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

1   Maternal odor is known to play an important role in mother-infant-interaction in

2   many altricial species such as rodents. However, we only know very little about

3   its role in early human development. The present study therefore investigated the

4   impact of maternal odor on infant brain responses to threat signals. We recorded

5   the electroencephalographic (EEG) signal of seven-month-old infants watching

6   happy and fearful facial expressions. While infants in two control groups showed

7   the expected EEG fear response, this response was markedly absent in the group

8   exposed to their mother's odor. Thus, infants respond differently to fear signals in

9   the presence of their mother and the mother's odor is a sufficiently strong signal

10   to elicit this effect. Our data suggest that olfaction, a sensory modality that has

11   been largely neglected as a social signal in our own species, might function as a

12   crucial modulator in early social learning.

13   <u>Keywords:</u> infancy, emotion perception, odor, breastfeeding, fear processing, EEG

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16   INTRODUCTION

17   As members of an altricial species, newborn humans completely rely on their

18   social environment for survival. To foster and support the care they receive,

19   newborns show a number of mechanisms to support social bonding, including a

20   strong preference for faces (Johnson, Dziurawiec, Ellis, & Morton, 1991) and their

21   mother's voice (DeCasper & Fifer, 1980). One modality however that is potentially

22   of equal importance but has received far less attention in human research is

23   olfaction as a form of extremely potent chemosensory signaling (Semin & Groot,

24   2013).

25   The importance of olfaction for early social development has been amply

26   investigated in other species, especially rodents. Rat pups form a strong

27   attachment to the dam which is crucially supported by a (learned) preference for

28   the maternal odor (Landers & Sullivan, 2012).

29   Initial research in human development suggests that olfaction and especially

30   maternal odor are important components for social development also in our

31   species (Lubke & Pause, 2015). Maternal odor cues for instance play a crucial role

32   in the successful initiation of breastfeeding (Porter & Winberg, 1999; Schaal et al.,

33   2009), essential for the survival of mammalian offsprings but also an important

34   player in the development of a secure bonding between mother and infant.

35   Furthermore, recent studies suggest that maternal odor impacts face perception,

36   in older infants (Durand, Baudouin, Lewkowicz, Goubet, & Schaal, 2013; Leleu et

37   al., 2019).

38   One setting in which this social learning is put to the test is in responses to adverse

39   situations such as stress and threat. Again, rodent research has provided us with

40   insights on the developmental trajectory of threat response and their modulation

41   by maternal presence and signals thereof. Very young pups who are highly

42   dependent on their mother show little fear responses but rather responses that

43   facilitate the formation of close bonding to their mother (Leon, 1992). Older pups

44   in contrast start to show more adult-like fear responses (Debiec & Sullivan, 2017).

45   Moreover, during a transition period, pups exhibit both types of responses; if their

46   mother is present, they show affiliative responses facilitating mother-infant-

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47   bonding, if their mother is absent, they show fear learning typically seen in older

48   pups (Debiec & Sullivan, 2017; Landers & Sullivan, 2012; Moriceau & Sullivan,

49   2006). Hence, maternal presence appears to be a key player in determining the

50   processing of and response to threat in early development of rodents, and maternal

51   odor is assumed to be a strong signal of maternal presence.

52   Studying responses to threat signals in human infants is more challenging. One

53   well-investigated phenomenon in this context is the development of an attentional

54   bias towards fearful expressions around 7 months of age (Vaish, Grossmann, &

55   Woodward, 2008). Interestingly, recent work suggests that this phenomenon can

56   be strongly influenced by secondary factors, such as parental sensitivity (Taylor-

57   Colls & Pasco Fearon, 2015), infant temperament (Martinos, Matheson, & de Haan,

58   2012), and breastfeeding experience (Krol, Rajhans, Missana, & Grossmann, 2014).

59   Crucially, all these factors are linked to the interplay between the infant and her

60   social environment, providing initial evidence for a modulation by social factors.

61   However, all the above-mentioned components are typically stable factors relating

62   to interindividual differences rather than flexible changes in a given situation. It is

63   therefore unclear whether threat responses in human infants can be modulated in

64   the same way as has been suggest for rodents. Does maternal presence, as a social

65   short-term rather than long-term factor, impact infants' responses to threat

66   signals? And is maternal odor a sufficient strong cue to elicit an effect of maternal

67   presence also in humans?

68   To address these questions, we designed an experiment to investigate the impact

69   of maternal odor on the neural response to threat signals in human infants. In an

70   electroencephalographic (EEG) set-up, infants were presented with happy and

71   fearful facial expressions while they were exposed to either the familiar maternal

72   odor, to an unfamiliar mother's odor, or to no specific odor at all. To quantify

73   infants' fear response, we investigated the amplitude of the *Nc*, an infant event-

74   related potential (ERP) component observed between 400 and 800 ms after the

75   onset of a stimulus at frontocentral electrodes. The Nc amplitude has been linked

76   to the allocation of attention and is typically enhanced in response to fearful faces

77   in 7-month-old infants (Peltola, Leppänen, Mäki, & Hietanen, 2009). Seven months

78   marks a crucial transitional period in human infants, and is associated not only

79   with the onset of stronger fear responses but also with the onset of locomotion

80   (Leppänen & Nelson, 2012). Hence, this age may be a period in humans analogous

81   to the transitional period described for rodents above; a shift from dependence to

82   increasing independence.

83   We therefore predict that infants show an increased threat response in the absence

84   of their mother (or an odor signaling her presence), but we expect this response to

85   be reduced in their mother's presence, even if only signaled via maternal odor.

86

87   METHODS

88   *Participants*. 76 7-month-old infants were included in the final sample (age: 213 ± 8

89   days [mean ± standard deviation (SD)]; range: 200-225, 38 female, see Table 1 for

90   description of the individual groups). An additional 15 infants had been tested but

91   were not included in the final sample because they did not provide at least 10

92   artifact-free trials per condition (n=11); had potential neurological problems (n=1);

93   were erroneously invited too young (n=1); the mean ERP response in the time-

94   window and electrodes of interest was more than 4 standard deviations from the

95   mean (n=1, see below); or because of technical problems during the recording

96   (n=1).

97   The sample size was determined by statistical considerations and practical

98   conventions in the field. First, for practical considerations and the known high

99   attrition rates in infant EEG studies, we had planned a priori to keep collecting

100   data until 25 useable data sets per each of the three experimental manipulation

101   groups were obtained. Second, as outlined in Albers & Lakens (2018), a smallest

102   effect size of interest was critical here, as too small true effects sizes for odor

103   manipulations would not be of practical or translational relevance. In the present

104   study, a total sample size of n=75 in three groups, was thus powered with 80% or

105   more to detect medium and large effects (i.e., Cohen's d of 0.8 or larger) at a

106   conventional type I error level of 5 %.

107   Infants were recruited via the maternity ward at the local hospital

108   (Universitätsklinikum Schleswig-Holstein), were born full-term (38–42 weeks

109   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

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136   that groups did not differ in gender, age, or breastfeeding experience. Infants in

137   the *Maternal odor* group were administered the t-shirt previously worn by their

138   mother during the experiment. Infants in the *No odor* group were administered an

139   unworn t-shirt. Infants in the *Stranger odor* group were administered a t-shirt

140   previously worn by the mother of one of the other infants. The t-shirt of their own

141   mother was stored in a freezer to be used as a stimulus for a different infant in the

142   *Stranger odor* group. Except in one case, both, parents and the experimenter

143   administering the t-shirt, were blind to the group assignment.

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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.

153   *Procedure and experimental design.* Before the laboratory visit, families were sent the

154   t-shirt (as described above) as well as a set of questionnaires, in particular the EPDS

155   (Cox, Holden, & Sagovsky, 1987), the IBQ-R (Gartstein & Rothbart, 2003;

156   Vonderlin, Ropeter, & Pauen, 2012), and a lab-internal questionnaire assessing

157   demographic information as well as feeding and sleeping routines of the infant

158   (One family, whose infant was assigned to the *Stranger odor* group, did not fill in

159   the IBQ-R and the EPDS and is therefore not included in the control analyses with

160   these two factors). After arriving in the laboratory, parents and infant were

161   familiarized with the environment and parents were informed about the study and

162   signed a consent form. The EEG recording was prepared while the infant was

163   sitting on his/her parent's lap. For recording, we used an elastic cap (BrainCap,

164   Easycap GmbH) in which 27 AgAgCl-electrodes were mounted according to the

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

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

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

179   The experiment was programmed using the Presentation software (Version 18.1).
180   Faces were presented for 800 ms, preceded by a fixation cross presented for
181   300 ms, and followed by an intertrial interval jittered between 800 and 1200 ms.
182   The faces had a height of approximately 28 cm. If necessary, short video clips
183   containing colorful moving shapes and ringtones were played during the
184   experiment to redirect the infant's attention to the screen. Each infant saw a
185   maximum of 216 trials, arranged in miniblocks of 24 trials containing 12 happy
186   and 12 fearful faces and played consecutively without interruption. Trials were
187   presented in a pseudorandomized order, ensuring that no stimulus category
188   (happy, fearful) was repeated more than once. The experiment continued until the
189   infant had seen all trials or became too fussy to continue the experiment. During
190   the experiment, the infant was video-recorded using a small camera mounted on
191   top of the monitor to offline exclude trials in which the infant did not attend to the
192   screen.

193   *Data Analysis.* We analyzed the data using Matlab 2013b (The MathWorks, Inc.,
194   Natick, MA), the Matlab toolbox FieldTrip (Oostenveld, Fries, Maris, & Schoffelen,
195   2011), and for statistical analysis the package JASP (JASP Team, version 0.10.2).

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

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

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

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228   also performed the equivalent analysis using Bayesian statistics; BF_{10} values above

229   1 are interpreted as anecdotal evidence, above 3 as moderate evidence, and above

230   10 as strong evidence for the research hypothesis (Wagenmakers et al., 2018).

231   To further analyze the Emotion effect without any a priori assumption about its

232   latency and topography, we ran a cluster-based permutation test (Maris &

233   Oostenveld, 2007) with 1000 permutations contrasting responses to happy and

234   fearful faces separately for each *Odor* group. A cluster had to comprise at least 2

235   adjacent electrodes, was computed across time and electrode position, and a type-

236   1-error probability of less than 0.05 at the cluster-level was ensured.

237   *Negative Affect.* Negative affect was computed as the mean of the IBQ-R scales

238   Sadness, Fear, and Distress to Limitations (Aktar et al., 2018).

239   RESULTS

240   *Influence of maternal odor on the Nc response.* We observed an overall enhanced Nc

241   amplitude in response to fearful faces, confirming the expected heightened threat

242   response (Peltola et al., 2009; significant main effect of Emotion [$F(1,72) = 11.60$, p

243    $= .001$, $\eta_p^2 = 0.14$; $BF_{10} = 2.578$]).

244   Most importantly, however, the threat response differed between odor groups.

245   That is, this emotion effect critically depended on the odor group an infant had

246   been assigned to (significant interaction Emotion × Odor [$F(2,72) = 5.57$, $p = .006$,

247    $\eta_p^2 = 0.13$; $BF_{10} = 4.564$; Figure 2]).


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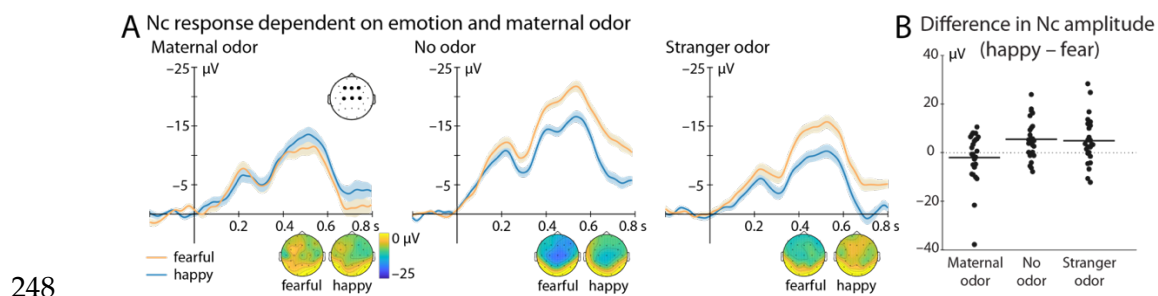
249   *Figure 2. ERP response in the different odor groups. A) Shows the Nc response at frontocentral*

250   *electrodes (F3, Fz, F4, C3, Cz, C4, marked by black dots) to fearful (orange) and happy (blue) facial*

251   *expressions. While no difference in response was observed in the Maternal odor group, infants in*

252   *the No odor and the Stranger odor group showed a significantly enhanced Nc response to fearful*

253   *faces. Topographic representations averaged between 400 and 800 ms after face onset are shown at*

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254   *the bottom. B) Depicts the difference between Nc response to fearful and happy faces for each*

255   *individual subject separately for the odor groups at the same electrodes and timewindow as in A.*

256   *Mean difference is marked by horizontal black lines. Note that the interaction Odor × Emotion*

257   *reaches significance even when excluding the two participants with the largest difference between*

258   *happy and fear in the Maternal odor group.*

259   Follow-up tests confirmed the Nc effect to fear signals was critically absent in the

260   *Maternal odor* group [$t(24) = -0.95$, $p = .35$, $d = -.19$; $BF_{10} = 0.32$; fearful: -6.51 ± 2.99

261   µV, happy: -8.53 ± 3.17 µV]. In contrast, the typical enhancement of the Nc

262   response to fearful (compared to happy) faces was present in the *Stranger odor*

263   group [$t(24) = 2.51$, $p = .019$, $d = .50$; $BF_{10} = 2.78$; fearful: -10.57 ± 2.34 µV (mean ±

264   SE), happy: -5.66 ± 1.78 µV] as well as in the *No odor* group [$t(25) = 3.50$, $p = .002$, d

265     $= .68$; $BF_{10} = 21.02$; fearful: -16.94 ± 2.19 µV, happy: -11.43 ± 2.53 µV].

266   *Corroborating analysis using a cluster-based permutation approach.* While the electrode

267   and time window selection for this analysis had not been data derived but

268   followed standards set by previous studies (Jessen & Grossmann, 2014, 2016, 2019),

269   we aimed to corroborate this main result by a more data-driven search for potential

270   effects using a cluster-based permutation test (Figure 3). In both, the *No odor* group

271   and the *Stranger odor* group, nearly identical clusters indicating a significantly

272   response enhancement to fearful (compared to happy) faces was found (No odor:

273     $p = .006$, $T_{sum} = 3063.8$; Stranger odor: $p = .021$, $T_{sum} = 1272.8$). Importantly, both

274   clusters exhibit the latency and topographic distribution typical for an Nc

275   response. Most importantly, no such cluster of significant differences was found

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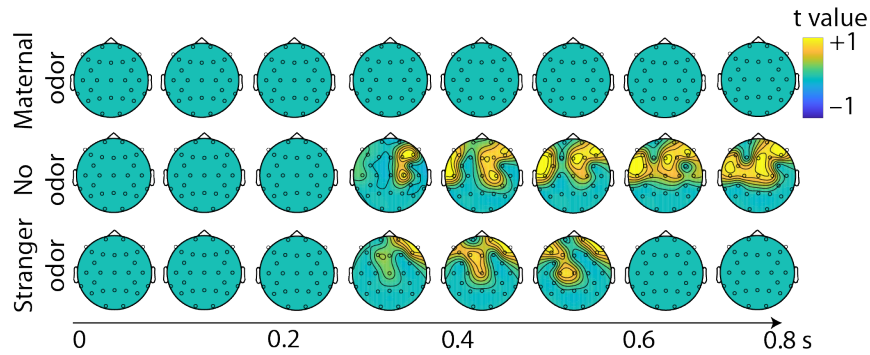
Figure 3. Cluster-based permutations test comparing responses to fearful and happy faces in the different odor groups. Depicted are topographic representations of t-values starting from the picture onset in steps of 100 ms.

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].

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302 Importantly, this was independent of (i.e., additionally true but not interacting

303 with) the *odor group* manipulation, as there was no meaningful Emotion ×

304 Breastfeeding × Odor interaction [$F(2,70) = 2.20$, $p = .12$, $\eta_p^2 = 0.06$, $BF_{10} = 1.081$].
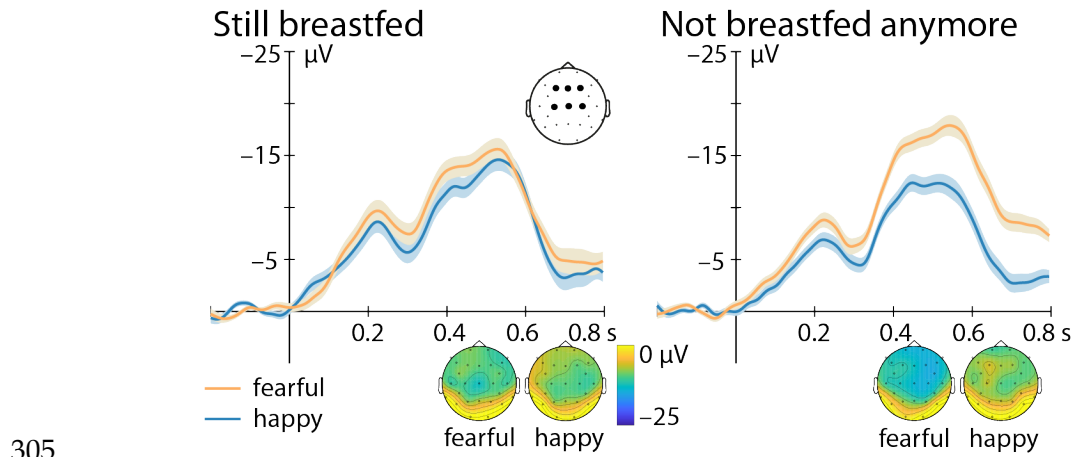
Figure 4. Nc response depending on breastfeeding status. Nc response is depicted at frontocentral electrodes (F3, Fz, F4, C3, Cz, C4, marked by black dots) to fearful (orange) and happy (blue) facial expressions for infants who are still breastfed (left) and not breastfed anymore (right). Infants who 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.

313 DISCUSSION

314 Our results demonstrate that maternal odor is a sufficiently strong signal to reduce

315 an established neural marker of the fear response in 7-month-old infants. A highly

316 consonant effect was found for breastfeeding, suggesting that not only momentary

317 states but also longer-lasting effects of maternal presence impact fear processing

318 in infants. Our results point to a previously unknown flexibility in fear processing

319 in infancy and its dependency on context and experience, which is in line with

320 findings in other species (Landers & Sullivan, 2012).

321 *Maternal odor as a momentary modulator of infant fear processing*

322 We suggest that such a response pattern might be characteristic for a developing

323 system that on the one hand needs to establish a close bonding to a caregiver,

324 typically the mother, while on the other hand learning to respond to potential

325 threat signals in the environment. This has been indirectly suggested by studies in

326 older children (Gee et al., 2014) as well as rodent research (Landers & Sullivan,

327 2012). Our findings, however, provide first evidence for flexible processing of

328 threat-related information depending on maternal signals in early human

329 development.

330 A diminished response to threat signals in maternal presence might facilitate

331 bonding, as a positive evaluation of information and less attention to potential

332 negative aspects may increase positive affect towards the caregiver even in the

333 presence of negative signals. In addition, if maternal presence works as a "safety

334 signal", requiring the infant to allocate less attention to potential threats, this might

335 also free cognitive capacities in the infant for other processes, akin to previously

336 reported improved cognitive performance in rat pups in the presence of familiar

337 odor (Wigal, Kucharski, & Spear, 1984).

338 At the same time, as the infant grows more independent, detecting and responding

339 to threat becomes of growing importance, especially if the mother is not present.

340 Crucially, 7 months is an important turning point in early human development,

341 characterized not only by qualitative changes in emotion development, but also by

342 the onset of locomotion, an important step towards growing independence

343 (Leppänen & Nelson, 2012). During this period, flexible threat processing might

344 be of particular importance, akin to what has been suggested in the rodent

345 literature (Landers & Sullivan, 2012).

346 Our results further underscore the importance of odor in early social development.

347 Two recent studies have suggested a modulation of infant face processing in

348 general by the presence of maternal odor (Durand et al., 2013; Leleu et al., 2019).

349 Our study is the first to show that the absence or presence of maternal odor can

350 impact highly specific aspects of infant face processing. Maternal odor might

351 therefore be an important guiding factor in emotional learning in infancy.

352 Specifically, we found an impact on the attention-related Nc component (Webb,

353 Long, & Nelson, 2005) but no influence on early visual processing (see

354 supplementary material) or on the number of trials the infants watched. Therefore,

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355   we found no evidence for a general impact of maternal odor on sensory processing

356   or compliance with the experiment, but rather odor specifically impacted the

357   evaluation of facial information, further underscoring its potential role in early

358   social learning.

359   Importantly, we assume that the observed effects are due to a *learned* odor

360   preference for familiar maternal signals rather than a specific preference for

361   maternal body odor. This assumption is in line with rodent work, suggesting that

362   effects akin to the ones reported for maternal odor can also be found other types

363   of highly familiar odor (Wigal et al., 1984). Accordingly, the present manipulation

364   did not differentiation between body odor and other odor components (such as

365   deodorant used or specific food consumed by the mother), thereby reflecting the

366   mélange of odors the infant experiences in maternal presence in everyday life.

367   *Breastfeeding as a long-term modulator of infant fear processing*

368   While maternal odor as a direct or phasic signal of maternal presence influenced

369   fear processing, so did the more tonic variable of an infant's breastfeeding

370   experience. In line with our interpretation of the above-mentioned odor effect, this

371   finding suggests a further modulatory impact of mother-infant-bonding in fear

372   processing: Our findings are in line with prior studies reporting an increased bias

373   towards expressions of happiness with increasing breastfeeding experience (Krol,

374   Monakhov, Lai, Ebstein, & Grossmann, 2015; Krol et al., 2014). How exactly

375   breastfeeding experience interacts with emotion processing is not certain, but a

376   possible explanation is an increased closeness between mother and infants;

377   breastfed infants on average spend more time interacting with their mother (Smith

378   & Forrester, 2017) and show a higher attachment security (Gibbs, Forste, &

379   Lybbert, 2018).

380   Maternal presence may therefore not only modulate fear processing directly, as

381   suggested by the influence of maternal odor, but might also exert a longer-lasting

382   impact.

383

384

385 *Future Directions*

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

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

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

408 *Conclusions*

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

16

415   fear response in infants. Furthermore, our data provide evidence for the potency

416   of odor as a social signal in humans and in particular in early ontogeny.

417   *Acknowledgements*

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