

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

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15

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-

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 (Martinis, 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:  $213 \pm 8$   
89 days [mean  $\pm$  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%  
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

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.



145 *Figure 1. Overview of experimental set-up. A) Mothers were asked to wear a provided t-shirt for 3*  
146 *nights in a row prior to the experiment. The infant was randomly assigned to one of three groups; a*  
147 *Maternal odor group (exposed to the t-shirt worn by the infant's mother), a Stranger odor group*  
148 *(exposed to a t-shirt worn by a different infant's mother), or a No odor group (exposed to an unworn*  
149 *t-shirt). We recorded the EEG signal while the infants were seated in a car seat with the t-shirt*  
150 *positioned over their chest area and watched happy and fearful facial expressions. B) Example of*  
151 *fearful and happy faces used as stimulus material, the colored circles are for illustration purpose*  
152 *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).



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  $\mu\text{V}$  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 ( $4 \pm 2$  components per participants  
205 [mean  $\pm$  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  $\mu\text{V}$ . 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-hoc tests and  
227 effect sizes are reported as partial eta squared ( $\eta_p^2$ ) and Cohen's *d*. In addition, we

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).

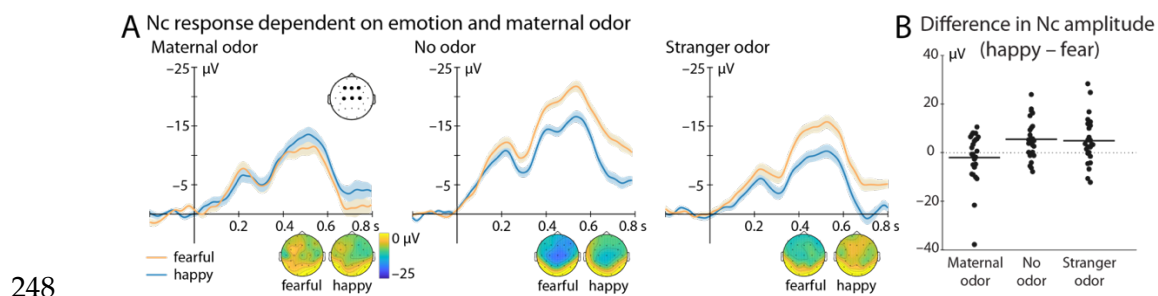
231 To further analyze the Emotion effect without any a priori assumption about its  
232 latency and topography, we ran a cluster-based permutation test (Maris &  
233 Oostenveld, 2007) with 1000 permutations contrasting responses to happy and  
234 fearful faces separately for each *Odor* group. A 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  $\times$  Odor [ $F(2,72) = 5.57, p = .006,$   
247  $\eta_p^2 = 0.13; BF_{10} = 4.564$ ; Figure 2]).

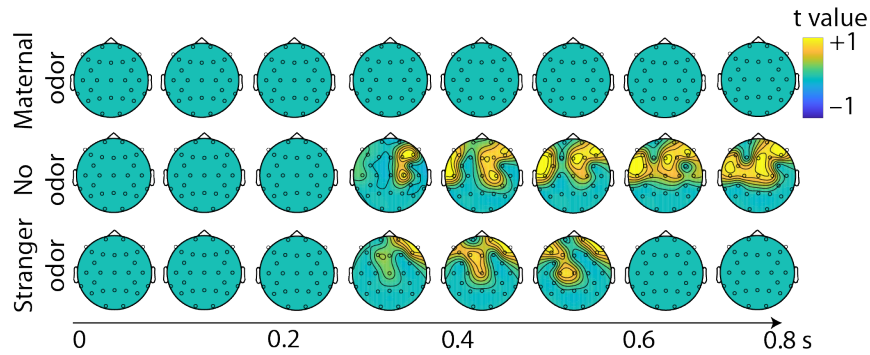


249 *Figure 2. ERP response in the different odor groups*. A) Shows the Nc response at frontocentral  
250 electrodes (F3, Fz, F4, C3, Cz, C4, marked by black dots) to fearful (orange) and happy (blue)  
251 facial expressions. While no difference in response was observed in the Maternal odor group, 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

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:  $-6.51 \pm 2.99$   
261  $\mu\text{V}$ , happy:  $-8.53 \pm 3.17 \mu\text{V}$ ]. 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:  $-10.57 \pm 2.34 \mu\text{V}$  (mean  $\pm$   
264 SE), happy:  $-5.66 \pm 1.78 \mu\text{V}$ ] as well as in the *No odor* group [ $t(25) = 3.50, p = .002, d$   
265  $= .68; BF_{10} = 21.02$ ; fearful:  $-16.94 \pm 2.19 \mu\text{V}$ , happy:  $-11.43 \pm 2.53 \mu\text{V}$ ].

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.



277

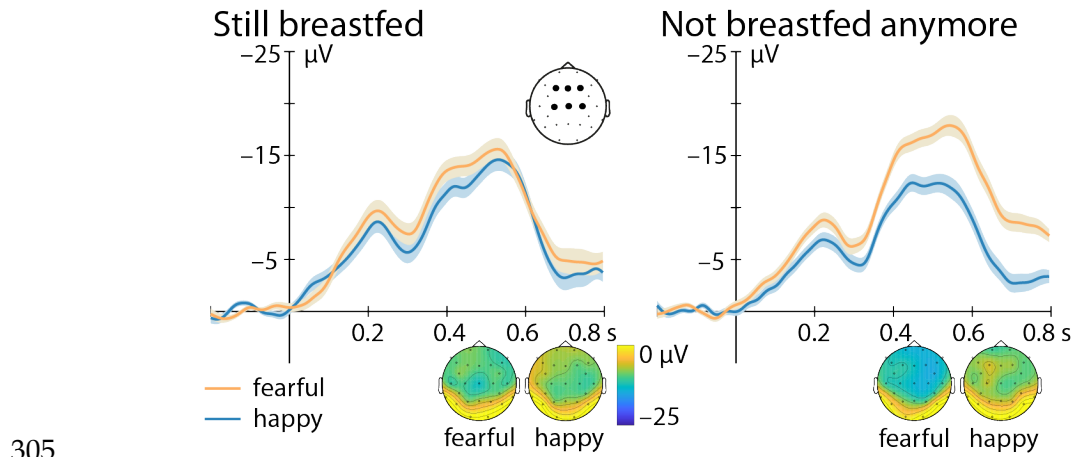
278 *Figure 3. Cluster-based permutations test comparing responses to fearful and happy faces in the*  
279 *different odor groups. Depicted are topographic representations of t-values starting from the picture*  
280 *onset in steps of 100 ms.*

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

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

293 *Effect of Breastfeeding.* A last finding supported our general line of reasoning.  
294 Namely, we did observe an interaction between Nc response to the emotional  
295 expression of the presented face and whether the infant was still breastfed or not  
296 [Emotion  $\times$  Breastfeeding,  $F(1,72) = 5.06, p = .028, \eta_p^2 = 0.07; BF_{10} = 1.632$ ; Figure 4].  
297 Only the infants who were not breastfed any more at the time of testing showed  
298 an enhanced Nc response to fearful faces [ $t(30) = 3.55, p = .001, d = .64; BF_{10} = 26.54$ ;  
299 fearful:  $-13.35 \pm 2.18 \mu V$ , happy:  $-7.90 \pm 2.00 \mu V$ ], while this enhancement was  
300 absent in the infants who were still breastfed [ $t(44) = 0.65, p = .52, d = 0.1; BF_{10} =$   
301  $0.20$ ; fearful:  $-10.08 \pm 2.08 \mu V$ , happy:  $-9.05 \pm 2.10 \mu V$ ].

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 [ $F(2,70) = 2.20, p = .12, \eta_p^2 = 0.06, BF_{10} = 1.081$ ].



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

312

## 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,

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 differentiate 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



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.

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