Maternal Odor Reduces the Neural Threat Response in Human Infants

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Short title: Maternal Odor and Fear Processing in Infancy

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ABSTRACT

Maternal odor is known to play an important role in mother-infant-interaction in many altricial species such as rodents. However, we only know very little about its role in early human development. The present study therefore investigated the impact of maternal odor on infant brain responses to threat signals. We recorded the electroencephalographic (EEG) signal of seven-month-old infants watching happy and fearful facial expressions. While infants in two control groups showed the expected EEG fear response, this response was markedly absent in the group exposed to their mother's odor. Thus, infants respond differently to fear signals in the presence of their mother and the mother's odor is a sufficiently strong signal to elicit this effect. Our data suggest that olfaction, a sensory modality that has been largely neglected as a social signal in our own species, might function as a crucial modulator in early social learning.

Keywords: infancy, emotion perception, odor, breastfeeding, fear processing, EEG

INTRODUCTION

As members of an altricial species, newborn humans completely rely on their social environment for survival. To foster and support the care they receive, newborns show a number of mechanisms to support social bonding, including a strong preference for faces (Johnson, Dziurawiec, Ellis, & Morton, 1991) and their mother's voice (DeCasper & Fifer, 1980). One modality however that is potentially of equal importance but has received far less attention in human research is olfaction as a form of extremely potent chemosensory signaling (Semin & Groot, 2013).

The importance of olfaction for early social development has been amply investigated in other species, especially rodents. Rat pups form a strong attachment to the dam which is crucially supported by a (learned) preference for the maternal odor (Landers & Sullivan, 2012).

Initial research in human development suggests that olfaction and especially maternal odor are important components for social development also in our species (Lubke & Pause, 2015). Maternal odor cues for instance play a crucial role in the successful initiation of breastfeeding (Porter & Winberg, 1999; Schaal et al., 2009), essential for the survival of mammalian offsprings but also an important player in the development of a secure bonding between mother and infant. Furthermore, recent studies suggest that maternal odor impacts face perception, in older infants (Durand, Baudouin, Lewkowicz, Goubet, & Schaal, 2013; Leleu et al., 2019).

One setting in which this social learning is put to the test is in responses to adverse situations such as stress and threat. Again, rodent research has provided us with insights on the developmental trajectory of threat response and their modulation by maternal presence and signals thereof. Very young pups who are highly dependent on their mother show little fear responses but rather responses that facilitate the formation of close bonding to their mother (Leon, 1992). Older pups in contrast start to show more adult-like fear responses (Debiec & Sullivan, 2017). Moreover, during a transition period, pups exhibit both types of responses; if their mother is present, they show affiliative responses facilitating mother-infant-

bonding, if their mother is absent, they show fear learning typically seen in older pups (Debiec & Sullivan, 2017; Landers & Sullivan, 2012; Moriceau & Sullivan, 2006). Hence, maternal presence appears to be a key player in determining the processing of and response to threat in early development of rodents, and maternal odor is assumed to be a strong signal of maternal presence.

Studying responses to threat signals in human infants is more challenging. One well-investigated phenomenon in this context is the development of an attentional bias towards fearful expressions around 7 months of age (Vaish, Grossmann, & Woodward, 2008). Interestingly, recent work suggests that this phenomenon can be strongly influenced by secondary factors, such as parental sensitivity (Taylor-Colls & Pasco Fearon, 2015), infant temperament (Martinos, Matheson, & de Haan, 2012), and breastfeeding experience (Krol, Rajhans, Missana, & Grossmann, 2014). Crucially, all these factors are linked to the interplay between the infant and her social environment, providing initial evidence for a modulation by social factors.

However, all the above-mentioned components are typically stable factors relating to interindividual differences rather than flexible changes in a given situation. It is therefore unclear whether threat responses in human infants can be modulated in the same way as has been suggest for rodents. Does maternal presence, as a social short-term rather than long-term factor, impact infants' responses to threat signals? And is maternal odor a sufficient strong cue to elicit an effect of maternal presence also in humans?

To address these questions, we designed an experiment to investigate the impact of maternal odor on the neural response to threat signals in human infants. In an electroencephalographic (EEG) set-up, infants were presented with happy and fearful facial expressions while they were exposed to either the familiar maternal odor, to an unfamiliar mother's odor, or to no specific odor at all. To quantify infants' fear response, we investigated the amplitude of the *Nc*, an infant event-related potential (ERP) component observed between 400 and 800 ms after the onset of a stimulus at frontocentral electrodes. The Nc amplitude has been linked to the allocation of attention and is typically enhanced in response to fearful faces in 7-month-old infants (Peltola, Leppänen, Mäki, & Hietanen, 2009). Seven months marks a crucial transitional period in human infants, and is associated not only

with the onset of stronger fear responses but also with the onset of locomotion (Leppänen & Nelson, 2012). Hence, this age may be a period in humans analogous to the transitional period described for rodents above; a shift from dependence to increasing independence.

We therefore predict that infants show an increased threat response in the absence of their mother (or an odor signaling her presence), but we expect this response to be reduced in their mother's presence, even if only signaled via maternal odor.

METHODS

Participants. 76 7-month-old infants were included in the final sample (age: 213 ± 8 days [mean ± standard deviation (SD)]; range: 200-225, 38 female, see Table 1 for description of the individual groups). An additional 15 infants had been tested but were not included in the final sample because they did not provide at least 10 artifact-free trials per condition (n=11); had potential neurological problems (n=1); were erroneously invited too young (n=1); the mean ERP response in the time-window and electrodes of interest was more than 4 standard deviations from the mean (n=1, see below); or because of technical problems during the recording (n=1).

The sample size was determined by statistical considerations and practical conventions in the field. First, for practical considerations and the known high attrition rates in infant EEG studies, we had planned a priori to keep collecting data until 25 useable data sets per each of the three experimental manipulation groups were obtained. Second, as outlined in Albers & Lakens (2018), a smallest effect size of interest was critical here, as too small true effects sizes for odor manipulations would not be of practical or translational relevance. In the present study, a total sample size of n=75 in three groups, was thus powered with 80% or more to detect medium and large effects (i.e., Cohen's d of 0.8 or larger) at a conventional type I error level of 5 %.

Infants were recruited via the maternity ward at the local hospital (Universitätsklinikum Schleswig-Holstein), were born full-term (38–42 weeks gestational age), had a birth weight of at least 2500 g, and had no known

110 neurological deficits. The study was conducted according to the Declaration of
111 Helsinki, approved by the ethics committee at the University of Lübeck, and
112 parents provided written informed consent.

113 *Table 1. Overview of participants included in the final analysis. An additional 15 infants were tested*
114 *but not included in the final analysis for various reasons (see text).*

	N	female	age (in days)*	still breastfed	trials (happy)*	trials (fearful)*	Inf Neg Temp*#	EPDS*#
Maternal odor	25	13	213 ± 7	14	38 ± 18	38 ± 17	3.03 ± 0.68	4.32 ± 3.74
No odor	26	9	214 ± 8	18	45 ± 21	45 ± 23	3.34 ± 0.68	5.08 ± 4.77
Stranger odor	25	16	215 ± 7	13	37± 18	37± 17	3.25 ± 0.76	4.54 ± 3.96

115 ** mean ± standard deviation; # excluding one participant in the Stranger odor group, who did not fill in the questionnaire; Inf Neg Temp = Infant Negative Temperament, see text; EPDS = Edinburgh Postpartum Depression Screening, see text*

116 *Stimulus*. As emotional face stimuli, we used colored photographs of happy and
117 fearful facial expressions by 6 actresses from the FACES database (Ebner, Riediger,
118 & Lindenberger, 2010 [actress-ID 54, 63, 85, 90, 115, 173]). Photographs were
119 cropped so that only the face was visible in an oval shape, and have successfully
120 been used in prior studies to investigate fear processing in infancy (Jessen &
121 Grossmann, 2015, 2017).

122 *Odor manipulation.* Prior to a scheduled experimental recording, all infants'
123 mothers were given a white cotton t-shirt and instructed to wear this t-shirt for
124 three nights in a row. The mother was asked to store the t-shirt in a provided zip-
125 lock bag during the day, and use her normal shampoo, soap, deodorant etc. as
126 usual but refrain from using new products. Before the t-shirt was given to the
127 mother, it had been washed with the same detergent for all t-shirts.

128 If the mother wore the t-shirt during the three nights directly preceding the
129 experiment, the mother was asked to simply bring the t-shirt along. If the three
130 nights did not directly precede the experiment, the mother was asked to store the
131 t-shirt in a zip-lock bag in the freezer, as freezing has been shown to conserve odor
132 (Lenochova, Roberts, & Havlicek, 2009).

133 *Randomization.* Infants were randomly assigned to either the *Maternal odor* group
134 or one of the control groups (*No odor* group or *Stranger odor* group; Figure 1). As
135 only constraint to fully random assignment, we monitored as the study proceeded

that groups did not differ in gender, age, or breastfeeding experience. Infants in the *Maternal odor* group were administered the t-shirt previously worn by their mother during the experiment. Infants in the *No odor* group were administered an unworn t-shirt. Infants in the *Stranger odor* group were administered a t-shirt previously worn by the mother of one of the other infants. The t-shirt of their own mother was stored in a freezer to be used as a stimulus for a different infant in the *Stranger odor* group. Except in one case, both, parents and the experimenter administering the t-shirt, were blind to the group assignment.

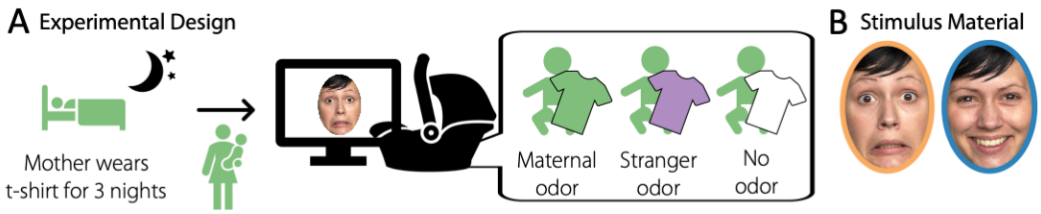

Figure 1. Overview of experimental set-up. A) Mothers were asked to wear a provided t-shirt for 3 nights in a row prior to the experiment. The infant was randomly assigned to one of three groups; a Maternal odor group (exposed to the t-shirt worn by the infant's mother), a Stranger odor group (exposed to a t-shirt worn by a different infant's mother), or a No odor group (exposed to an unworn t-shirt). We recorded the EEG signal while the infants were seated in a car seat with the t-shirt positioned over their chest area and watched happy and fearful facial expressions. B) Example of fearful and happy faces used as stimulus material, the colored circles are for illustration purpose only and correspond to the color coding used in the following figures.

Procedure and experimental design. Before the laboratory visit, families were sent the t-shirt (as described above) as well as a set of questionnaires, in particular the EPDS (Cox, Holden, & Sagovsky, 1987), the IBQ-R (Gartstein & Rothbart, 2003; Vonderlin, Ropeter, & Pauen, 2012), and a lab-internal questionnaire assessing demographic information as well as feeding and sleeping routines of the infant (One family, whose infant was assigned to the *Stranger odor* group, did not fill in the IBQ-R and the EPDS and is therefore not included in the control analyses with these two factors). After arriving in the laboratory, parents and infant were familiarized with the environment and parents were informed about the study and signed a consent form. The EEG recording was prepared while the infant was sitting on his/her parent's lap. For recording, we used an elastic cap (BrainCap, Easycap GmbH) in which 27 AgAgCl-electrodes were mounted according to the

international 10-20-system. An additional electrode was attached below the infant's right eye to record the electrooculogram. The EEG signal was recorded with a sampling rate of 250 Hz using a BrainAmp amplifier and the BrainVision Recorder software (both Brain Products).

For the EEG recording, the infant was sitting in an age appropriate car seat (Maxi Cosi Pebble) positioned on the floor. The t-shirt was positioned over the chest area of the infant, folded along the vertical axis of the t-shirt and with the armpit region of the t-shirt directed towards the infant's face. The t-shirt was fixated using the safety straps of the car seat as closely to the chin of the infant as possible and adjusted during the experiment if necessary.

In front of the infant (approximately 60 cm from the infant's feet), a 24-inch monitor with a refresh rate of 60 Hz was positioned at a height of about 40 cm (bottom edge of the screen). The parent was seated approximately 1.5 m behind the infant and instructed not to interact with the infant during the experiment.

The experiment was programmed using the Presentation software (Version 18.1). Faces were presented for 800 ms, preceded by a fixation cross presented for 300 ms, and followed by an intertrial interval jittered between 800 and 1200 ms. The faces had a height of approximately 28 cm. If necessary, short video clips containing colorful moving shapes and ringtones were played during the experiment to redirect the infant's attention to the screen. Each infant saw a maximum of 216 trials, arranged in miniblocks of 24 trials containing 12 happy and 12 fearful faces and played consecutively without interruption. Trials were presented in a pseudorandomized order, ensuring that no stimulus category (happy, fearful) was repeated more than once. The experiment continued until the infant had seen all trials or became too fussy to continue the experiment. During the experiment, the infant was video-recorded using a small camera mounted on top of the monitor to offline exclude trials in which the infant did not attend to the screen.

Data Analysis. We analyzed the data using Matlab 2013b (The MathWorks, Inc., Natick, MA), the Matlab toolbox FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011), and for statistical analysis the package JASP (JASP Team, version 0.10.2).

EEG Preprocessing. For purposes of artefact removal including an independent component analysis (ICA) routine, all data were first referenced to the average of all electrodes (average reference), filtered using a 100-Hz lowpass and a 1-Hz highpass filter, and segmented into 1-sec-epochs. To detect epochs obviously contaminated by artifacts, the standard deviation was computed in a sliding window of 200 msec. If the standard deviation exceeds 100 µV at any electrode, the entire epoch was discarded. Next, an independent component analysis (ICA) was computed on the remaining concatenated data. Components were inspected visually and rejected if classified as artefactual (4 ± 2 components per participants [mean ± SD], range 0–10 components).

After removal of ICA components, the data was re-segmented into epochs ranging from 200 ms before to 800 ms after the onset of the stimulus, re-referenced to the linked mastoids (mean of TP9 and TP10), and a 0.2 to 20 Hz bandpass filter was applied. A last step of automatic artifact detection was applied, rejecting all epochs in which the standard deviation exceeded 80 µV. Data was inspected visually for remaining artifacts, and all trials in which the infant did not attend to the screen (as assessed via the video recording during the experiment) were rejected (see Table 1 for number of remaining trials).

ERP analysis. To analyze the Nc response, we computed the mean response in a time-window of 400–800 ms after stimulus onset across frontocentral electrodes (F3, Fz, F4, C3, Cz, C4; see Supplementary Material for an analysis of occipital electrodes, where no significant effect was found). One participant was rejected from further analysis because the difference in the mean response to happy and fearful faces in this time-window and electrode cluster was more than 4 standard deviations from the mean across all other participants. Mean responses were entered into a repeated measures ANOVA with the within-subject factor Emotion (happy, fear) and the between-subject factor Odor (maternal, stranger, no odor). Furthermore, we included the infant's current breastfeeding status (whether s/he was still breastfed at the time of testing or not) as reported by the mother (Breastfed [yes,no]) as a covariate, as lactation may impact the mother's body odor (McClintock et al., 2005). Student's t-tests are computed as post-how tests and effect sizes are reported as partial eta squared (η_p^2) and Cohen's *d*. In addition, we

also performed the equivalent analysis using Bayesian statistics; BF_{10} values above 1 are interpreted as anecdotal evidence, above 3 as moderate evidence, and above 10 as strong evidence for the research hypothesis (Wagenmakers et al., 2018).

To further analyze the Emotion effect without any a priori assumption about its latency and topography, we ran a cluster-based permutation test (Maris & Oostenveld, 2007) with 1000 permutations contrasting responses to happy and fearful faces separately for each *Odor* group. A cluster had to comprise at least 2 adjacent electrodes, was computed across time and electrode position, and a type-1-error probability of less than 0.05 at the cluster-level was ensured.

Negative Affect. Negative affect was computed as the mean of the IBQ-R scales Sadness, Fear, and Distress to Limitations (Aktar et al., 2018).

RESULTS

Influence of maternal odor on the Nc response. We observed an overall enhanced Nc amplitude in response to fearful faces, confirming the expected heightened threat response (Peltola et al., 2009; significant main effect of Emotion [$F(1,72) = 11.60$, $p = .001$, $\eta_p^2 = 0.14$; $BF_{10} = 2.578$]).

Most importantly, however, the threat response differed between odor groups. That is, this emotion effect critically depended on the odor group an infant had been assigned to (significant interaction Emotion × Odor [$F(2,72) = 5.57$, $p = .006$, $\eta_p^2 = 0.13$; $BF_{10} = 4.564$; Figure 2]).

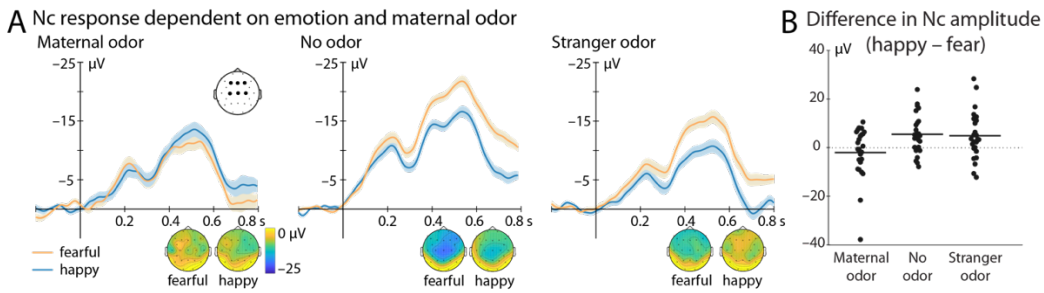

Figure 2. ERP response in the different odor groups. A) Shows the Nc response at frontocentral electrodes (F3, Fz, F4, C3, Cz, C4, marked by black dots) to fearful (orange) and happy (blue) facial expressions. While no difference in response was observed in the Maternal odor group, infants in the No odor and the Stranger odor group showed a significantly enhanced Nc response to fearful faces. Topographic representations averaged between 400 and 800 ms after face onset are shown at

the bottom. B) Depicts the difference between Nc response to fearful and happy faces for each individual subject separately for the odor groups at the same electrodes and timewindow as in A. Mean difference is marked by horizontal black lines. Note that the interaction Odor × Emotion reaches significance even when excluding the two participants with the largest difference between happy and fear in the Maternal odor group.

Follow-up tests confirmed the Nc effect to fear signals was critically absent in the *Maternal odor* group [$t(24) = -0.95$, $p = .35$, $d = -.19$; $BF_{10} = 0.32$; fearful: –6.51 ± 2.99 µV, happy: –8.53 ± 3.17 µV]. In contrast, the typical enhancement of the Nc response to fearful (compared to happy) faces was present in the *Stranger odor* group [$t(24) = 2.51$, $p = .019$, $d = .50$; $BF_{10} = 2.78$; fearful: –10.57 ± 2.34 µV (mean ± SE), happy: –5.66 ± 1.78 µV] as well as in the *No odor* group [$t(25) = 3.50$, $p = .002$, $d = .68$; $BF_{10} = 21.02$; fearful: –16.94 ± 2.19 µV, happy: –11.43 ± 2.53 µV].

Corroborating analysis using a cluster-based permutation approach. While the electrode and time window selection for this analysis had not been data derived but followed standards set by previous studies (Jessen & Grossmann, 2014, 2016, 2019), we aimed to corroborate this main result by a more data-driven search for potential effects using a cluster-based permutation test (Figure 3). In both, the *No odor* group and the *Stranger odor* group, nearly identical clusters indicating a significantly response enhancement to fearful (compared to happy) faces was found (No odor: $p = .006$, $T_{sum} = 3063.8$; Stranger odor: $p = .021$, $T_{sum} = 1272.8$). Importantly, both clusters exhibit the latency and topographic distribution typical for an Nc response. Most importantly, no such cluster of significant differences was found in the *Maternal odor* group when contrasting responses to happy and fearful faces.

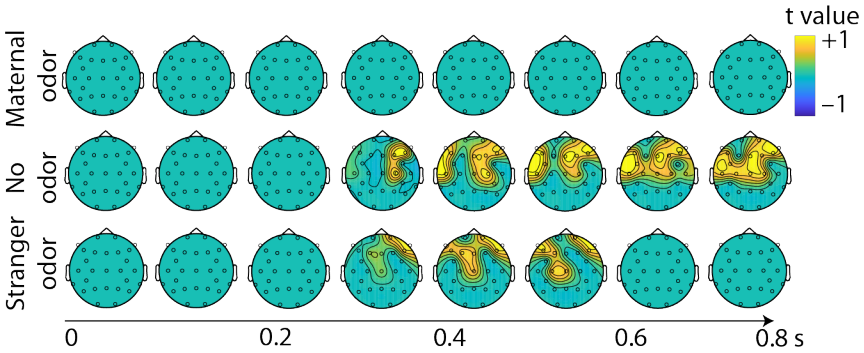

Figure 3. Cluster-based permutations test comparing responses to fearful and happy faces in the different odor groups. Depicted are topographic representations of t-values starting from the picture onset in steps of 100 ms.

Hence, while both control groups (*No group* and *Stranger odor* group) showed the age-typical enhanced Nc response to fearful, threat-signalling faces, a heightened fear response was absent in the *Maternal odor* group. Our results suggest that maternal odor, as a signal of familiarity and maternal presence, reduces infant's attention allocation to threat signals.

No effect of potential confounds. Importantly, we did not find a difference between the three groups with respect to a number of potential confounds: There were no group differences in the number of included trials per infant in either Emotion condition [happy: $F(2,73) = 1.49$, $p = .23$, $BF_{10} = 0.355$; fearful: $F(2,73) = 1.25$, $p = .29$, $BF_{10} = 0.296$]; age [$F(2,73) = 0.49$, $p = .61$, $BF_{10} = 0.165$]; in maternal depression scores as assessed via the EPDS [$F(2,72) = 0.22$, $p = .80$, $BF_{10} = 0.136$]; or in infant negative temperament as assessed via the IBQ-R [$F(2,72) = 1.23$, $p = .30$, $BF_{10} = 0.294$].

Effect of Breastfeeding. A last finding supported our general line of reasoning. Namely, we did observe an interaction between Nc response to the emotional expression of the presented face and whether the infant was still breastfed or not [Emotion × Breastfeeding, $F(1,72) = 5.06$, $p = .028$, $\eta_p^2 = 0.07$; $BF_{10} = 1.632$; Figure 4]. Only the infants who were not breastfed any more at the time of testing showed an enhanced Nc response to fearful faces [$t(30) = 3.55$, $p = .001$, $d = .64$; $BF_{10} = 26.54$; fearful: –13.35 ± 2.18 µV, happy: –7.90 ± 2.00 µV], while this enhancement was absent in the infants who were still breastfed [$t(44) = 0.65$, $p = .52$, $d = 0.1$; $BF_{10} = 0.20$; fearful: –10.08 ± 2.08 µV, happy: –9.05 ± 2.10 µV].

Importantly, this was independent of (i.e., additionally true but not interacting with) the *odor group* manipulation, as there was no meaningful Emotion × Breastfeeding × Odor interaction [$F(2,70) = 2.20$, $p = .12$, $\eta_p^2 = 0.06$, $BF_{10} = 1.081$].

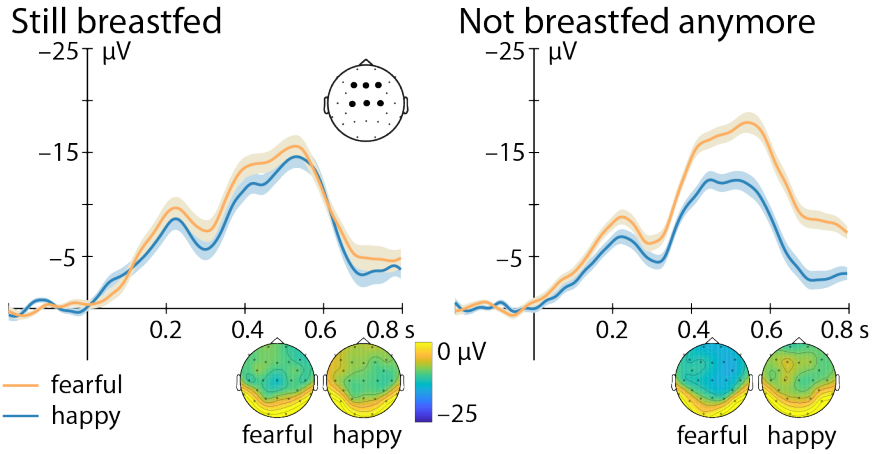

Figure 4. Nc response depending on breastfeeding status. Nc response is depicted at frontocentral electrodes (F3, Fz, F4, C3, Cz, C4, marked by black dots) to fearful (orange) and happy (blue) facial expressions for infants who are still breastfed (left) and not breastfed anymore (right). Infants who are not breastfed any more show an enhanced Nc response to fearful faces, while this effect was absent in the group of infants who were still breastfed. Topographic representations averaged between 400 and 800 ms after face onset are shown at the bottom.

Discussion

Our results demonstrate that maternal odor is a sufficiently strong signal to reduce an established neural marker of the fear response in 7-month-old infants. A highly consonant effect was found for breastfeeding, suggesting that not only momentary states but also longer-lasting effects of maternal presence impact fear processing in infants. Our results point to a previously unknown flexibility in fear processing in infancy and its dependency on context and experience, which is in line with findings in other species (Landers & Sullivan, 2012).

Maternal odor as a momentary modulator of infant fear processing

We suggest that such a response pattern might be characteristic for a developing system that on the one hand needs to establish a close bonding to a caregiver,

typically the mother, while on the other hand learning to respond to potential threat signals in the environment. This has been indirectly suggested by studies in older children (Gee et al., 2014) as well as rodent research (Landers & Sullivan, 2012). Our findings, however, provide first evidence for flexible processing of threat-related information depending on maternal signals in early human development.

A diminished response to threat signals in maternal presence might facilitate bonding, as a positive evaluation of information and less attention to potential negative aspects may increase positive affect towards the caregiver even in the presence of negative signals. In addition, if maternal presence works as a "safety signal", requiring the infant to allocate less attention to potential threats, this might also free cognitive capacities in the infant for other processes, akin to previously reported improved cognitive performance in rat pups in the presence of familiar odor (Wigal, Kucharski, & Spear, 1984).

At the same time, as the infant grows more independent, detecting and responding to threat becomes of growing importance, especially if the mother is not present. Crucially, 7 months is an important turning point in early human development, characterized not only by qualitative changes in emotion development, but also by the onset of locomotion, an important step towards growing independence (Leppänen & Nelson, 2012). During this period, flexible threat processing might be of particular importance, akin to what has been suggested in the rodent literature (Landers & Sullivan, 2012).

Our results further underscore the importance of odor in early social development. Two recent studies have suggested a modulation of infant face processing in general by the presence of maternal odor (Durand et al., 2013; Leleu et al., 2019). Our study is the first to show that the absence or presence of maternal odor can impact highly specific aspects of infant face processing. Maternal odor might therefore be an important guiding factor in emotional learning in infancy.

Specifically, we found an impact on the attention-related Nc component (Webb, Long, & Nelson, 2005) but no influence on early visual processing (see supplementary material) or on the number of trials the infants watched. Therefore,

we found no evidence for a general impact of maternal odor on sensory processing or compliance with the experiment, but rather odor specifically impacted the evaluation of facial information, further underscoring its potential role in early social learning.

Importantly, we assume that the observed effects are due to a *learned* odor preference for familiar maternal signals rather than a specific preference for maternal body odor. This assumption is in line with rodent work, suggesting that effects akin to the ones reported for maternal odor can also be found other types of highly familiar odor (Wigal et al., 1984). Accordingly, the present manipulation did not differentiation between body odor and other odor components (such as deodorant used or specific food consumed by the mother), thereby reflecting the mélange of odors the infant experiences in maternal presence in everyday life.

Breastfeeding as a long-term modulator of infant fear processing

While maternal odor as a direct or phasic signal of maternal presence influenced fear processing, so did the more tonic variable of an infant's breastfeeding experience. In line with our interpretation of the above-mentioned odor effect, this finding suggests a further modulatory impact of mother-infant-bonding in fear processing: Our findings are in line with prior studies reporting an increased bias towards expressions of happiness with increasing breastfeeding experience (Krol, Monakhov, Lai, Ebstein, & Grossmann, 2015; Krol et al., 2014). How exactly breastfeeding experience interacts with emotion processing is not certain, but a possible explanation is an increased closeness between mother and infants; breastfed infants on average spend more time interacting with their mother (Smith & Forrester, 2017) and show a higher attachment security (Gibbs, Forste, & Lybbert, 2018).

Maternal presence may therefore not only modulate fear processing directly, as suggested by the influence of maternal odor, but might also exert a longer-lasting impact.

Future Directions

An important aspect in further assessing the relevance of maternal odor in infancy are potential changes across development. If the impact of maternal presence on fear responses follows a similar trajectory as has been reported for rodents (Landers & Sullivan, 2012), this predicts a specific time-window during which infants show flexible fear responses depending on the presence and by extension the odor of their mother. This time-window might be around seven months of age, when infants first acquire the ability to locomote (Leppänen & Nelson, 2012), but future studies tracing the impact of maternal odor longitudinally are clearly warranted to solidify this suggestion.

In the present approach, we assume that the reported influence of maternal odor is the result of early learning processes, during which the infants learns to associate her mother with a certain odor, the maternal odor, consisting of a combination of the mother's body odor and familiar home scents. Hence, future studies need to consider the differential contributions of body odor in comparison to other types of odor the infant might be highly familiar with.

Finally, the generalizability to other types of adverse signals needs to be assessed in future work. We show that maternal odor reduced attention to fearful faces, and we predict that maternal odor should also impact infant responses to other negative signals, such as pain or aversive sounds. However, since recent studies suggest a link between maternal odor and the processing of faces in infancy (Durand et al., 2013; Leleu et al., 2019), one could also expect a more specific effect of maternal odor on negative social information.

Conclusions

The current study demonstrates that maternal odor influences fear processing in infancy. While infants in two control groups of different specificity (a stranger's odor or no specific odor at all) showed an expectably enhanced attentional response to fear signals, this response was absent in infants who could smell their mother. Our results establish that the mother's presence, even if just signaled by the mother's familiar odor, can result in a marked reduction of the neurobiological

fear response in infants. Furthermore, our data provide evidence for the potency of odor as a social signal in humans and in particular in early ontogeny.

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