildam et al., 2000; Harrison & Magill-Evans, 1996; Tikotzky et al., 2011). An increased exposure to the odor of the primary caregiver should lead to a higher familiarity, resulting possibly in a stronger impact on other types of social processing. In addition, since breastfeeding is an inherently positive experience (with not only a nutritious but also an emotion regulatory function (see e.g., Schaal et al., 2020; Schäfer & Croy, 2023), maternal odor is not only more familiar but also has very strong positive associations.

On the other hand, social odor is a learned odor and continuously updated (Damon et al., 2021; Schaal et al., 2020; Sullivan & Opendak, 2020), which is important, since a person's odor changes due to natural variations, for instance, in food intake and health status, but also due to artificial factors such as a new deodorant used. Importantly, previous studies investigating the impact of maternal odor on sociocognitive aspects such as face processing have not focused on a specific component of the mother's body odor (such as mamillary odor). Rather, they considered the entire odor of the mother, encompassing different types of body odor and potentially also artificial sources of odor such as deodorant in combination, as one social odor. Hence, infants need to constantly adapt their representation of their mother's odor, and there is no reason why postnatal learning and updating should be limited to one single odor and not also occur for other familiar odors, such as the father's odor. While maternal odor may be more familiar, other social odor could be familiar enough to have a similar effect on sociocognitive processing.

As the familiarity of the odor on infant face processing may be of particular importance for emotion processing (Jessen, 2020; Düfeld et al., in press), our main aim was to investigate whether paternal odor impacts the neural processing of fearful faces in 7-month-old infants, as has been previously reported for maternal odor (Jessen, 2020). At 7 months, infants typically show an enhanced response to fearful compared to happy facial expressions (see e.g., Leppänen et al., 2007; Peltola et al., 2009; Vaish et al., 2008), impacting ERP components linked to structural face processing (N290, P400; De Haan et al., 2003; De Haan et al., 2007; De Haan et al., 2002) as well as attention-allocation (Nc, Conte et al., 2020; Reynolds & Richards, 2005). Based on Jessen (2020), we expected infants to show a reduction in Nc response to fearful faces when exposed to their own fathers compared to an unfamiliar father's odor.

One important aspect to consider is the gender of the face expressing the emotions. Not only do infants in many societies spend more time with their mother than their father, as mentioned above; they typically also see more female than male faces in general (Liu et al., 2015; Quinn et al., 2008; Rennels & Davis, 2008). This increased familiarity with female faces has been suggested to result in a processing bias in favor of female faces (Quinn et al., 2002; Ramsey et al., 2005; Ramsey-Rennels & Langlois, 2006; Rennels et al., 2016; Righi et al., 2014), which has prompted developmental researchers to rely on female faces as stimulus material in many studies (see e.g., (Aran et al., 2023; Vanderwert et al., 2015; Xie et al., 2019). Hence, we know little about the processing of emotions from male faces in infancy, and whether it differs from that of female faces. When investigating the role of paternal odor, however, it is essential to not only use female faces, as this would result in an inherent mismatch between olfactory and visual information. The second aim of our study is therefore to investigate the processing of male compared to female emotional facial expressions, and to what extent the impact of paternal odor is modulated by face gender.

Methods

Sample size and main analyses were preregistered and can be found here: https://aspredicted.org/CLG_DBM.

Participants

64 7-month-old infants were invited to participate in the study. Data of 30 infants (*age at appointment 1:* 209 ± 6 days (mean ± SD), range: 199 - 225 days; *age at appointment 2:* 217 ± 6 days, range: 206 – 231 days; 15 girls) were included in the final sample for the main analysis. 31 infants were excluded because they did not contribute at least 10 artifact-free trials per condition at each appointment (n=26), did not show up for the second appointment (n=3), because of technical problems (n=2), and an Nc amplitude more than 2 SD from the mean across all conditions (n=3). The sample size of n=30 was determined a priori (see preregistration) and allowed us to detect effects of f=.22 with a power of .8. For the corroborating analysis using general linear mixed models, we included all infants who contributed at least 10 artifact-free trials for at least one appointment (n=41).

Infants were recruited via the maternity ward at the *Universitätsklinikum Schleswig-Holstein* in Lübeck, were born full-term (gestation weeks 37 to 42), had a birth weight of at least 2500 g, and no known visual or neurological deficits or other known significant health problems.

The study was conducted according to the Declaration of Helsinki and approved by the ethics committee at the University of Luebeck. Written informed consent was obtained from the guardians of the infant prior to data collection. Parents received a reimbursement of 35 Euro in total for their participation as well as a small toy for the infant.

Visual Stimuli

Infants were presented with a total of 24 colored photographs from the FACES database (Ebner et al., 2010), showing 6 women (actress-ID: 010, 034, 040, 054, 063, 069) and 6 men (actor-ID: 008, 049, 062, 066, 114, 167) between 19 and 31 years. Each person was shown once with a happy and once with a fearful expression, and expressions had been recognized with an accuracy above 90% in a prior rating study (Ebner et al., 2010).

Odor Manipulation

To manipulate the presence of paternal odor, we employed the "worn t-shirt paradigm" (see Figure 1 for general procedure), in which paternal odor was captured by using worn cotton t-shirts, as successfully used in previous studies (see e.g., Durand et al., 2013; Jessen, 2020). Prior to the scheduled appointment, participating families were provided with a white, same-sized, 100% cotton t-shirt in a zip-lock bag. All t-shirts were pre-washed in the same way with a skin-friendly and unscented detergent (Persil Sensitive Gel). The infants' fathers were asked to wear the t-shirt during sleep for three consecutive nights, storing it in the zip-lock bag throughout the day. Additionally, the fathers were instructed to use their usual toiletries and refrain from using any new soap, perfume, etc. or change their eating and drinking habits during these days. After odor exposure, the t-shirt was stored in a household freezer to preserve its odor (Lenochova et al., 2009), only removed again on the testing date, and brought along to the experiment by the parent. Parents were asked to freeze the t-shirt for at least one day, which all families did. For practical reasons and to further conserve the odor, we kept all t-shirts in the lab's freezer (-16 °C) between appointments to swap them between father-infant-dyads for the stranger odor condition. Each t-shirt was used twice, once for the paternal odor condition for the father's own child and once for the stranger odor condition for a different infant. The t-shirt used in the father condition was not previously used in the stranger condition.

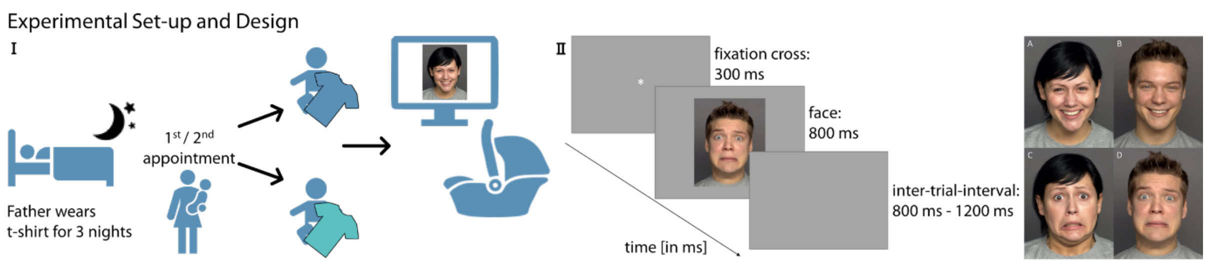

Figure 1. Experimental Set-up and Design. *I The fathers wore a t-shirt for three nights in a row before coming to the experiment. At one appointment, infants were exposed to their father's odor, while at the other, they were exposed to a stranger's odor (order randomized). During the EEG recording, the t-shirt was positioned over the infant's chest area while the infant was sitting in a car seat in front of a computer screen. II In the right part, a sample of one trial of the stimulus presentation as well as examples of all four stimulus categories are shown (A: female happy, B: male happy, C: female fearful, D: male fearful).*

Design

The experiment followed a within group design (2 x 2 x 2 design) with the factors Odor (father, stranger), Emotion (happy, fear), and FaceGender (male, female). Infants were tested on two separate EEG appointments within 4 weeks' time. All infants were exposed to their father's odor on one appointment and a stranger's odor on the other appointment, with the order being counterbalanced across participants.

Procedure

Prior to the lab visit, participating families were sent a set of four questionnaires and asked to fill them in at home and bring them along for the first appointment: the German short version of the Infant Behavior Questionnaire (IBQ-R) (Gartstein & Rothbart, 2003; validated in (Vonderlin et al., 2012), the Edinburgh Postnatal Depression Scale (EPDS) (Cox et al., 1987), and the Early Motor Questionnaire (EMQ) (Libertus & Landa, 2013), and a lab internal questionnaire (LAB-Q), obtaining information on parameters pertaining to the infant and their environment. Relevant to the current analysis, parents were asked (a) whether the infant had ever been, and if so, was still, breastfed, and (b) how many hours the mother respectively the father spend with the infant on an average day.

All experiments in the lab were carried out by two female experimenters, who refrained from using perfume or perfumed products on the day of the testing to avoid odor contamination during the experiment. Upon arrival at the lab, families and infants were given time to familiarize themselves with the lab environment and the two experimenters. Parents were informed about the exact procedure of the experiment, had the opportunity to ask questions, and signed a consent form. For all except one appointment, the infant was accompanied by their mother, sometimes additionally by the father or other family members.

Testing took place in a light-attenuated room, with consistent conditions (closed blinds and dimmed light) maintained across sessions to minimize external variability. The room was thoroughly aired between each measurement session.

Preparation for the EEG recording was done while the infant was sitting on their parent's lap. An elastic cap (BrainCap, Easycap GmbH) with 27 AgAgCl electrodes arranged according to the international 10-20 system was used for recording, and skin-friendly, slightly warmed EEG gel was applied to reduce impedances ideally below 20 kΩ. The EEG signal was recorded at a sampling rate of 500 Hz using a BrainAmp MR Plus amplifier and BrainVision Recorder Software (Brain Products). During the measurement, data were referenced to the Cz electrode.

After EEG preparation, the infants were seated in an age-appropriate car seat (Maxi Cosi Pebble), which was placed on the lab's floor in a semi-reclining position. For the father's odor condition, a t-shirt worn by the father was placed over the infant's chest area, whereas for the stranger's odor, a t-shirt worn by the father of one of the other infants was used. The t-shirt was folded vertically and placed horizontally, with the armpit area facing towards the infant's chin as well as nose, making sure that the axillary area was as close to the chin as possible to maximize odor exposure. During the recording, the t-shirt was maintained in the proper position and loosely secured by the seat's safety belts. If possible, both, the experimenter placing the t-shirt and the accompanying parents, were blind to the odor condition, except in six cases, where this was not possible for practical reasons (such as parents having forgotten to bring the t-shirt along for the first appointment). All other parents were not debriefed until after the second experimental session.

A 24-inch monitor (resolution 1680X1050, refresh rate: 60Hz) was positioned at a distance of 60 cm from the car seat at a height of approximately 35 cm from the ground to the bottom edge of the screen. Two loudspeakers were positioned on either side of the monitor. Furthermore, a small camera was placed on top of the screen to monitor the infant's attention and to exclude any trials in which the infant was too inattentive or did not look at the screen.

The experiment was implemented using the software Presentation (version 22.1). Images were presented in isolation at the center of the screen on a grey background at a size of 24 x 30 cm. A trial started with a fixation cross, shown for 300 ms, followed by the face stimulus for 800 ms, and a jittered inter-trial interval of 800-1200 ms (see Figure 1). The infants saw a maximum of 216 trials, arranged in nine blocks, consisting of 24 trials each with 12 happy and 12 fearful faces. Blocks were presented subsequently without interruption. Stimuli were shown in a pseudo-randomized order, with no condition repeated more than once. The order of visual stimuli was randomized for each infant and for each of the two measurement appointments. To redirect the infants' attention to the screen, colorful, dynamic video clips accompanied by ringtones could be presented by the experimenter as attention-getters whenever the infant looked away.

During the measurement, the mother (in one case the father) remained in the same room but was seated approximately 1.5 m behind the infant, so as not to influence the testing or distract the infant from the visual stimuli. The parent was instructed not to interact or engage with the infant during the experiment, and one experimenter remained in the room at all times. If the father also came along to the appointment, he waited in an adjacent room during the experiment, except for the one case, where the father was in the room while measurement took place, as he was the only accompanying parent.

EEG Processing

Preprocessing and further analysis of the EEG data was done using Matlab 2022b (The MathWorks, Inc., Natick, MA) and customized scripts as well as the FieldTrip toolbox (Oostenveld et al., 2011).

All trials were segmented into one-second epochs around the time window of interest (200 ms pre- to 800 ms post-stimulus onset). The data were re-referenced offline to the linked mastoids, correspondingly the mean of TP9 and TP10. Subsequently, a bandpass filter was applied, ranging from 0.2 Hz to 20 Hz. All electrode channels deviating more than two standard deviations from the mean in at least 50 % of the segments were identified and interpolated using spherical spline interpolation; this was the case for at least one electrode in 26 out of 60 data sets.

After interpolation, all trials in which the standard deviation exceeded 80 μV at any electrode in a sliding window of 200 ms were excluded from further analysis. The remaining data were inspected visually to screen for any remaining artifacts and any trials in which the infant did not attend to the screen based on the video recording were excluded from further analysis. Infants had to provide a minimum of at least 10 artifact-free trials per condition (female-happy, male-happy, female-fearful, male-fearful) at each of the two appointments to be included in the final sample for the main analysis.

Table 1. Trial information. *Overview of the mean trial number based on odor exposure (father and stranger). Shown are mean ± standard deviation.*

	female happy	female fearful	male happy	male fearful
Father Odor	25 ± 9	26 ± 9	24 ± 8	24 ± 10
Stranger Odor	23 ± 8	24 ± 9	24 ± 8	25 ± 8

ERP Analysis

For the main statistical analysis, initially data from a total of 33 7-month-old infants were included.

Following preprocessing, the data were statistically analyzed in Matlab (version 2022b) and Jamovi (version 2.3.28). The Nc response was analyzed at frontocentral electrodes (F3, Fz, F4, C3, Cz, C4) in a time window of 400 to 800 ms after stimulus onset. The N290 was analyzed in a time window of 100–300 ms and the P400 in a time window of 300–500 ms after stimulus onset at occipital electrodes (O1, O2). Both, electrodes and time windows, corresponded to the preregistration and were determined prior to data collection. In addition, we also analyzed the P400 in a time-window of 280 – 430 ms based on visual inspection.

For Nc, N290, and P400, mean responses were computed over the respective time windows and electrodes. Three participants had a mean Nc amplitude of more than 2 standard deviations from the mean across all conditions, and were excluded from further analysis. Data from the remaining 30 participants were entered into a repeated measures ANOVA with the within-subject factors Emotion (happy, fearful), FaceGender (female, male), and Odor (paternal, stranger). As post-hoc tests, Student's t-tests are computed. Effect sizes are reported as partial eta squared (η^2p) and Cohen's *d*.

In addition and to corroborate the findings from the repeated measures ANOVA in a larger sample, we computed a general linear mixed model, which allowed us to include the data from infants who only contributed a sufficient number of trials at one appointment. Here, we did not exclude entire participants as outliers but only those data points which were more than 2 standard deviations from the mean (i.e., we excluded single conditions for individual infants). Using the GAMLj package (version 2.4.0) in jamovi, we computed the following model (plus the interactions between the three factors) for all three ERP components:

ERPamplitude ~ 1 + Odor + FaceGender + Emotion + (1 | SubjectID)

where *SubjectID* was included to account for interindividual variance. The model also included all interactions between the three factors Odor, FaceGender, and an Emotion.

Results

Sample

Infants in the main sample spent on average 21.0 ± 3.04 (mean ± standard deviation) hours/day with their mother and 9.29 ± 4.26 hours/day with their father, and all infants spent more time with their mother than with their father. At the time of the first appointment, 22 (out of 30) infants were still breastfed.

ERP analysis

We computed a repeated measures ANOVA with the factors Odor (father, stranger), Emotion (happy, fearful) and FaceGender (female, male) for the Nc, the N290 and the P400.

For the Nc, we observed an interaction between all three factors ($F(1,29) = 6.48$, $p=.016$, $\eta_p^2=0.18$; see Figure 2), revealing an interaction between Emotion and Odor for male ($F(1,29) = 7.99$, $p= .008$, $\eta_p^2=0.22$) but not for female faces ($F(1,29) = 0.61$, $p=0.44$, $\eta_p^2=0.02$). When smelling their father, infants showed an enhanced Nc response to fearful male compared to happy male faces ($t(29) = 2.45$, $p=.021$, $d=0.45$, fearful = -18.48 ± 17.5 µV [mean ±SD], happy = -8.55 ± 12.9 µV). When smelling a stranger, infants did not differentiate between the two emotions ($t(29) = -0.99$, $p=.33$, $d=-.18$).

For the N290, we observed an interaction between FaceGender and Emotion ($F(1,29) = 5.149$, $p=.031$, $\eta_p^2=0.15$; see Figure 3), but this interaction was not further influenced by Odor ($p>.23$). Only for male faces, infants showed a larger N290 amplitude for happy compared to fearful faces ($t(29) = -2.13$, $p=.042$, $d=-0.39$, fearful = 7.00 ± 7.17 µV, happy = 3.78 ± 6.24 µV).

For the P400, we observed a marginally significant interaction between FaceGender and Emotion ($F(1,29) = 4.16$, $p=.051$, $\eta_p^2=0.13$; see Figure 3) between 300 and 500 ms as defined a priori. For male faces, infants showed a more positive P400 for fearful compared to happy faces ($t(29) = -2.12$, $p=.042$, $d=-0.39$, fearful = 10.3 ± 10.9 µV, happy = 5.4 ± 10.6 µV). In the exploratory time window of 280 – 430 ms based on visual inspection, we observed the same pattern of results (FaceGender*Emotion: $F(1,29) = 4.364$, $p=.046$, $\eta_p^2=.013$; male faces: $t(29) = -2.05$, $p=.050$, $d=-0.37$, fearful = 8.55 ± 10 µV, happy = 4.30 ± 9.7 µV; female faces: $t(29) = 0.42$, $p=.677$, $d=0.08$, fearful = 4.93 ± 7.2 µV, happy = 5.59 ± 9.2 µV).

Including breastfeeding experience as a factor in the model (Breastfeeding (yes, no), coding whether the infant was still breastfed at the time of the first appointment) did not change the outcome, nor did including time spent with the father (z-scored) as a covariate.

To corroborate these analyses, we computed a linear mixed model for the larger sample of infants (i.e., n=41, including all infants who contributed ten trials per condition for at least one appointment). Our model yielded the same results for the interaction FaceGender*Odor*Emotion on the Nc ($b = -12.20$, $SE = 5.88$, $t(261.5) = -2.08$, $p = .039$), the interaction FaceGender*Emotion on the N290 ($b = 4.05$, $SE = 2.05$, $t(254.5) = 1.98$, $p=.048$) and the interaction FaceGender*Emotion on the P400 ($b = 4.94$, $SE = 2.75$, $t(263.0) = 1.79$, $p = .074$), confirming results from the repeated measures ANOVA in the increased sample.

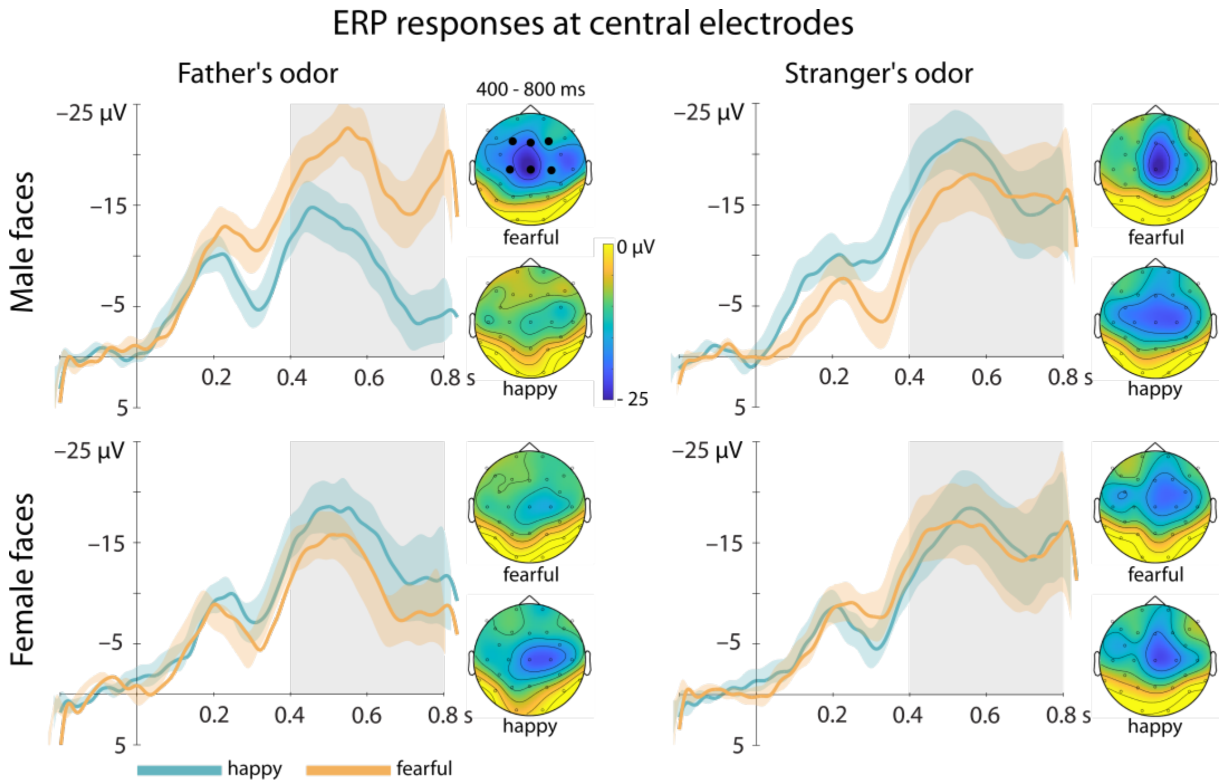

Figure 2. ERP responses at the central electrodes. *Shown are the ERPs for the Nc response at frontocentral electrodes (F3, Fz, F4, C3, Cz, C4; marked by black dots) to male and female faces in the two emotion conditions, happy (blue) and fearful (orange), in both the father's odor condition (left panel) as well as the stranger's odor condition (right panel). While no difference in response was observed for female faces and the stranger's odor condition, infants show an enhanced Nc response to male fearful compared to male happy faces in the father's odor condition. Next to the ERP curves, topoplots of the EEG signal across all electrodes averaged in the time window of interest (400-800 ms) post stimulus onset are presented.*

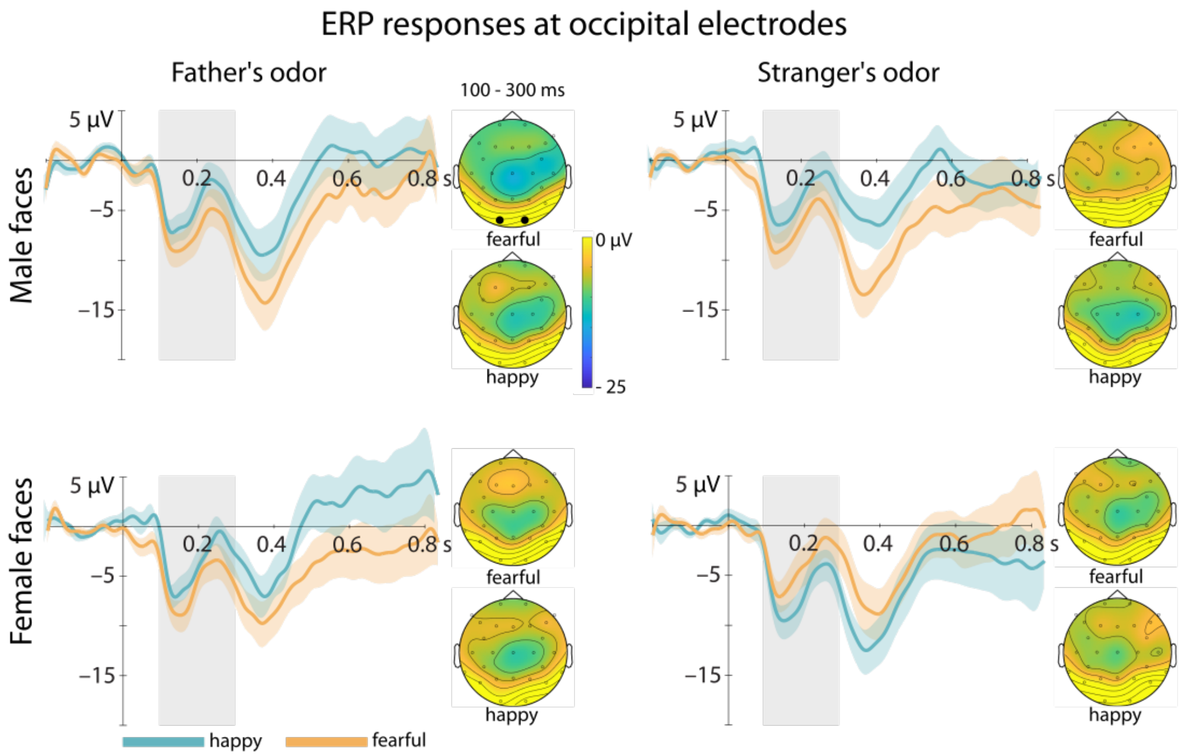

Figure 3. ERP responses at the occipital electrodes. *Shown are the ERPs for the N290 and P400 responses at occipital electrodes (O1, O2; marked by black dots) to male and female faces in the two emotion conditions, happy (blue) and fearful (orange), in both the father's odor condition (left panel) as well as the stranger's odor condition (right panel). For both components, there seems to be no odor effect, irrespective of familiarity. However, infants showed a more positive amplitude in response to fearful compared to happy male faces. Next to the ERP curves, topoplots of the EEG signal across all electrodes averaged in the time window of interest (100-300 ms) post stimulus onset are presented.*

Discussion

We investigated the impact of the father's odor on the processing of fearful and happy facial expressions in 7-month-old infants. Infants who smelled their father showed an enhanced Nc response to male fearful compared to male happy faces, while no difference in Nc response was observed for either female faces or infants smelling a different infant's father. Furthermore, on the N290 and P400 response, we found no influence of paternal odor but infants showed a more positive amplitude in response to fearful compared to happy male but not female faces.

Paternal odor enhances Nc response to fearful male faces

As predicted, the presence of paternal odor had an impact on emotion processing in 7-month-old infants by influencing the Nc response to fearful faces. Hence, paternal odor does influence sociocognitive processing in infancy, as had previously only been shown for the mother's odor (Durand et al., 2020; Jessen, 2020). This effect was specific to the Nc component and not observed at the occipital components N290 or P400. As the Nc has been linked to attention allocation (Ackles & Cook, 2007; Conte et al., 2020), this suggests that paternal odor affected attention related processes rather than perceptual or structural processing of faces predominantly observed at occipital electrodes (De Haan et al., 2003; De Haan et al., 2007).

Interestingly, this effect was specific for male faces, and did not modulate processing of female facial expressions. Several explanations for this pattern are possible. While it has previously been suggested that infants learn to associate faces with odor (Leleu et al., 2020; Rekow et al., 2020), thereby facilitating face categorization, it may be the case that this association is gender-specific. If infants have learned to associate male faces with male odor and female faces with female odor, paternal odor might specifically influence the processing of male faces. Since social odor differs markedly between men and women (Mutic et al., 2016; Penn et al., 2007; Russell, 1976; Troccaz et al., 2008), it seems plausible that infants may also be sensitive to this difference.

Another explanation could be general processing differences between male and female faces. While we did not find an effect of paternal odor on occipital face processing, also here, we only observed differential emotion processing for male faces. This suggests a more general difference in emotion processing between male and female faces, irrespective of odor. Since most prior studies investigating emotional face processing in infants used only female faces (Aran et al., 2023; Vanderwert et al., 2015; Xie et al., 2019) or did not systematically compare the processing of male and female faces (Hoehl & Striano, 2008; 2010), we know little about how infants process emotions from male faces. However, since infants show a processing bias for neutral female faces (e.g., Marquis & Sugden, 2019; Righi et al., 2014), it is likely that infants also process emotional information differently.

A likely interpretation of the present pattern of results is therefore that infants overall showed a structural differentiation between fearful and happy male faces, which was further modulated at an attentional level by the presence of paternal odor.

Absence of differential emotion processing when smelling an unfamiliar father

An interesting difference to previous work using maternal odor is the fact that we found an enhanced response to fearful faces in the presence of the father's but not a stranger's odor, while the reverse pattern has been reported for maternal odor (i.e., an enhanced response to fearful faces only in the presence of a stranger's but not the mother's odor, Jessen, 2020).

One explanation for this different pattern could be differences in odor familiarity. Infants in our sample spent on average twice as much time with their mother compared to their father (20.9 vs. 9.21 hours/day), making the mother the primary caregiver. Hence, while the father's odor certainly is familiar (as shown by the reported odor effect), it is likely less familiar than the mother's odor and hence might have a different impact on other social processes. This experience-driven account would be in line with research on face processing, which suggests that the amount of time infants spend with their father impacts their processing of male vs. female faces (e.g., Gredebäck et al., 2012; Liu et al., 2015). It might be the case that the father's odor draws attention but does not have the same buffering effect as maternal odor due to lower exposure. In this respect, the observed difference would be explained by different responses to primary vs. secondary caregiver rather than maternal vs. paternal odor. We did not find direct evidence for such an exposure-based explanation in our data – including time spent with the father in the model did not have an impact on the results. However, since in all cases, the mother spent more time with the infant than the father, the variance in the sample might be too small to detect an effect of exposure. Hence, future studies including infants with larger variation in parenting exposure and a larger overall sample could shed further light on an experience-based account underlying an odor impact.

Another potential influence could have been the mother, who was present during the measurement. As in previous studies on maternal odor (e.g., Durand et al., 2020; Jessen, 2020; Leleu et al., 2020), the mother was instructed to remain behind the infant at a distance to avoid any influence of her odor, but remained in the testing room at all times. However, in contrast to previous studies, this implied that the odor donor (i.e. the father) was absent, while in studies on maternal odor, the odor donor was in the room. This may have inadvertently caused a mismatch between the presence of one caregiver (the mother) while infants smelled the absent caregiver (the father), which in turn could impact concomitant face processing.

Absence of differential emotion processing for female faces

While infants showed a differential response to fearful compared to happy male faces at both, occipital and central electrodes, we found no evidence for emotion discrimination from female faces. This lack of a discrimination effect contrasts with many prior studies who reported enhanced response to fearful female faces as central and/or occipital electrodes (e.g., Aran et al., 2023; Peltola et al., 2009; Xie et al., 2019) in comparable age groups.

It may have been the case that – in addition to influencing the processing of male faces – paternal odor hampered the processing of female faces. If male odor is indeed associated with male faces, both, father's as well as stranger's odor, create a mismatch with female faces, which may have an impact on face processing, as has been reported for audiovisual emotion processing in infancy (Grossmann et al., 2006; Vogel et al., 2012).

Another interpretation might be that the use of male and female faces as stimulus material caused infants to pay more attention to male faces as the less familiar stimulus, which may have resulted in a reduced processing of information from female faces. However, such an account would contradict the assumed attentional bias for female face (Quinn et al., 2002; Ramsey et al., 2005; Rennels et al., 2016; Righi et al., 2014). Furthermore, prior studies using both, male and female faces, did report differential processing at central and/or occipital electrodes (Hoehl & Striano, 2008, 2010), providing evidence against such an explanation (though the factor gender was not systematically investigated and the effect may have been driven by male or female faces).

Clearly, future studies are needed to shed further light on the mechanisms behind the observed pattern. A first important step would be to directly compare the impact of maternal to that of paternal odor in the same sample of infants and using the same set of visual stimuli. Furthermore, a more systematic investigation of the infants' familiarity with male vs. female faces in general and the time spent with mother vs. father in particular is necessary to address the role of familiarity for the influence of paternal odor on face processing.

Conclusion

In recent years, several studies have explored the impact of maternal odor on sociocognitive processing in infancy. Here, for the first time, we provide evidence that this impact is not limited to maternal odor, but that paternal odor influences infants' processing of emotional faces as well. Interestingly, the observed effects were specific to male faces, and suggested a stronger emotion discrimination in the presence of paternal odor. Our results therefore provide an important first step for our understanding of the role different types of social odor play in early human development.

References

Ackles, P. K., & Cook, K. G. (2007). Attention or Memory? Effects of Familiarity and Novelty on the Nc Component of Event-Related Brain Potentials in Six-Month-Old Infants. *International Journal of Neuroscience*, *117*(6), 837–867. https://doi.org/10.1080/00207450600909970

Aran, Ö., Garcia, S. E., Hankin, B. L., Hyde, D. C., & Davis, E. P. (2023). Signatures of emotional face processing measured by event-related potentials in 7-month-old infants. *Developmental Psychobiology*, *65*(2), e22361. https://doi.org/10.1002/dev.22361

Baildam, E. M., Hillier, V. F., Menon, S., Bannister, R. P., Bamford, F. N., Moore, W. M. O., & Ward, B. S. (2000). Attention to infants in the first year. *Child: Care, Health and Development*, *26*(3), 199–216. https://doi.org/10.1046/j.1365-2214.2000.00144.x

Conte, S., Richards, J. E., Guy, M. W., Xie, W., & Roberts, J. E. (2020). Face-sensitive brain responses in the first year of life. *NeuroImage*, *211*, 116602. https://doi.org/10.1016/j.neuroimage.2020.116602

Cox, J. L., Holden, J. M., & Sagovsky, R. (1987). Detection of Postnatal Depression: Development of the 10-item Edinburgh Postnatal Depression Scale. *British Journal of Psychiatry*, *150*(6), 782–786. https://doi.org/10.1192/bjp.150.6.782

Damon, F., Mezrai, N., Magnier, L., Leleu, A., Durand, K., & Schaal, B. (2021). Olfaction in the Multisensory Processing of Faces: A Narrative Review of the Influence of Human Body Odors. *Frontiers in Psychology*, *12*, 750944. https://doi.org/10.3389/fpsyg.2021.750944

De Haan, M., Johnson, M. H., & Halit, H. (2003). Development of face-sensitive event-related potentials during infancy: A review. *International Journal of Psychophysiology*, *51*(1), 45–58. https://doi.org/10.1016/S0167-8760(03)00152-1

De Haan, M., Johnson, M. H., & Halit, H. (2007). *Development of face-sensitive event-related potentials during infancy*. Psychology Press.

Düfeld, A., Nehler, R., Peplies, E., & Jessen, S. (2025). Social Odor as a Source of Learning in Human Infants. *In Press; Trends in Cognitive Sciences*.

Durand, K., Baudouin, J.-Y., Lewkowicz, D. J., Goubet, N., & Schaal, B. (2013). Eye-Catching Odors: Olfaction Elicits Sustained Gazing to Faces and Eyes in 4-Month-Old Infants. *PLoS ONE*, *8*(8), e70677. https://doi.org/10.1371/journal.pone.0070677

Durand, K., Schaal, B., Goubet, N., Lewkowicz, D. J., & Baudouin, J. (2020). Does any mother’s body odor stimulate interest in mother’s face in 4-month-old infants? *Infancy*, *25*(2), 151–164. https://doi.org/10.1111/infa.12322

Ebner, N. C., Riediger, M., & Lindenberger, U. (2010). FACES—A database of facial expressions in young, middle-aged, and older women and men: Development and validation. *Behavior Research Methods*, *42*(1), 351–362. https://doi.org/10.3758/BRM.42.1.351

Gartstein, M. A., & Rothbart, M. K. (2003). Studying infant temperament via the Revised Infant Behavior Questionnaire. *Infant Behavior and Development*, *26*(1), 64–86. https://doi.org/10.1016/S0163-6383(02)00169-8

Gredebäck, G., Eriksson, M., Schmitow, C., Laeng, B., & Stenberg, G. (2012). Individual Differences in Face Processing: Infants’ Scanning Patterns and Pupil Dilations are Influenced by the Distribution of Parental Leave. *Infancy*, *17*(1), 79–101. https://doi.org/10.1111/j.1532-7078.2011.00091.x

Grossmann, T., Striano, T., & Friederici, A. D. (2006). Crossmodal integration of emotional information from face and voice in the infant brain. *Developmental Science*, *9*(3), 309–315. https://doi.org/10.1111/j.1467-7687.2006.00494.x

Haan, M. D., Pascalis, O., & Johnson, M. H. (2002). Specialization of Neural Mechanisms Underlying Face Recognition in Human Infants. *Journal of Cognitive Neuroscience*, *14*(2), 199–209. https://doi.org/10.1162/089892902317236849

Harrison, M. J., & Magill-Evans, J. (1996). Mother and father interactions over the first year with term and preterm infants. *Research in Nursing & Health*, *19*(6), 451–459. https://doi.org/10.1002/(SICI)1098-240X(199612)19:6<451::AID-NUR1>3.0.CO;2-N

Hoehl, S., & Striano, T. (2008). Neural Processing of Eye Gaze and Threat-Related Emotional Facial Expressions in Infancy. *Child Development*, *79*(6), 1752–1760. https://doi.org/10.1111/j.1467-8624.2008.01223.x

Hoehl, S., & Striano, T. (2010). The development of emotional face and eye gaze processing. *Developmental Science*, *13*(6), 813–825. https://doi.org/10.1111/j.1467-7687.2009.00944.x

Jessen, S. (2020). Maternal odor reduces the neural response to fearful faces in human infants. *Developmental Cognitive Neuroscience*, *45*, 100858. https://doi.org/10.1016/j.dcn.2020.100858

Leleu, A., Rekow, D., Poncet, F., Schaal, B., Durand, K., Rossion, B., & Baudouin, J. (2020). Maternal odor shapes rapid face categorization in the infant brain. *Developmental Science*, *23*(2), e12877. https://doi.org/10.1111/desc.12877

Lenochova, P., Roberts, S. C., & Havlicek, J. (2009). Methods of Human Body Odor Sampling: The Effect of Freezing. *Chemical Senses*, *34*(2), 127–138. https://doi.org/10.1093/chemse/bjn067

Leppänen, J. M., Moulson, M. C., Vogel-Farley, V. K., & Nelson, C. A. (2007). An ERP Study of Emotional Face Processing in the Adult and Infant Brain. *Child Development*, *78*(1), 232–245. https://doi.org/10.1111/j.1467-8624.2007.00994.x

Libertus, K., & Landa, R. J. (2013). The Early Motor Questionnaire (EMQ): A parental report measure of early motor development. *Infant Behavior and Development*, *36*(4), 833–842. https://doi.org/10.1016/j.infbeh.2013.09.007

Liu, S., Xiao, N. G., Quinn, P. C., Zhu, D., Ge, L., Pascalis, O., & Lee, K. (2015). Asian infants show preference for own-race but not other-race female faces: The role of infant caregiving arrangements. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.00593

Marquis, A. R., & Sugden, N. A. (2019). Meta-analytic review of infants' preferential attention to familiar and unfamiliar face types based on gender and race. *Developmental Review*, *53*, 100868. https://doi.org/10.1016/j.dr.2019.100868

Mutic, S., Moellers, E. M., Wiesmann, M., & Freiherr, J. (2016). Chemosensory Communication of Gender Information: Masculinity Bias in Body Odor Perception and

Femininity Bias Introduced by Chemosignals During Social Perception. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.01980

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Computational Intelligence and Neuroscience*, *2011*, 1–9. https://doi.org/10.1155/2011/156869

Peltola, M. J., Leppänen, J. M., Mäki, S., & Hietanen, J. K. (2009). Emergence of enhanced attention to fearful faces between 5 and 7 months of age. *Social Cognitive and Affective Neuroscience*, *4*(2), 134–142. https://doi.org/10.1093/scan/nsn046

Penn, D. J., Oberzaucher, E., Grammer, K., Fischer, G., Soini, H. A., Wiesler, D., Novotny, M. V., Dixon, S. J., Xu, Y., & Brereton, R. G. (2007). Individual and gender fingerprints in human body odour. *Journal of The Royal Society Interface*, *4*(13), 331–340. https://doi.org/10.1098/rsif.2006.0182

Porter, RichardH., & Winberg, J. (1999). Unique salience of maternal breast odors for newborn infants. *Neuroscience & Biobehavioral Reviews*, *23*(3), 439–449. https://doi.org/10.1016/S0149-7634(98)00044-X

Quinn, P. C., Uttley, L., Lee, K., Gibson, A., Smith, M., Slater, A. M., & Pascalis, O. (2008). Infant preference for female faces occurs for same- but not other-race faces. *Journal of Neuropsychology*, *2*(1), 15–26. https://doi.org/10.1348/174866407X231029

Quinn, P. C., Yahr, J., Kuhn, A., Slater, A. M., & Pascalis, O. (2002). Representation of the Gender of Human Faces by Infants: A Preference for Female. *Perception*, *31*(9), 1109–1121. https://doi.org/10.1068/p3331

Ramsey, J. L., Langlois, J. H., & Marti, N. C. (2005). Infant categorization of faces: Ladies first. *Developmental Review*, *25*(2), 212–246. https://doi.org/10.1016/j.dr.2005.01.001

Ramsey-Rennels, J. L., & Langlois, J. H. (2006). Infants' Differential Processing of Female and Male Faces. *Current Directions in Psychological Science*, *15*(2), 59–62. https://doi.org/10.1111/j.0963-7214.2006.00407.x

Rekow, D., Baudouin, J.-Y., Poncet, F., Damon, F., Durand, K., Schaal, B., Rossion, B., & Leleu, A. (2021). Odor-driven face-like categorization in the human infant brain. *Proceedings of the National Academy of Sciences*, *118*(21), e2014979118. https://doi.org/10.1073/pnas.2014979118

Rekow, D., Leleu, A., Poncet, F., Damon, F., Rossion, B., Durand, K., Schaal, B., & Baudouin, J.-Y. (2020). Categorization of objects and faces in the infant brain and its sensitivity to maternal odor: Further evidence for the role of intersensory congruency in perceptual development. *Cognitive Development*, *55*, 100930. https://doi.org/10.1016/j.cogdev.2020.100930

Rennels, J. L., & Davis, R. E. (2008). Facial experience during the first year. *Infant Behavior and Development*, *31*(4), 665–678. https://doi.org/10.1016/j.infbeh.2008.04.009

Rennels, J. L., Kayl, A. J., Langlois, J. H., Davis, R. E., & Orlewicz, M. (2016). Asymmetries in infants' attention toward and categorization of male faces: The potential role of experience. *Journal of Experimental Child Psychology*, *142*, 137–157. https://doi.org/10.1016/j.jecp.2015.09.026

Reynolds, G. D., & Richards, J. E. (2005). Familiarization, Attention, and Recognition Memory in Infancy: An Event-Related Potential and Cortical Source Localization Study. *Developmental Psychology*, *41*(4), 598–615. https://doi.org/10.1037/0012-1649.41.4.598

Righi, G., Westerlund, A., Congdon, E. L., Troller-Renfree, S., & Nelson, C. A. (2014). Infants' experience-dependent processing of male and female faces: Insights from eye tracking and event-related potentials. *Developmental Cognitive Neuroscience*, *8*, 144–152. https://doi.org/10.1016/j.dcn.2013.09.005

Russell, M. J. (1976). Human olfactory communication. *Nature*, *260*(5551), 520–522. https://doi.org/10.1038/260520a0

Schaal, B. (1988). Olfaction in infants and children: Developmental and functional perspectives. *1988*.

Schaal, B., Marlier, L., & Soussignan, R. (1998). Olfactory function in the human fetus: Evidence from selective neonatal responsiveness to the odor of amniotic fluid. *Behavioral Neuroscience*, *112*(6), 1438–1449. https://doi.org/10.1037/0735-7044.112.6.1438

Schaal, B., Saxton, T. K., Loos, H., Soussignan, R., & Durand, K. (2020). Olfaction scaffolds the developing human from neonate to adolescent and beyond. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1800), 20190261. https://doi.org/10.1098/rstb.2019.0261

Schäfer, L., & Croy, I. (2023). An integrative review: Human chemosensory communication in the parent-child relationship. *Neuroscience & Biobehavioral Reviews*, *153*, 105336. https://doi.org/10.1016/j.neubiorev.2023.105336

Sullivan, R. M., & Opendak, M. (2020). Defining immediate effects of sensitive periods on infant neurobehavioral function. *Current Opinion in Behavioral Sciences*, *36*, 106–114. https://doi.org/10.1016/j.cobeha.2020.08.006

Tikotzky, L., Sadeh, A., & Glickman-Gavrieli, T. (2011). Infant Sleep and Paternal Involvement in Infant Caregiving During the First 6 Months of Life. *Journal of Pediatric Psychology*, *36*(1), 36–46. https://doi.org/10.1093/jpepsy/jsq036

Tristão, R. M., Lauand, L., Costa, K. S. F., Brant, L. A., Fernandes, G. M., Costa, K. N., Spilski, J., & Lachmann, T. (2021). Olfactory sensory and perceptual evaluation in newborn infants: A systematic review. *Developmental Psychobiology*, *63*(7), e22201. https://doi.org/10.1002/dev.22201

Troccaz, M., Borchard, G., Vuilleumier, C., Raviot-Derrien, S., Niclass, Y., Beccucci, S., & Starkenmann, C. (2008). Gender-Specific Differences between the Concentrations of Nonvolatile (R)/(S)-3-Methyl-3-Sulfanylhexan-1-Ol and (R)/(S)-3-Hydroxy-3-Methyl-Hexanoic Acid Odor Precursors in Axillary Secretions. *Chemical Senses*, *34*(3), 203–210. https://doi.org/10.1093/chemse/bjn076

Vaish, A., Grossmann, T., & Woodward, A. (2008). Not all emotions are created equal: The negativity bias in social-emotional development. *Psychological Bulletin*, *134*(3), 383–403. https://doi.org/10.1037/0033-2909.134.3.383

Vanderwert, R. E., Westerlund, A., Montoya, L., McCormick, S. A., Miguel, H. O., & Nelson, C. A. (2015). Looking to the eyes influences the processing of emotion on face-sensitive event-related potentials in 7-month-old infants. *Developmental Neurobiology*, *75*(10), 1154–1163. https://doi.org/10.1002/dneu.22204

Varendi, H., Porter, R., & Winberg, J. (1997). Natural odour preferences of newborn infants change over time. *Acta Paediatrica*, *86*(9), 985–990. https://doi.org/10.1111/j.1651-2227.1997.tb15184.x

Vogel, M., Monesson, A., & Scott, L. S. (2012). Building biases in infancy: The influence of race on face and voice emotion matching. *Developmental Science*, *15*(3), 359–372. https://doi.org/10.1111/j.1467-7687.2012.01138.x

Vonderlin, E., Ropeter, A., & Pauen, S. (2012). Erfassung des frühkindlichen Temperaments mit dem Infant Behavior Questionnaire Revised: Psychometrische Merkmale einer deutschen Version. *Zeitschrift für Kinder- und Jugendpsychiatrie und Psychotherapie*, *40*(5), 307–314. https://doi.org/10.1024/1422-4917/a000187

Xie, W., McCormick, S. A., Westerlund, A., Bowman, L. C., & Nelson, C. A. (2019). Neural correlates of facial emotion processing in infancy. *Developmental Science*, *22*(3), e12758. https://doi.org/10.1111/desc.12758