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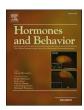
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## Facing infant cuteness: How nurturing care motivation and oxytocin system gene methylation are associated with responses to baby schema features

Hannah Spencer<sup>a,\*</sup>, Franca H. Parianen Lesemann<sup>b</sup>, Renate S.M. Buisman<sup>a</sup>, Eline J. Kraaijenvanger<sup>c</sup>, Susan Branje<sup>d</sup>, Marco P.M. Boks<sup>e</sup>, Peter A. Bos<sup>a</sup>

- <sup>a</sup> Institute of Education and Child Studies, Leiden University, Leiden, the Netherlands
- <sup>b</sup> Department of Experimental Psychology, Utrecht University, Utrecht, the Netherlands
- <sup>c</sup> Department of Child and Adolescent Psychiatry and Psychotherapy, Central Institute of Mental Health, Medical Faculty Mannheim /Heidelberg University, Mannheim,
- <sup>d</sup> Department of Youth and Family, Utrecht University, Utrecht, the Netherlands
- e Brain Centre University Medical Centre Utrecht, Utrecht, the Netherlands

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#### ABSTRACT

Baby schema features are a specific set of physical features—including chubby cheeks, large, low-set eyes, and a large, round head—that have evolutionary adaptive value in their ability to trigger nurturant care. In this study among nulliparous women (N = 81; M age = 23.60, SD = 0.44), we examined how sensitivity to these baby schema features differs based on individual variations in nurturant care motivation and oxytocin system gene methylation. We integrated subjective ratings with measures of facial expressions and electroencephalography (EEG) in response to infant faces that were manipulated to contain more or less pronounced baby schema features. Linear mixed effects analyses demonstrated that infants with more pronounced baby schema features were rated as cuter and participants indicated greater motivation to take care of them. Furthermore, infants with more pronounced baby schema features elicited stronger smiling responses and enhanced P2 and LPP amplitudes compared to infants with less pronounced baby schema features. Importantly, individual differences significantly predicted baby schema effects. Specifically, women with low OXTR methylation and high nurturance motivation showed enhanced differentiation in automatic neurophysiological responses to infants with high and low levels of baby schema features. These findings highlight the importance of considering individual differences in continued research to further understand the complexities of sensitivity to child cues, including facial features, which will improve our understanding of the intricate neurobiological system that forms the basis of caregiving behavior.

#### 1. Introduction

Human infants fully depend on nurturance from caretakers for basic survival and healthy development for an extended period. Infants' morphology has evolutionary adaptive value in its ability to trigger such nurturant care. In particular, a specific set of physical features—including chubby cheeks, large, low-set eyes, and a large, round head—serve as 'releasing' stimuli for affectionate feelings and behaviors, which promote care responses (Lorenz, 1943). These 'baby schema' features are generally perceived as cute (Alley, 1981; Almanza-Sepúlveda et al., 2018; Hildebrandt and Fitzgerald, 1979; Sternglanz et al., 1977), and both parents and non-parents report greater motivation to

take care of infants with more pronounced baby schema features (e.g., Aragón et al., 2015; Endendijk et al., 2018; Glocker et al., 2009a). Furthermore, people exert effort to look at these infants longer, which is indicative of greater reward value (Hahn et al., 2015, 2013). Importantly, baby schema features may also elicit differential caregiving responses. Indeed, increased carefulness was triggered when women perceived infants with more pronounced baby schema features (Sherman et al., 2013). Also, infant cuteness was associated with increased affection, playfulness, and positive attitudes of mothers towards their children (Langlois et al., 1995). These effects of cuteness warrant a more comprehensive understanding of the psychophysiological processing of baby schema features that might be related to caregiving behavior. The

<sup>\*</sup> Corresponding author at: Leiden University, Institute of Education and Child Studies, Wassenaarseweg 52, 2333 AK Leiden, the Netherlands. E-mail address: h.spencer@fsw.leidenuniv.nl (H. Spencer).

current study examined sensitivity to baby schema features on subjective ratings, measures of facial expressions and electroencephalography (EEG). Crucially, the moderating role of nurturant care motivation and oxytocin system functioning in this sensitivity to baby schema was examined.

Facial expressions play a significant role in non-verbal communication. They convey emotions and intentions, and are therefore essential for facilitating dyadic interactions (Kraaijenvanger et al., 2017). Infants in particular rely on caregivers' facial expressions to guide their feelings and behaviors, with positive expressions encouraging social and explorative behavior (Feinman, 1982). Infants automatically elicit positive facial expressions (i.e. smiles) in perceivers, which is accompanied by elevated experiences of positive affect (Hildebrandt and Fitzgerald, 1978; Lang et al., 1993; Nittono and Ihara, 2017). Since rewarding facial stimuli elicit stronger automatic positive facial expressions, similar effects might be expected for infants with more pronounced baby schema features (Hahn et al., 2015, 2013; Sims et al., 2012). Infants with more pronounced baby schema features did elicit reduced automatic negative facial expressions (i.e. sneers; Löwenbrück and Hess, 2021). Nevertheless, previous studies do not find differences in positive facial expressions for varying baby schema features, even though more pronounced baby schema features elicited elevated positive affect (Hildebrandt and Fitzgerald, 1978; Löwenbrück and Hess, 2021). Automatic facial expressions are, however, subtle and can show a rapid, dynamic changing time-course in response to affective images (Bos et al., 2016; Tassinary and Cacioppo, 1992; van Boxtel, 2010). So far, studies examining automatic facial expressions in relation to baby schema features have not taken this time course into account, which might reduce sensitivity to detect differential responses.

In addition to facial expressions, it is noteworthy to consider the initial neural processing when facing infants. Neuroimaging evidence shows that humans respond to infants rapidly and distinctively, which may be explained by baby schema features (Hahn and Perrett, 2014; Kringelbach et al., 2016). Furthermore, brain reward pathways show specific responses to infants, and this activation increases when baby schema features are more pronounced (Glocker et al., 2009b; Wang et al., 2018, but see Endendijk et al., 2020). This effect may further relate to the general saliency of infant faces, where less pronounced baby schema features are perceived as less typical for infant faces, thereby triggering distinctive neural responses (Bos et al., 2018). The saliency of faces is widely studied with event related potential (ERP) components measured with electroencephalography (EEG). The initial processing of faces is captured by the P1 and N170 component, respectively, with stronger components associated with enhanced attentional capture of stimuli (Schindler and Bublatzky, 2020). The following P2 component is associated with face typicality, with less typical faces eliciting decreased amplitudes (Schweinberger and Neumann, 2016). Subsequently, the late positive potential (LPP) is linked to sustained attention and reflective of stimulus saliency, including the valence and arousal of stimuli (Schindler and Bublatzky, 2020). Given the saliency and reward value of baby schema features, one may expect differentiations in early and later processing stages when perceiving infants with more pronounced baby schema features. However, studies so far show mixed findings (Endendijk et al., 2018; Hahn et al., 2016), which necessitates further research.

Importantly, individual differences may further account for the inconsistent findings when examining baby schema effects. A key aspect of nurturant and sensitive care involves promptly and adequately perceiving children's signals and needs (Ainsworth, 1969). Consequently, reduced sensitivity to infant cues, including baby schema features, may impede care responses (Vuoriainen et al., 2022). Women with strong maternal tendencies showed a greater sensitivity to the rewarding value of infant faces with more pronounced baby schema features (Hahn et al., 2015). Similarly, women with more prosocial tendencies were more sensitive to slight variations in baby schema features (Sherman et al., 2013). Nurturance motivation—one's general

tendency to provide nurturant care to promote infant's healthy development—may be of particular significance for sensitivity to baby schema features (Buckels et al., 2015; Hofer et al., 2018). Indeed, adults with increased trait nurturance motivation showed enhanced reward value of and neural responses to infants (Bos et al., 2018; Buckels et al., 2015; Endendijk et al., 2020, 2018). Yet, thus far, no discernible association has been found between nurturance motivation and sensitivity to baby schema features (Bos et al., 2018; Endendijk et al., 2020, 2018).

On a physiological level, the oxytocin system is intricately linked with caregiving and thus might also impact sensitivity towards baby schema features (Feldman, 2017). Elevated levels of the neuropeptide oxytocin are positively associated with responsiveness to infant cues and care responses (e.g., Feldman et al., 2007; Riem et al., 2011; Strathearn et al., 2009). However, administration studies provide inconsistent findings regarding how oxytocin might increase sensitivity to baby schema features (Bos et al., 2018; Holtfrerich et al., 2018). One study showed increased neural responses to infants with more pronounced baby schema features after oxytocin administration (Holtfrerich et al., 2018). However, another study found no interaction between oxytocin administration and baby schema features affecting neural responses. Instead, neural responses were reduced to all infants regardless of baby schema features after oxytocin administration (Bos et al., 2018). These inconsistencies may be due to context-dependent effects, possibly stemming from the use of different tasks (Carter et al., 2020). Compelling evidence suggest the feasibility of measuring oxytocin system functioning through gene methylation, which can downregulate gene expression, and is associated with oxytocin sensitivity (Carter et al., 2020). Elevated methylation levels of the Oxytocin (OXT) and Oxytocin Receptor (OXTR) genes, where OXT encodes a precursor hormone crucial in oxytocin synthesis, and OXTR encodes oxytocin receptors through which oxytocin influences brain function and behavior, are associated with a reduced responsiveness to socially salient stimuli (see e.g., Haas et al., 2016; Krol et al., 2019; Puglia et al., 2015; Spencer et al., 2022). Methylation in the promotor area of these genes is associated with reduced function and therefore low methylation may be associated with higher sensitivity to baby schema features (Szyf and Bick, 2013).

The current study aimed to gain a more comprehensive understanding of the processing of baby schema features, as well as to examine individual characteristics that might moderate sensitivity to these features and may underlie disparities in the literature. We focused on nurturance motivation and oxytocin system gene methylation, and expected that increased nurturance motivation and lower methylation of the *OXT* and *OXTR* genes were associated with enhanced sensitivity to variations in baby schema features.

#### 2. Methods

#### 2.1. Participants

All participants were recruited from the RADAR (Research on Adolescent Development and Relationships) Young cohort (Branje and Meeus, 2018). A total of 154 female participants were initially eligible for study participation and eventually 81 participants were included in the study ( $M_{\rm age}=23.60$ , SD=0.44, range = 22.30–24.76 years). All participants were Dutch (n=2 with dual nationality). Reasons for not being included were opting out of participation in the lab study (n=44), meeting exclusion criteria (n=18), or not reachable via telephone or email (n=11).

#### 2.2. Procedure

The current study was part of a larger research project focused on caregiving behavior prior to motherhood and therefore nulliparous women were contacted for participation (Parianen Lesemann et al., 2020; Spencer et al., 2022). For the larger research project, we initially

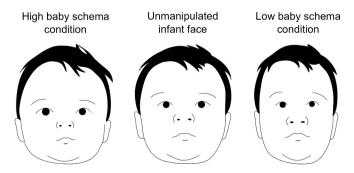
aimed for a sample size of 84 participants, based on power calculation for a multiple regression analysis with four independent predictors, a medium effect size, 80 % power, and a 0.05 alpha level (Cohen, 1992). Eligible participants were invited to participate and received information about study participation through a letter. Next, they were contacted via phone, where further information about study participation was provided. After participants expressed interest to participate in the study, they underwent a screening to establish their eligibility based on the following exclusion criteria: 1) pregnancy or motherhood, 2) history of endocrinal, neurological, or psychiatric conditions, and 3) use or previous use of medication that influences endocrinal, neurological, or psychological functioning. The study was conducted in accordance with the latest version of the Declaration of Helsinki and approved by the  $medical\ ethical\ committee\ of\ the\ UMC\ Utrecht\ (NL57474.041.16,METC$ 16/244). Upon arrival in the lab, all participants were informed about task procedures and provided written informed consent prior to study participation. As part of the larger research project, all participants provided two saliva samples for DNA methylation and steroid hormone assessment. Additionally, they completed five experimental computer tasks followed by a series of questionnaires. We describe the measures that were part of the current study below.

#### 2.3. Stimuli and baby schema task

Participants were presented with an experimental computer task designed to measure responses to different levels of baby schema features based on Glocker et al. (2009a, 2009b). The stimuli used in the task consisted of full color photographs of nine infant faces with neutral facial expressions that were manipulated with standardized measures to contain more and less pronounced baby schema features in accordance with Borgi et al. (2014). This resulted in three conditions (unmanipulated; high baby schema features; and low baby schema features) and a total of 27 distinct stimuli. Detailed information on the stimuli can be found elsewhere (Endendijk et al., 2020); for an illustration of the stimuli used see Fig. 1. The dimension of all stimuli was  $800 \times 800$ pixels. All stimuli were presented once in a randomized order in the center of the screen for a duration of 2000 ms and were preceded by a 1000 ms fixation cross. After each stimulus presentation, participants were asked to rate the stimuli on cuteness of the infant (from 1: not at all cute to 9: very cute) and motivation to care for the infant (from 1: not at all to 9: very much). There was no time limitation on participant's responses and responses were followed by a blank screen with a duration of 1000 ms. Intertrial durations varied according to participants' reaction time.

#### 2.4. Electromyography (EMG) data collection and reduction

Automatic facial expressions in response to baby schema features were measured with EMG, which was recorded using the Biosemi ActiveTwo system (Biosemi, Amsterdam, The Netherlands) at 2048 Hz



**Fig. 1.** An Illustration of Infant Stimuli Used in the Study. Note. During the study, participants were presented with full-color photographs of infant faces. Due to copyright and privacy concerns, we provide line drawings as an illustration of the images used in the task.

sampling rate from bipolar electrode montages placed over the left zygomaticus major (ZYG) to measure smiling responses, and over the left corrugator supercilii (COR) to measure frowning responses (Fridlund and Cacioppo, 1986). The ground consisted of the active common mode sense (CMS) and passive driven right leg (DRL) electrodes (see below).

Data reduction was performed using Brain Vision Analyser 2.2. Raw EMG data were 30-500 Hz band pass filtered with a 24 dB roll-off per octave. For each trial, data were segmented into -1000-2000 ms epochs time-locked to stimulus onset, rectified, and averaged into 250 ms intervals. Next, signals were normalized by calculating the proportion of mean rectified activity for each 250 ms interval compared to the mean rectified baseline activity (-1000-0 ms) for each trial. Therefore, data at each timepoint represent the EMG activity relative to the baseline activity observed during the trial, with a value of 1.00 signifying an equal level of activity to the average baseline. Trials were rejected as artifacts if mean rectified baseline EMG activity and/or mean normalized poststimulus onset (0–2000 ms) EMG activity was  $\pm 3$  SD from the mean activity within subjects. Next, remaining trials containing extreme EMG activity, where mean normalized post-stimulus onset EMG activity was  $\pm 3$  SD from the mean activity across subjects, were identified as outliers and omitted from analyses. In total 6.17 % of trials for the ZYG and 2.88 % of trials for the COR were omitted from analyses. For the ZYG activity, an average of 0.28 more trials were omitted from the high baby schema condition compared to the unmanipulated condition within participants (p = .02), but there was no significant difference when comparing number of omitted trials for the high versus low baby schema condition or for the low baby schema versus unmanipulated condition (p's  $\geq$  .29). There were no differences in number of trials omitted per condition within participants for the COR activity (p's  $\geq$  .99). The eight time-points during stimulus presentation were used for analyses and EMG activity was log transformed due to positive skewness.

#### 2.5. Electroencephalography (EEG) data collection and reduction

Neural responses to baby schema features were measured with EEG that was simultaneously recorded using the Biosemi ActiveTwo system (Biosemi, Amsterdam, The Netherlands) at 2048 Hz sampling rate from 32 AG/AgCl pin electrodes placed according to the International 10/20 electrode placement standard. The ground reference point consisted of the active common mode sense (CMS) and passive driven right leg (DRL) electrode placed on central sagittal midline scalp locations. Horizontal and vertical eye movements were measured with electrodes placed besides the outer canthus of both eyes and above and below the right eye.

Data reduction was performed using Brain Vision Analyser 2.2. Raw EEG traces were down-sampled to 256 Hz, 0.1-30 Hz band pass filtered with a 24 dB roll-off per octave and re-referenced to the average activity of all electrodes. Data were segmented (200 ms pre-stimulus – 1000 ms post-stimulus) and segments containing eye movements and blinks were corrected using the Gratton & Coles method (Gratton et al., 1983). Artifacts were rejected through semi-automatic inspection of EEG channels, with maximal allowed difference of 55  $\mu V$  between maximum and minimum value in any 100 ms interval measured over Fp1 or Fp2. For three participants AF3 and AF4 were used to detect artifacts, since Fp1 and Fp2 were too noisy. Additional segments were deleted if visual inspection revealed residual artifacts. Individual channels were removed from segments if the difference between the maximum and minimum value within the channel and segment exceeded 200 μV or if the difference between the maximum and minimum value in any 100 ms window was less than  $0.5~\mu V$ . Data sets of five participants were not included in the final analyses due to excessive artifacts in the EEG signal (less than five artifact free trials per condition). On average, artifacts were detected in 13 % of all trials of participants included in the final analyses. The number of artifacts did not differ between the baby schema conditions (p's > .79). Segments were baseline corrected relative to the 200 ms pre-stimulus interval and averaged into the three separate conditions per participant.

Statistical analyses were performed for the following event-related potential (ERP) components: P1, N170, P2, and LPP. The selection of time windows and electrodes was extracted in coherence with previous studies (Endendijk et al., 2018; Hahn et al., 2016; Huffmeijer et al., 2018). Specifically, P1 was quantified post-stimulus as average activity from 129 to 156 ms (measured over O1, O2, and Oz), N170 from 172 to 211 ms (measured over P7 and P8), P2 from 242 to 281 ms (measured over PO3, PO4, P3, P4, Pz), and LPP from 300 to 800 ms (measured over PO3, PO4, P3, P4, Pz, CP1, and CP2).

#### 2.6. Nurturance motivation assessment

The *Nurturance* subscale of the Parental Care and Tenderness (PCAT) questionnaire measured individuals' nurturance motivation (Buckels et al., 2015; Hofer et al., 2018). Participants completed the full PCAT for which they first responded to 15 statements by indicating their levels of agreement on a 5-point scale from 1 (*strongly disagree*) to 5 (*strongly agree*; example item *Nurturance* subscale: "When I see infants, I want to hold them."). Next, participants indicated how much tenderness they would feel in 10 hypothetical situations on a 5-point scale from 1 (*no tenderness at all*) to 5 (*a lot of tenderness*; example item *Nurturance* subscale: "You make a baby laugh over and over again by making silly faces."). The *Nurturance* subscale contains 6 items (including responses to 2 statements and 4 hypothetical situations) and nurturance motivation was computing by averaging the responses to these items. Internal consistency of the *Nurturance* subscale was acceptable in the current study (Cronbach's  $\alpha = 0.75$ ).

#### 2.7. OXT and OXTR methylation assessment

After task execution, saliva samples (2.0 mL) were collected using the Oragene DNA (OG-500) Kit (DNA Genotek Inc., Ottowa, CA). Extracted DNA was submitted to bisulfite treatment before undergoing polymerase chain reaction (PCR) and Methylation Sensitive High-Resolution Melting (MS-HRM) analyses in duplo (Wojdacz and Dobrovic, 2007). Target sequences were determined based on previous studies demonstrating associations between OXT and OXTR methylation levels and socio-behavioral outcomes (Bell et al., 2015; Haas et al., 2016; Kraaijenvanger et al., 2019). Specifically, the primer set for OXT covered the target sequence GRCh38/hg38, chr20: 3,071,297-3,071,697 (containing 17 CpG sites) and the primer set for OXTR covered target sequence GRCh38/hg38, chr3: 8,769,043-8,769,159 (containing CpG sites -860, -901, -924, -934, and -959 (hg38, 3: 8769047, 8,769,088, 8,769,111, 8,769,121, and 8,769,146); Bell et al., 2015; Haas et al., 2016; Kraaijenvanger et al., 2019). Specifics of the OXT and OXTR primer sets are reported elsewhere in the Supplemental material (Parianen Lesemann et al., 2020). MS-HRM analyses recorded the melting profile, with the area under the curve estimating methylation levels across all CpG sites in the target sequences. Replicates were averaged and the average across replicate coefficient of variation (CV) was 3.67 % for the OXT gene and 1.68 % for the OXTR gene.

#### 2.8. Statistical analyses

Mixed-effects models were used to deal with the hierarchical data structure, that is, responses to different stimuli per condition were measured repeatedly within participants. Analyses were conducted in "R" Version 4.2.2 using the lmerTest (Kuznetsova et al., 2017) and lme4 (Bates et al., 2015) packages to compute the linear mixed-effects analyses using the lmer function with maximum-likelihood estimation and bound optimization by quadratic approximation with a set maximum of 100,000 iterations. For each model, we used the maximal random effects structure justified by our design and supported by the data, including random slopes for main fixed effects to control for Type 1 error (Barr et al., 2013; Volpert-Esmond et al., 2021). If necessary, random effects

were removed to avoid singularity or convergence issues (Barr et al., 2013). Missing values (i.e., artifacts and outlier trials) were omitted from analyses and all continuous predictors were scaled. We reported the estimated marginal means (EMM) and EMM of linear trends including comparisons computed with the emmeans package (Lenth, 2023). Degrees of freedom were calculated using the Satterthwaite method. We first conducted manipulation checks to assess the effectiveness of the image manipulation in our study. Consistent with our expectations, we observed the most pronounced differences in outcome measures when comparing the high baby schema condition to the low baby schema condition, with the unmanipulated condition exhibiting intermediate responses (see supplemental material). Therefore, we proceeded with our main hypotheses-driven analyses by comparing responses to infants with high compared to low baby schema features and used the Benjamini-Hochberg procedure to address the issue of multiple comparisons (Benjamini and Hochberg, 1995). The False Discovery Rate (FDR) was set at 0.10, acknowledging the subtle effects commonly revealed by neurobiological mechanisms of caregiving which offer valuable insights into individual differences that can inform future research and interventions. This aligns with the consideration that an FDR of 0.05 is often too low for many experiments and using an FDR of 0.10 to 0.20 is suggested if the cost of a false negative is higher (Lee and Lee, 2018). Analyses examining the effects of baby schema features, as well as moderating effects of nurturance motivation and oxytocin system gene methylation, were treated as three distinct families of tests separately for each outcome measure category. These outcome measures encompassed subjective ratings, EMG responses, and ERP components, resulting in a total correction for nine distinct families of tests. The total number of fixed effects accounted for ranged from 4 (to examine effects of baby schema features on subjective ratings) to 32 (to examine effects of oxytocin system gene methylation for both the EMG responses and ERP components).

#### 2.8.1. Subjective rating effects

For the subjective ratings, we first tested the unconditional means (UM) model which decomposed the variance into three independent components: participant, stimulus, and error. This model was used to compute the proportion of explained variance (ICC) at the participant and stimulus level. Next, we included the fixed effect of condition with additional random slopes of condition over participant to test effects of baby schema features on subjective ratings (Task effect model). Finally, we tested the moderating effects of nurturance motivation, OXT methylation, and OXTR methylation on sensitivity to baby schema features by including these measures into separate models as main effects and in interaction with the fixed effect of the task effect model (NURT model, OXT model, and OXTR model). This resulted in the following maximal model for the subjective ratings: Subjective rating ~ Condition \* Moderator + (1 + Condition|Participant) + (1|Stimulus). We only interpreted results if model fit significantly improved with increasing complexity. Analyses were conducted separately for the cuteness and care motivation ratings.

#### 2.8.2. EMG effects

For the EMG responses, we first tested the UM model which decomposed the variance into three independent components: participant, stimulus, and error. This model was used to compute the ICC at the participant and stimulus level. Next, we included the fixed effect of time with additional random slopes of time over participant and stimulus to test the unconditional growth (UG) model. Then, we included the interaction between condition and time with additional random slopes of condition over participant to test the effect of baby schema on EMG activity over time (Task effect model). Finally, we tested the moderating effects of nurturance motivation, *OXT* methylation, and *OXTR* methylation on sensitivity to baby schema features by including these measures into separate models as main effects and in interaction with the fixed effect of the task effect model (NURT model, *OXT* model, and *OXTR* 

model). This resulted in the following maximal model for the EMG responses: Muscle activity  $\sim$  Condition \* Time \* Moderator + (1 + Condition + Time|Participant) + (1 + Time|Stimulus). We only interpreted results if model fit significantly improved with increasing complexity. Analyses were conducted separately for the ZYG and COR activity.

#### 2.8.3. ERP effects

ERP components were averaged across conditions and exported individually for each electrode, as defined previously for each ERP component. Therefore, for the ERP components, we first tested the UM model which decomposed the variance into three independent components: participant, electrode, and error (Volpert-Esmond et al., 2021). This model was used to compute the ICC at the participant and electrode level. Next, we included the fixed effect of condition with additional random slopes of condition over participant to test effects of baby schema on ERP components (Task effect model). Finally, we tested the moderating effects of nurturance motivation, OXT methylation, and OXTR methylation on sensitivity to baby schema features by including these measures into separate models as main effects and in interaction with the fixed effect of the task effect model (NURT model, OXT model, and OXTR model). This resulted in the following maximal model for the ERP components: ERP amplitude  $\sim$  Condition \* Moderator + (1 + Condition|Participant) + (1|Electrode). We only interpreted results if model fit significantly improved with increasing complexity. Analyses were conducted separately for the P1, N170, P2, and LPP components.

#### 3. Results

#### 3.1. Subjective ratings

An overview of the results of the mixed-effects model analyses for subjective ratings is presented in Table 1.

#### 3.1.1. Cuteness ratings

The UM model revealed that the proportion of explained variance (ICC) was 0.26 at the participant level and 0.31 at the stimulus level, indicating that 26 % of the total variance in cuteness ratings can be explained by differences between participants and 31 % can be explained by differences between stimuli. The task effect model revealed that baby schema condition was significantly associated with cuteness ratings, t = 3.83, p = .001,  $\beta = 0.36$ . Participants rated infants with high levels of baby schema features as cuter (M = 6.08, 95 % CI[5.30, 6.85]) than infants with low levels baby schema features (M = 4.45, 95 % CI [3.66, 5.24]; see Fig. 2A). The task effect model fit the data significantly better than the UM model ( $\chi^2$  (3) = 29.58, p < .001). The NURT model demonstrated that nurturance motivation was significantly associated with cuteness ratings, t = 5.83, p < .001,  $\beta = 0.36$ . Overall, higher nurturance scores were associated with higher cuteness ratings across all stimuli. Nurturance motivation scores did not interact with condition to predict cuteness ratings, p = .50. The NURT model fit the data significantly better than the task effect model ( $\chi^2$  (2) = 33.28, p < .001). The OXT and OXTR models did not fit the data significantly better than the task effect model, p's > .05, and therefore we did not interpret further

#### 3.1.2. Care motivation ratings

The UM model revealed that the proportion of explained variance (ICC) was 0.56 at the participant level and 0.12 at the stimulus level, indicating that 56 % of the total variance in care motivation ratings can be explained by differences between participants and 12 % can be explained by differences between stimuli. The task effect model revealed that baby schema condition was significantly associated with care motivation ratings,  $t=3.98,\,p<.001,\,\beta=0.24.$  Participants indicated higher motivation to care for infants with high levels of baby schema features ( $M=5.29,\,95$  % CI[4.64, 5.94]) compared to infants with low levels of baby schema features ( $M=4.15,\,95$  % CI[3.50, 4.79]; see Fig. 2B). The task effect model fit the data significantly better than the

 Table 1

 Results of mixed-effects model analyses for subjective ratings.

		Cuteness ratings				Care motivation ratings					
		UM	Task	NURT	OXT	OXTR	UM	Task	NURT	OXT	OXTR
Fixed effects		Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)
	Intercept	5.26 (0.32)***	4.45 (0.34)***	4.45 (0.32)***	4.45 (0.34)***	4.45 (0.34)***	4.72 (0.28)***	4.15 (0.28)***	4.15 (0.25)***	4.15 (0.28)***	4.15 (0.28)***
	Condition		1.63 (0.43)**	1.63 (0.42)**	1.63 (0.42)**	1.63 (0.42)**		1.14 (0.29)***	1.14 (0.27)***	1.14 (0.29)***	1.14 (0.29)***
	Nurturance			0.81 (0.14)***					1.07 (0.17)***		
Condition x Nurturance				-0.07 (0.09)					-0.01 (0.10)		
	OXT				-0.04 (0.16)					0.08 (0.21)	
Condition x OXT					-0.10 (0.10)					-0.10 (0.10)	
	OXTR					-0.05 (0.74)					0.07 (0.21)
Condition x OXTR						0.08 (0.09)					0.01 (0.10)
Variance components		Variance (SD)	Variance (SD)	Variance (SD)	Variance (SD)	Variance (SD)	Variance (SD)	Variance (SD)	Variance (SD)	Variance (SD)	Variance (SD)
Participant level	Intercept	1.71 (1.31)	2.02 (1.42)	1.36 (1.17)	2.02 (1.42)	2.02 (1.42)	3.21 (1.79)	3.26 (1.81)	2.12 (1.46)	3.26 (1.80)	3.26 (1.81)
	Condition		0.33 (0.58)	0.33 (0.57)	0.32 (0.57)	0.33 (0.57)		0.40 (0.63)	0.40 (0.63)	0.39 (0.63)	0.40 (0.63)
Stimulus level	Intercept	1.43 (1.20)	0.77 (0.88)	0.76 (0.87)	0.77 (0.88)	0.78 (0.88)	0.66 (0.81)	0.33 (0.57)	0.33 (0.57)	0.33 (0.57)	0.33 (0.57)
Residual level		1.97 (1.41)	1.88 (1.37)	1.88 (1.37)	1.88 (1.37)	1.88 (1.37)	1.83 (1.35)	1.72 (1.32)	1.72 (1.31)	1.72 (1.31)	1.72 (1.31)
Model fit improved?		n/a	<b>√</b>	✓	×	×	n/a	✓	<b>√</b>	×	×
Fit statistics	AIC	5434.2	5410.6	5381.4	5412.9	5414.0	5364.9	5334.8	5305.0	5337.8	5338.7
	BIC	5455.4	5447.6	5428.9	5460.5	5461.6	5389.0	5371.8	5352.6	5385.4	5386.3

Note. Condition: -1 = low baby schema condition, 1 = logh baby schema condition; UM = Unconditional Means Model; Task = Task effects model; Task = Task

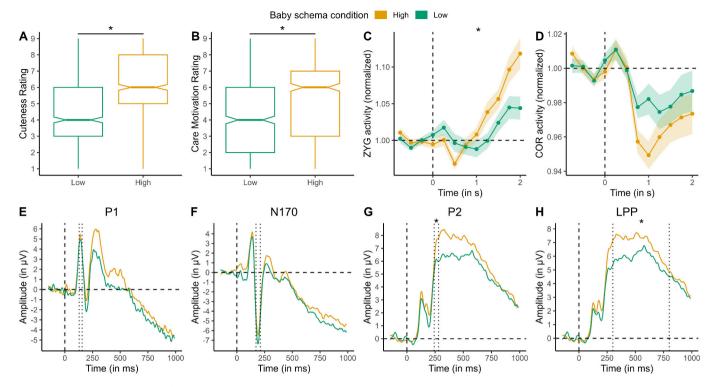


Fig. 2. Responses to Infants with High and Low Baby Schema Features Measured with A) Cuteness Ratings; B) Care Motivation Ratings; C) ZYG Activity Over Time; D) COR Activity Over Time; E) P1 Amplitudes; F) N170 Amplitudes; G) P2 Amplitudes; H) LPP Amplitudes

Note. Dotted vertical lines in panels E–H represent the boundaries of the time windows for each ERP component; ZYG = Zygomaticus major; COR = Corrugator supercilli.

UM model ( $\chi 2$  (3) = 36.04, p < .001). The NURT model demonstrated that nurturance motivation was significantly associated with care motivation ratings,  $t=6.31,\ p<.001,\ \beta=0.44.$  Overall, higher nurturance scores were associated with higher care motivation ratings across all stimuli. Nurturance motivation scores did not interact with condition to predict care motivation ratings, p=.89. The NURT model fit the data significantly better than the task effect model ( $\chi 2$  (2) = 33.84, p<.001). The *OXT* and *OXTR* models did not fit the data significantly better than the task effect model, p's > .05, and therefore we did not interpret further results.

#### 3.2. Facial expression responses

An overview of the results of the mixed-effects model analyses for facial expression responses is presented in Table 2.

#### 3.2.1. ZYG activity

The UM model revealed that the proportion of explained variance (ICC) was 0.08 at the participant level and 0.01 at the stimulus level, indicating that 8 % of the total variance in ZYG activity can be explained by differences between participants and 1 % can be explained by differences between stimuli. The UG model revealed that ZYG activity significantly increased over time towards all infants,  $t = 2.33, p = .02, \beta$ = 0.06. The UG model fit the data significantly better than the UM model  $(\chi 2 (5) = 253.59, p < .001)$ . The task effect model revealed that baby schema condition significantly associated with ZYG activity over time, t = 2.47, p = .02,  $\beta$  = 0.06. ZYG activity over time was stronger in response to infants with high levels of baby schema features (M = 0.028, 95 % CI[0.010, 0.046]), compared to infants with low levels of baby schema features (M = 0.004, 95 % CI[-0.014, 0.022]; see Fig. 2C). The task effect model fit the data significantly better than the UG model ( $\chi 2$ (5) = 204.92, p < .001). The OXTR model demonstrated that OXTR methylation levels interacted with baby schema condition to predict ZYG activity over time,  $t=-3.01, p=.003, \beta=-0.04$ . For participants with low *OXTR* methylation levels (M-1 SD), ZYG activity over time was significantly higher in response to infants with high levels of baby schema features compared to infants with low levels of baby schema features ( $M\Delta=0.039, 95$  % CI[0.011, 0.066]), z=3.57, p=.002. For participants with high *OXTR* methylation levels (M+1 SD), ZYG activity over time was not significantly different between baby schema conditions ( $M\Delta=0.009, 95$  % CI[-0.018, 0.037]), z=0.87, p=.82 (see Fig. 3). The *OXTR* model fit the data significantly better than the task effect model ( $\chi 2$  (4) = 18.03, p=.001). The NURT and *OXT* models did not fit the data significantly better than the task effect model, p's > .05, and therefore we did not interpret further results.

#### 3.2.2. COR activity

The UM model revealed that the proportion of explained variance (ICC) was 0.09 at the participant level and 0.02 at the stimulus level, indicating that 9 % of the total variance in COR activity can be explained by differences between participants and 2 % can be explained by differences between stimuli. The UG model revealed that COR activity significantly decreased over time in response to all infants, t=-3.31, p=.002,  $\beta=-0.09$ . The UG model fit the data significantly better than the UM model ( $\chi 2$  (5) = 486.36, p<.001). The task effect model revealed that COR activity over time did not differ between the baby schema conditions, t=-0.52, p=.61,  $\beta=-0.01$  (see Fig. 2D). The task effect model did fit the data significantly better than the UG model ( $\chi 2$  (5) = 165.31, p<.001). The NURT, *OXT*, and *OXTR* models did not fit the data significantly better than the task effect model, p's >.05, and therefore we did not interpret further results.

#### 3.3. ERP components

An overview of the results of the mixed-effects model analyses for ERP components is presented in Table 3.

<sup>\*</sup> Significant difference in responses at p < .05.

**Table 2**Results of mixed-effects model analyses for facial expression responses.

		ZYG activity						COR activity					
		UM	UG	Task	NURT	OXT	OXTR	UM	UG	Task	NURT	OXT	OXTR
Fixed effects		Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)					
	Intercept	-0.013 (0.011)	-0.013 (0.011)	-0.023 (0.014)	-0.023 (0.014)	-0.023 (0.014)	-0.023 (0.014)	-0.047(0.012)***	-0.047(0.012)***	-0.039 (0.014)**	-0.039 (0.014)**	-0.039 (0.014)**	-0.039 (0.014)**
	Condition			0.022 (0.018)	0.022 (0.018)	0.022 (0.018)	0.022 (0.017)			-0.016 (0.018)	-0.016 (0.018)	-0.016 (0.018)	-0.016 (0.018)
	Time		0.016 (0.007)*	0.004 (0.008)	0.004 (0.008)	0.004 (0.008)	0.004 (0.008)		-0.020 (0.006)**	-0.018 (0.007)*	-0.018 (0.007)*	-0.018 (0.007)*	-0.018 (0.007)*
Conc	dition x Time			0.024 (0.010)*	0.024 (0.010)*	0.024 (0.010)*	0.024 (0.010)*			-0.004 (0.008)	-0.004 (0.008)	-0.004 (0.008)	-0.004 (0.008)
	Nurturance				0.003 (0.011)						-0.003 (0.008)		
Condition	x Nurturance				0.004 (0.011)						-0.012 (0.008)		
Time :	x Nurturance				0.009 (0.005)						-0.002 (0.005)		
Condition x	Time x Nurt				0.000 (0.005)						-0.008 (0.004)		
	OXT					-0.005 (0.011)						-0.002 (0.008)	
Conc	dition x OXT					0.009 (0.011)						0.001 (0.008)	
Time x OXT						0.003 (0.005)						-0.000 (0.005)	
Condition x Time x OXT						0.005 (0.005)						0.001 (0.004)	
	OXTR						0.027 (0.010)**						0.007 (0.008)
Condit	tion x OXTR						-0.018 (0.011)						-0.002 (0.008)
T	ime x OXTR						0.018 (0.005)***						0.011 (0.005)*
Condition x T	ime x OXTR						-0.015 (0.005)**						-0.008 (0.004)
Variance com	ponents	Variance (SD)	Variance (SD)	Variance (SD)	Variance (SD)	Variance (SD)	Variance (SD)	Variance (SD)					
Participant level	Intercept	0.006 (0.075)	0.006 (0.076)	0.008 (0.091)	0.009 (0.091)	0.008 (0.091)	0.008 (0.087)	0.005 (0.071)	0.005 (0.071)	0.005 (0.071)	0.005 (0.071)	0.005 (0.071)	0.005 (0.071)
	Condition			0.008 (0.089)	0.008 (0.089)	0.008 (0.089)	0.008 (0.087)			0.005 (0.069)	0.005 (0.068)	0.005 (0.069)	0.004 (0.069)
	Time slope		0.001 (0.038)	0.001 (0.038)	0.001 (0.037)	0.001 (0.037)	0.001 (0.036)		0.002 (0.042)	0.002 (0.042)	0.002 (0.041)	0.002 (0.042)	0.002 (0.041)
Stimulus level	Intercept	0.001 (0.031)	0.001 (0.031)	0.001 (0.29)	0.001 (0.029	0.001 (0.029)	0.001 (0.029)	0.001 (0.034)	0.001 (0.034)	0.001 (0.033)	0.001 (0.033)	0.001 (0.033)	0.001 (0.033)
	Time slope		0.000 (0.021)	0.000 (0.018)	0.000 (0.018)	0.000 (0.018)	0.000 (0.018)		0.000 (0.015)	0.000 (0.015)	0.000 (0.015)	0.000 (0.015)	0.000 (0.015)
Residual level		0.068 (0.261)	0.066 (0.257)	0.064 (0.253)	0.064 (0.253)	0.064 (0.253)	0.064 (0.253)	0.051 (0.226)	0.049 (0.221)	0.048 (0.218)	0.048 (0.218)	0.048 (0.218)	0.048 (0.218)
Model fit improved?		n/a	✓	✓	×	×	✓	n/a	✓	✓	×	×	×
Fit statistics	AIC	1871.6	1628.0	1433.0	1436.7	1438.0	1423.0	-1231.9	-1708.3	-1863.6	-1862.0	-1856.2	-1862.2
	BIC	1900.7	1693.6	1535.1	1568.0	1569.3	1554.3	.1202.6	-1642.3	-1760.9	-1730.0	-1724.2	-1730.2

Note. Condition: -1 = low baby schema condition, 1 = high baby schema condition; UM = Unconditional Means Model; UG = Unconditional Growth Model; Task = Task effects model; NURT = Nurturance motivation model; OXT = OXT methylation model. p < 0.05, p < 0.01, p < 0.01, p < 0.01.

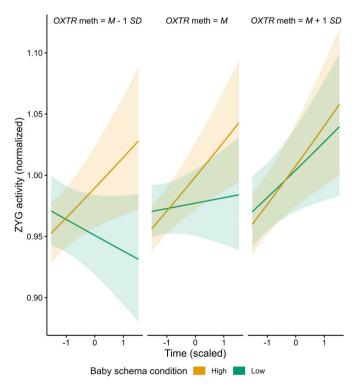


Fig. 3. ZYG Activity Over Time in Response to Infants with High and Low Baby Schema Features for Participants with Low (M - 1 SD), Average (M), and High (M + 1 SD) Levels of OXTR Methylation.

#### 3.3.1. P1

The UM model revealed that the proportion of explained variance (ICC) was 0.69 at the participant level and 0.02 at the electrode level, indicating that 69 % of the total variance in P1 amplitudes can be explained by differences between participants and 2 % can be explained by differences between electrodes. The task effect model revealed that baby schema condition did not associate with P1 amplitudes, p = .53(see Fig. 2E). The task effect model fit the data significantly better than the UM model ( $\chi 2$  (3) = 49.05, p < .001). The OXTR model demonstrated that OXTR methylation levels were significantly associated with P1 amplitudes, t = 3.26, p = .002,  $\beta = 0.32$ . Overall, higher levels of OXTR methylation were associated with higher P1 amplitudes across all stimuli. OXTR methylation did not interact with condition to predict P1 amplitudes, p = .62. The OXTR model fit the data significantly better than the task effect model ( $\chi 2$  (2) = 10.27, p = .006). The NURT and OXT models did not fit the data significantly better than the task effect model, p's > .05, and therefore we did not interpret further results.

#### 3.3.2. N170

The UM model revealed that the proportion of explained variance (ICC) was 0.44 at the participant level and 0.01 at the electrode level, indicating that 44 % of the total variance in N170 amplitudes can be explained by differences between participants and 1 % can be explained by differences between electrodes. Due to singularity issues, we had to drop the random slopes of condition over participant from further model analyses for N170 amplitudes. The resulting task effect, NURT, OXT, and OXTR models did not fit the data significantly better than the UM model, p's > .05, and therefore we did not interpret further results.

#### 3.3.3. P2

The UM model revealed that the proportion of explained variance

**Table 3**Results of mixed-effects model analyses for ERP components.

		P1 amplitudes					N170 amplitude	es			
		UM	Task	NURT	OXT	OXTR	UM	Task	NURT	OXT	OXTR
Fixed effects		Estimate (SE)									
	Intercept	4.82 (0.66)***	4.69 (0.68)***	4.69 (0.68)***	4.69 (0.68)***	4.69 (0.65)***	-5.96(0.78)***	-6.38(0.83)***	-6.38(0.82)***	-6.38(0.83)***	-6.38(0.83)***
	Condition		0.25 (0.39)	0.25 (0.38)	0.25 (0.39)	0.25 (0.40)		0.84 (0.54)	0.84 (0.54)	0.84 (0.54)	0.84 (0.54)
	Nurturance			0.44 (0.55)					-0.91 (0.62)		
Condition x	Nurturance			-0.03 (0.40)					0.04 (0.54)		
OXT					0.61 (0.54)					0.61 (0.62)	
Condi	ition x OXT				-0.55 (0.39)					-0.66 (0.54)	
	OXTR					1.68 (0.52)**					0.40 (0.62)
Conditi	on x OXTR					-0.20 (0.40)					0.03 (0.54)
Variance cor	nponents	Variance (SD)									
Participant level	Intercept	19.22 (4.38)	21.06 (4.59)	20.86 (4.57)	20.68 (4.55)	18.23 (4.27)	18.32 (4.28)	18.38 (4.29)	17.58 (4.19)	18.34 (4.28)	18.21 (4.27)
	Condition		8.19 (2.86)	8.19 (2.86)	7.89 (2.81)	8.15 (2.85)					
Electrode level	Intercept	0.48 (0.69)	0.49 (0.70)	0.50 (0.70)	0.50 (0.70)	0.49 (0.70)	0.60 (0.78)	0.60 (0.77)	0.60 (0.77)	0.60 (0.77)	0.60 (0.77)
Residual level		8.25 (2.87)	5.76 (2.40)	5.76 (2.40)	5.76 (2.40)	5.76 (2.40)	22.45 (4.74)	22.22 (4.71)	22.22 (4.71)	22.07 (4.70)	22.22 (4.71)
Model fit imp	roved?	n/a	✓	×	×	✓	n/a	×	×	×	×
Fit statistics	AIC	2475.2	2432.1	2435.4	2433.7	2425.9	1929.1	1928.7	1930.1	1930.9	1932.1
	BIC	2491.7	2461.0	2472.5	2470.8	2463.0	1944.0	1947.3	1956.1	1957.0	1958.2
		P2 amplitudes					LPP amplitudes	ı			
		UM	Task	NURT	OXT	OXTR	UM	Task	NURT	OXT	OXTR
Fixed effects		Estimate (SE)	Estimate (SE								
	Intercept	6.44 (0.76)***	5.81 (0.76)***	5.81 (0.76)***	5.81 (0.76)***	5.81 (0.76)***	6.37 (0.39)***	5.81 (0.40)***	5.81 (0.40)***	5.81 (0.40)***	5.81 (0.40)**
	Condition		1.25 (0.36)***	1.25 (0.34)***	1.25 (0.36)***	1.25 (0.36)***		1.12 (0.26)***	1.12 (0.25)***	1.12 (0.26)***	1.12 (0.26)**
	Nurturance			-0.38 (0.40)					0.17 (0.33)		
Condition x	Nurturance			1.14 (0.34)***					0.55 (0.25)*		
	OXT				0.07 (0.40)					0.12 (0.33)	
Condi	ition x OXT				-0.43 (0.36)					-0.09 (0.26)	
	OXTR					-0.15 (0.40)					0.09 (0.33)
Conditi	on x OXTR					-0.02 (0.36)					-0.27 (0.26)
Variance cor	nponents	Variance (SD)									
Participant level	Intercept	11.03 (3.32)	10.16 (3.19)	10.01 (3.16)	10.15 (3.19)	10.13 (3.18)	6.34 (2.52)	6.56 (2.56)	6.53 (2.56)	6.54 (2.56)	6.55 (2.56)
	Condition		6.01 (2.45)	4.64 (2.15)	5.83 (2.41)	6.01 (2.45)		2.09 (1.15)	1.79 (1.34)	2.09 (1.44)	2.02 (1.42)
Electrode level	Intercept	2.06 (1.43)	2.07 (1.44)	2.07 (1.44)	2.07 (1.44)	2.07 (1.44)	0.39 (0.62)	0.39 (0.63)	0.39 (0.63)	0.39 (0.63)	0.39 (0.63)
Residual level		11.93 (3.46)	9.82 (3.13)	9.82 (3.13)	9.82 (3.13)	9.82 (3.13)	11.59 (3.40)	10.68 (3.27)	10.68 (3.27)	10.68 (3.27)	10.68 (3.27)
Model fit improved?		n/a	<b>√</b>	<b>√</b>	×	×	n/a	✓	<b>√</b>	×	×
Fit statistics	AIC	4240.4	4180.0	4172.6	4182.6	4183.8	5810.0	5775.2	5772.7	5779.1	5778.1

Note. Condition: -1 = low baby schema condition, 1 = high baby schema condition; UM = Unconditional Means Model; Task = Task effects model; Task = Task

(ICC) was 0.44 at the participant level and 0.08 at the electrode level, indicating that 44 % of the total variance in P2 amplitudes can be explained by differences between participants and 8 % can be explained by differences between electrodes. The task effect model revealed that baby schema condition was significantly associated with P2 amplitudes,  $t=3.45,\,p<.001,\,\beta=0.13.$  P2 amplitudes were higher in response to

infants with high levels of baby schema features (M=7.06, 95 % CI [4.99, 9.13]) compared to infants with low levels of baby schema features (M=5.81, 95 % CI[3.78, 7.85]; see Fig. 2G). The task effect model fit the data significantly better than the UM model ( $\chi 2$  (3) = 66.41, p<.001). The NURT model demonstrated that nurturance motivation scores interacted with baby schema condition to predict P2 amplitudes, t=

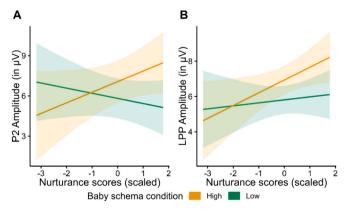
3.49, p<.001,  $\beta=0.17$ . For participants scoring high on nurturance motivation (M+1 SD), P2 amplitudes were significantly higher in response to infants with high levels of baby schema features compared to infants with low levels of baby schema features ( $M\Delta=2.42$ , 95 % CI [1.18, 3.67]), t=5.10, p<.001. For participants with low nurturance motivation scores (M-1 SD), P2 amplitudes were not significantly different between baby schema conditions ( $M\Delta=0.08$ , 95 % CI[-1.17, 1.32]), t=0.16, p=.99 (see Fig. 4A). The NURT model fit the data significantly better than the task effect model ( $\chi 2$  (2) = 11.40, p=.003). The OXT and OXTR models did not fit the data significantly better than the task effect model, p's >.05, and therefore we did not interpret further results.

#### 3.3.4. LPP

The UM model revealed that the proportion of explained variance (ICC) was 0.35 at the participant level and 0.02 at the electrode level, indicating that 35 % of the total variance in LPP amplitudes can be explained by differences between participants and 2 % can be explained by differences between electrodes. The task effect model revealed that baby schema condition was significantly associated with LPP amplitudes, t = 4.32, p < .001,  $\beta = 0.13$ . LPP amplitudes were higher in response to infants with high levels of baby schema features (M = 6.93, 95 % CI[5.96, 7.90]) compared to infants with low levels of baby schema features (M = 5.81, 95 % CI[4.86, 6.75]; see Fig. 2H). The task effect model fit the data significantly better than the UM model ( $\chi 2$  (3) = 40.79, p < .001). The NURT model demonstrated that nurturance motivation scores interacted with baby schema condition to predict LPP amplitudes, t = 2.20, p = .03,  $\beta = 0.09$ . For participants scoring high on nurturance motivation (M + 1 SD), LPP amplitudes were significantly higher in response to infants with high levels of baby schema features compared to infants with low levels of baby schema features ( $M\Delta$  = 1.68, 95 % CI[0.74, 2.61]), t = 4.70, p < .001. For participants with low nurturance motivation scores (M - 1 SD), LPP amplitudes were not significantly different between baby schema conditions ( $M\Delta = 0.57, 95$ % CI[-0.37, 1.51]), t = 1.59, p = .39 (see Fig. 4B). The NURT model fit the data significantly better than the task effect model ( $\chi 2$  (2) = 6.55, p= .04). The OXT and OXTR models did not fit the data significantly better than the task effect model, p's > .05, and therefore we did not interpret further results.

#### 3.4. Associations between response measures

We conducted post-hoc exploratory analyses to assess associations between outcome measures. EMG activity was averaged per participant for each trial, followed by linear mixed models with random effects of participant and image to examine associations with subjective ratings. These associations were not explored for our ERP outcome measures,



**Fig. 4.** Associations Between Nurturance Motivation and A) P2 Amplitudes in Response to Infants with High and Low Baby Schema Features; and B) LPP Amplitudes in Response to Infants with High and Low Baby Schema Features.

since data was only available averaged per condition (rather than per trial) due to the nature of ERP analyses. Higher cuteness ratings were significantly associated with higher care motivation ratings ( $\beta=0.77$ ), stronger ZYG activity ( $\beta=0.06$ ), and decreased COR activity ( $\beta=-0.06$ ). Higher care motivation ratings were also significantly associated with stronger ZYG activity ( $\beta=0.04$ ; see Table 4).

#### 4. Discussion

In this study, our aim was to enhance the understanding of the psychophysiological processing of baby schema features. We specifically focused on moderating effects of nurturance motivation and oxytocin system gene methylation levels, and expected that increased nurturance motivation and decreased methylation of the oxytocin system genes would associate with enhanced sensitivity to variations in baby schema features.

First of all, our findings demonstrated distinct responses to high compared to low levels of baby schema features. In line with previous research, infants with more pronounced baby schema features were perceived as cuter and participants indicated greater motivation to take care of them (e.g., Almanza-Sepúlveda et al., 2018; Bos et al., 2018; Glocker et al., 2009a). Furthermore, our results indicated that strongly pronounced baby schema features elicited stronger automatic positive facial expressions, such as smiles, than weakly pronounced baby schema features. This is in contrast with previous research where no distinction between conditions was found and instead smiling responses were triggered in response to infants in general (Hildebrandt and Fitzgerald, 1978; Löwenbrück and Hess, 2021). While our findings also indicate that infants overall trigger a smiling response, our incorporation of the time course of facial expressions may have increased our sensitivity to discern differential responses between conditions (Bos et al., 2016; Tassinary and Cacioppo, 1992; van Boxtel, 2010). Moreover, these differential responses align with prior findings, underscoring the tendency for rewarding facial stimuli to elicit stronger automatic positive facial expressions (Sims et al., 2012). Further support is provided by significant associations within our data between subjective ratings and automatic facial responses; infants that were rated as cuter also elicited stronger smiling responses. Baby schema features were, however, not associated with negative facial expressions. While more pronounced baby schema features were previously associated with a reduction in sneering expressions (linked to disgust; Löwenbrück and Hess, 2021), our findings suggest that the corrugator supercilii—associated with frowning—relaxes in response to infant faces overall. At the same time, irrespective of baby schema condition, infants perceived as cuter did induce a lower level of frowning responses.

Additionally, both P2 and LPP amplitudes were higher in response to more pronounced baby schema features. The findings captured by the P2 component potentially signify that more pronounced baby schema features are perceived as more typical for infant faces (Bos et al., 2018). Indeed, less typical faces elicit decreased P2 amplitudes (Schweinberger and Neumann, 2016). This typicality effect is further suggested to account for diminished P2 amplitudes evoked by infant faces with a cleft lip/palate (Hahn et al., 2023; Huffmeijer et al., 2018). On the other hand, LPP amplitudes are reflective of sustained attention towards salient stimuli (Schindler and Bublatzky, 2020). This supports the

**Table 4**Associations between subjective ratings and EMG activity.

	Care motivation rating	COR activity	ZYG activity		
	Estimate (SE)	Estimate (SE)	Estimate (SE)		
Cuteness rating ZYG activity COR activity	0.73 (0.02)*** 0.48 (0.18)** -0.29 (0.23)	-0.79 (0.24)** -0.02 (0.02)	0.57 (0.19)**		

*Note.* EMG activity is averaged within trials during stimulus presentation. \* p < .05, \*\*p < .01, \*\*\* p < .001.

suggestion that more pronounced baby schema features also tend to be more salient. Notably, no differences were found in the P1 and N170 amplitudes associated with the early configurational processing of facial features. Effects of P1 are highly variable and prior studies report inconsistent findings, while N170 effects might be closer associated with emotional information in faces (Schindler and Bublatzky, 2020). Together, these findings suggest that initial stages of facial processing may not be affected by baby schema features, while differences do appear during subsequent processing stages suggesting a greater saliency of more pronounced baby schema features.

Importantly, we demonstrated that individual characteristics may explain sensitivity towards baby schema. First, women with stronger nurturance motivation showed a greater differentiation in P2 and LPP amplitudes when perceiving infants with varying levels of baby schema features. This aligns with previous findings demonstrating that women with strong prosocial and maternal tendencies exhibited enhanced sensitivity to differences in baby schema features (Hahn et al., 2015; Sherman et al., 2013). Stronger nurturance motivation was additionally associated with higher subjective ratings of cuteness and care motivation, regardless of baby schema features. Similarly, Hahn et al. (2015) demonstrated that strong maternal tendencies were associated with greater sensitivity to the reward value of infant faces with more pronounced baby schema features, while such effects were not found for subjective cuteness ratings. Yet, previous studies demonstrated no discernible association between nurturance motivation and neural responses to baby schema features (Bos et al., 2018; Endendijk et al., 2020, 2018). Since these studies were carried out with limited sample sizes (n's  $\leq$  33), this likely decreased the power to detect individual differences in sensitivity to baby schema features.

Moreover, participants with low levels of OXTR methylation were more sensitive to varying levels of baby schema features, as demonstrated by differences in smiling responses to infants with high and low schema features. This nuanced differentiation in responses contrasted with the relatively consistent smiling responses observed among individuals with high OXTR methylation levels. Previous administration studies provided inconsistent findings regarding how oxytocin might increase sensitivity to baby schema features. One study showed heightened neural responses after oxytocin administration that was specific to high baby schema infants (Holtfrerich et al., 2018), while another observed a decrease in neural responses to all infants irrespective of baby schema features (Bos et al., 2018). These disparities might be due to context-dependent effects, small samples sizes, or task differences (Carter et al., 2020). Also, recent administration studies highlight that effects of oxytocin may not follow linear dose responses, and furthermore, these effect may vary depending on sex (Borland et al., 2019; Quintana et al., 2021). Since sensitivity to oxytocin and oxytocin availability is influenced through methylation of associated genes, gene methylation may serve as a useful proxy for oxytocin system functioning to examine interactions with brain function and behavior (Carter et al., 2020; Kraaijenvanger et al., 2019). Our findings not only align with the increasing body of evidence that oxytocin system gene methylation may inhibit sensitivity to socially salient stimuli in general (see e.g., Haas et al., 2016; Krol et al., 2019; Puglia et al., 2015; Spencer et al., 2022), but also emphasize that this effect may extend to cues specifically relevant to infant care. While we recognize the need for replicating our selective effect for OXTR methylation, our methods struck a balance between minimizing Type I errors and remaining sensitive to effects aligned with previous research, generating hypotheses for future investigations.

Notably, though, methylation patterns may interact with peripheral oxytocin concentrations and genotype variation to predict behavioral outcomes (see, e.g., Bell et al., 2015; Ebner et al., 2019; Rijlaarsdam et al., 2017). Additionally, the oxytocin system functions as an integrated system with the vasopressin system, and many other molecules, including dopamine, serotonin, GABA, and opioids, interact with these systems to influence behavior (Carter et al., 2020). An integration of

further related biological measures, including peripheral oxytocin concentrations and genotype variation, in large research samples will aid our future understanding of this complex interplay of oxytocin system functioning and behavioral outcomes. Furthermore, we measured peripheral methylation patterns from saliva samples to examine behavioral effects likely stemming from differences in oxytocin signaling pathways in the brain (Spencer et al., 2022). Studies suggest that gene methylation patterns in saliva can serve as useful proxies for brain tissue methylation (Braun et al., 2019; Smith et al., 2015). Also, *OXTR* methylation levels in saliva correlated significantly with those in blood samples, and blood *OXTR* methylation was linked to gene expression in brain tissue (Gregory et al., 2009; Krol et al., 2019; Perkeybile et al., 2019; Puglia et al., 2020). Consequently, salivary methylation patterns may serve as a reliable non-invasive measure for studying behavioral effects related to brain epigenetics.

Our research shows that individuals with reduced nurturance motivation and increased *OXTR* methylation levels show similar responses towards all infants. On the one hand this may seem beneficial, facilitating care responses towards infants regardless of visual characteristics. Yet, decreased sensitivity towards visual characteristics may interfere with one's ability to quickly detect and interpret children's signals and cues (Vuoriainen et al., 2022). However, across all measures of individual differences, we did not show any indications of varying sensitivity to baby schema features as measured with subjective ratings. This divergence between automatic neurophysiological responses and subjective ratings underscores a nuanced relation between individual characteristics and the processing of baby schema features.

Crucially, we must be careful when attempting to infer the implications of sensitivity to baby schema features for actual caregiving behaviors, since there is still very limited evidence to support this connection. Preliminary evidence suggests a connection between neural responses, specifically LPP amplitudes in response to child and infant faces, and parenting quality. However, these findings are largely derived from underpowered studies (Endendijk et al., 2018; Vuoriainen et al., 2022). Further research is necessary to establish a conclusive link between neurophysiological processing of baby schema features and realworld care responses. Furthermore, of course, interactions with infants do not solely rely on visual morphological characteristics. For instance, both positive and negative auditory cues-such as laughter and crying-along with emotional expressions elicit enhanced and faster responses towards infants (Kringelbach et al., 2016). Additionally, infant and child temperament can influence cuteness perceptions and automatic facial expressions (Bos et al., 2016; Parsons et al., 2014). Since baby schema features are one of numerous cues that influence responses to infants, the effects of these features are likely small and this could potentially account for the variability in findings (Kringelbach et al., 2016).

Individual characteristics of research samples may have further compromised the pursuit of finding general patterns in baby schema effects. Our current study was conducted among a community sample of nulliparous females and found that such individual characteristics play a significant role in predicting outcomes. Research so far has mainly focused on specific subject groups, that is, either undergraduate students-mainly nulliparous females-or mothers, which raises questions about how well findings apply to a wider population. Numerous studies have consistently shown that women tend to be more sensitive to infants than men (Berman, 1980; Fullard and Reiling, 1976; Glocker et al., 2009a; Hildebrandt and Fitzgerald, 1978). Also, young women were more sensitive to variations in infant cuteness than post-menopausal women and men, with effects possibly driven by female reproductive hormones (Sprengelmeyer et al., 2009). As such, further research is necessary to elucidate plausible gender differences in sensitivity to baby schema features. Additionally, since our sample was nulliparous, we must consider how results may extend to parents. In a society where infants depend on a range of caretakers, including grandparents and childcare workers, it could be expected that humans are in general

predisposed to respond to infant signals and cues, including baby schema features (Hrdy, 2007). Indeed, baby schema effects—assessed with subjective ratings—have been demonstrated for both parents and non-parents (Bos et al., 2018; Endendijk et al., 2018; Hahn et al., 2015; Löwenbrück and Hess, 2021). Yet, neuroimaging studies revealed that parents exhibit stronger responses to infants compared to non-parents, as well as particular stronger responses to their own compared to unfamiliar infants (Vuoriainen et al., 2022). Accumulating evidence suggest that both pregnancy and cumulative experiences in infant care may profoundly impact parent's sensitivity to infant cues, likely due to structural changes in the brain and neural tuning (Abraham et al., 2014; Dudek et al., 2020; Hoekzema et al., 2017; Kim et al., 2014; Parsons et al., 2017). Notably, the oxytocin system undergoes corresponding physical transformations in response to pivotal experiences, such as pregnancy, birth, and breastfeeding, which include epigenetic modifications of associated genes (Carter et al., 2020). The intricate interplay of pregnancy and parenting-parallel structural alterations in brain regions and the oxytocin system—and heightened neural responsiveness to infants highlights the importance of continued research with larger and more diverse samples, including longitudinal examinations of transitions into parenthood.

#### 5. Conclusion

In the current study, we demonstrated that nulliparous women respond distinctively to infants with varying levels of baby schema features. Furthermore, individual differences significantly predicted baby schema effects. Specifically, individuals with low *OXTR* methylation and high nurturance motivation showed enhanced differentiation in automatic neurophysiological responses to infants with varying levels of baby schema features. These findings highlight the importance of considering individual differences in continued research to further understand the complexities of sensitivity to child cues, including baby schema features, which will improve our understanding of the intricate neurobiological system that forms the basis of caregiving behavior.

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#### CRediT authorship contribution statement

Hannah Spencer: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Data curation. Franca H. Parianen Lesemann: Writing – review & editing, Methodology, Formal analysis. Renate S.M. Buisman: Writing – review & editing, Supervision, Formal analysis. Eline J. Kraaijenvanger: Writing – review & editing, Investigation. Susan Branje: Writing – review & editing, Resources, Funding acquisition, Conceptualization. Marco P.M. Boks: Writing – review & editing, Resources, Funding acquisition, Conceptualization. Peter A. Bos: Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

### Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT 3.5 to improve readability and language at the sentence level. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.yhbeh.2024.105595.

#### References

- Abraham, E., Hendler, T., Shapira-Lichter, I., Kanat-Maymon, Y., Zagoory-Sharon, O., Feldman, R., 2014. Father's brain is sensitive to childcare experiences. Proc. Natl. Acad. Sci. U. S. A. 111, 9792–9797. https://doi.org/10.1073/pnas.1402569111.
- Ainsworth, M.D.S., 1969. Maternal sensitivity scales, the Baltimore longitudinal project, 1969. Johns Hopkins Univ. 1–15.
- Alley, T.R., 1981. Head shape and the perception of cuteness. Dev. Psychol. 17, 650–654. https://doi.org/10.1037/0012-1649.17.5.650.
- Almanza-Sepúlveda, M.L., Dudin, A., Wonch, K.E., Steiner, M., Feinberg, D.R., Fleming, A.S., Hall, G.B., 2018. Exploring the morphological and emotional correlates of infant cuteness. Infant Behav. Dev. 53, 90–100. https://doi.org/ 10.1016/j.infbeh.2018.08.001.
- Aragón, O.R., Clark, M.S., Dyer, R.L., Bargh, J.A., 2015. Dimorphous expressions of positive emotion: displays of both care and aggression in response to cute stimuli. Psychol. Sci. 26, 259–273. https://doi.org/10.1177/0956797614561044.
- Barr, D.J., Levy, R., Scheepers, C., Tily, H.J., 2013. Random effects structure for confirmatory hypothesis testing: keep it maximal. J. Mem. Lang. 68, 255–278. https://doi.org/10.1016/j.jml.2012.11.001.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.
- Bell, A.F., Carter, C.S., Steer, C.D., Golding, J., Davis, J.M., Steffen, A.D., Rubin, L.H., Lillard, T.S., Gregory, S.P., Harris, J.C., Connelly, J.J., 2015. Interaction between oxytocin receptor DNA methylation and genotype is associated with risk of postpartum depression in women without depression in pregnancy. Front. Genet. 6, 243. https://doi.org/10.3389/fgene.2015.00243.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. R. Stat. Soc. Ser. B 57, 289–300. https:// doi.org/10.1111/j.2517-6161.1995.tb02031.x.
- Berman, P.W., 1980. Are women more responsive than men to the young? A review of developmental and situational variables. Psychol. Bull. 88, 668–695. https://doi. org/10.1037/0033-2909.88.3.668.
- Borgi, M., Cogliati-Dezza, I., Brelsford, V., Meints, K., Cirulli, F., 2014. Baby schema in human and animal faces induces cuteness perception and gaze allocation in children. Front. Psychol. 5, 1–12. https://doi.org/10.3389/fpsyg.2014.00411.
- Borland, J.M., Rilling, J.K., Frantz, K.J., Albers, H.E., 2019. Sex-dependent regulation of social reward by oxytocin: an inverted U hypothesis. Neuropsychopharmacology 44, 97–110. https://doi.org/10.1038/s41386-018-0129-2.
- Bos, P.A., Jap-Tjong, N., Spencer, H., Hofman, D., 2016. Social context modulates facial imitation of Children's emotional expressions. PloS One 11, e0167991. https://doi. org/10.1371/journal.pone.0167991.
- Bos, P.A., Spencer, H., Montoya, E.R., 2018. Oxytocin reduces neural activation in response to infant faces in nulliparous young women. Soc. Cogn. Affect. Neurosci. 13, 1099–1109. https://doi.org/10.1093/scan/nsy080.
- Branje, S., Meeus, W.H.J., 2018. Research on adolescent development and relationships (young cohort). DANS. https://doi.org/10.17026/dans-zrb-v5wp.
- Braun, P.R., Han, S., Hing, B., Nagahama, Y., Gaul, L.N., Heinzman, J.T., Grossbach, A.J., Close, L., Dlouhy, B.J., Howard, M.A., Kawasaki, H., Potash, J.B., Shinozaki, G., 2019. Genome-wide DNA methylation comparison between live human brain and peripheral tissues within individuals. Transl. Psychiatry 9. https://doi.org/10.1038/s41398-019-0376-y.
- Buckels, E.E., Beall, A.T., Hofer, M.K., Lin, E.Y., Zhou, Z., Schaller, M., 2015. Individual differences in activation of the parental care motivational system: assessment, prediction, and implications. J. Pers. Soc. Psychol. 108, 1–18. https://doi.org/10.1037/pspp0000023.
- Carter, C.S., Kenkel, W.M., Maclean, E.L., Wilson, S.R., Perkeybile, A.M., Yee, J.R., Ferris, C.F., Nazarloo, H.P., Porges, S.W., Davis, J.M., Connelly, J.J., Kingsbury, M. A., 2020. Is oxytocin "nature's medicine"? Pharmacol. Rev. 72, 829–861. https://doi.org/10.1124/pr.120.019398.
- Cohen, J., 1992. A power primer. Psychol. Bull. 112, 155–159. https://doi.org/10.1037/0033-2909.112.1.155.
- Dudek, J., Colasante, T., Zuffianò, A., Haley, D.W., 2020. Changes in cortical sensitivity to infant facial cues from pregnancy to motherhood predict mother-infant bonding. Child Dev. 91, e198–e217. doi:https://doi.org/10.1111/cdev.13182.
- Ebner, N.C., Lin, T., Muradoglu, M., Weir, D.H., Plasencia, G.M., Lillard, T.S., Pournajafi-Nazarloo, H., Cohen, R.A., Sue Carter, C., Connelly, J.J., 2019. Associations between oxytocin receptor gene (OXTR) methylation, plasma oxytocin, and attachment across adulthood. Int. J. Psychophysiol. 136, 22–32. https://doi.org/10.1016/j.ijpsycho.2018.01.008.

- Endendijk, J.J., Spencer, H., van Baar, A.L., Bos, P.A., 2018. Mothers' neural responses to infant faces are associated with activation of the maternal care system and observed intrusiveness with their own child. Cogn. Affect. Behav. Neurosci. 18, 609–621. https://doi.org/10.3758/s13415-018-0592-6.
- Endendijk, J.J., Smit, A.K., van Baar, A.L., Bos, P.A., Bos, P.A., 2020. What a cute baby! Preliminary evidence from a fMRI study for the association between mothers' neural responses to infant faces and activation of the parental care system. Neuropsychologia 143, 107493. https://doi.org/10.1016/j.neuropsychologia.2020.107493.
- Feinman, S., 1982. Social referencing in infancy. Merrill. Palmer. Q. 28, 445–470. Feldman, R., 2017. The neurobiology of human attachments human attachments
- Feldman, R., 2017. The neurobiology of human attachments human attachments throughout life share underlying neurobiology. Trends Cogn. Sci. 21, 80–99. https:// doi.org/10.1016/j.tics.2016.11.007.
- Feldman, R., Weller, A., Zagoory-Sharon, O., Levine, A., 2007. Evidence for a Neuroendocrinological Foundation of Human Affiliation. Psychol. Sci. 18, 965–970. https://doi.org/10.1111/j.1467-9280.2007.02010.x.
- Fridlund, A.J., Cacioppo, J.T., 1986. Guidelines for human Electromyographic research. Psychophysiology 23, 567–589. https://doi.org/10.1111/j.1469-8986.1986.
- Fullard, W., Reiling, A.M., 1976. An Investigation of Lorenz's "Babyness." Child Dev. 47, 1191–1193. doi:https://doi.org/10.1111/j.1467-8624.1976.tb02306.x.
- Glocker, M.L., Langleben, D.D., Ruparel, K., Loughead, J.W., Gur, R.C., Sachser, N., 2009a. Baby Schema in infant faces induces cuteness perception and motivation for caretaking in adults. Ethology 115, 257–263. https://doi.org/10.1111/j.1439-0310.2008.01603.x.
- Glocker, M.L., Langleben, D.D., Ruparel, K., Loughead, J.W., Valdez, J.N., Griffin, M.D., Sachser, N., Gur, R.C., 2009b. Baby schema modulates the brain reward system in nulliparous women. Proc. Natl. Acad. Sci. 106, 9115–9119. https://doi.org/ 10.1073/pnas.0811620106.
- Gratton, G., Coles, M.G., Donchin, E., 1983. A new method for off-line removal of ocular artifact. Electroencephalogr. Clin. Neurophysiol. 55 (4), 468–484.
- Gregory, S.G., Connelly, J.J., Towers, A.J., Johnson, J., Biscocho, D., Markunas, C.A., Lintas, C., Abramson, R.K., Wright, H.H., Ellis, P., Persico, A., Pericak-Vance, M.A., 2009. Genomic and epigenetic evidence for oxytocin receptor deficiency in autism. BMC Med. 7 https://doi.org/10.1186/1741-7015-7-62.
- Haas, B.W., Filkowski, M.M., Cochran, R.N., Denison, L., Ishak, A., Nishitani, S., Smith, A.K., 2016. Epigenetic modification of OXT and human sociability. Proc. Natl. Acad. Sci. 113, E3816–E3823. https://doi.org/10.1073/pnas.1602809113.
- Hahn, A.C., Perrett, D.I., 2014. Neural and behavioral responses to attractiveness in adult and infant faces. Neurosci. Biobehav. Rev. 46, 591–603. https://doi.org/10.1016/j. neubjorev.2014.08.015.
- Hahn, A.C., Xiao, D., Sprengelmeyer, R., Perrett, D.I., 2013. Gender differences in the incentive salience of adult and infant faces. Q. J. Exp. Psychol. 66, 200–208. https:// doi.org/10.1080/17470218.2012.705860.
- Hahn, A.C., Debruine, L.M., Jones, B.C., 2015. Reported maternal tendencies predict the reward value of infant facial cuteness, but not cuteness detection. Biol. Lett. 11, 20140978 https://doi.org/10.1098/rsbl.2014.0978.
- Hahn, A.C., Symons, L.A., Kredel, T., Hanson, K., Hodgson, L., Schiavone, L., Jantzen, K. J.J., 2016. Early and late event-related potentials are modulated by infant and adult faces of high and low attractiveness. Soc. Neurosci. 11, 207–220. https://doi.org/10.1080/17470919.2015.1059361.
- Hahn, A.C., Riedelsheimer, J., Royer, Z., Frederick, J., Kee, R., Crimmins, R., Huber, B., Harris, D., Jantzen, K., 2023. Effects of cleft lip on visual scanning and neural processing of infant faces. Authorea 1–17. https://doi.org/10.22541/ au 168455102 24287447/v1
- Hildebrandt, K.A., Fitzgerald, H.E., 1978. Adults' responses to infants varying in perceived cuteness. Behav. Processes 3, 159–172. https://doi.org/10.1016/0376-6357(78)00042-6
- Hildebrandt, K.A., Fitzgerald, H.E., 1979. Facial feature determinants of perceived infant attractiveness. Infant Behav. Dev. 2, 329–339. https://doi.org/10.1016/S0163-6383 (79)80043-0.
- Hoekzema, E., Barba-Müller, E., Pozzobon, C., Picado, M., Lucco, F., García-García, D., Soliva, J.C., Tobeña, A., Desco, M., Crone, E.A., Ballesteros, A., Carmona, S., Vilarroya, O., 2017. Pregnancy leads to long-lasting changes in human brain structure. Nat. Neurosci. 20, 287–296. https://doi.org/10.1038/nn.4458.
- Hofer, M.K., Buckels, E.E., White, C.J.M., Beall, A.T., Schaller, M., 2018. Individual differences in activation of the parental care motivational system: an empirical distinction between protection and nurturance. Soc. Psychol. Personal. Sci. 9, 907–916. https://doi.org/10.1177/1948550617728994.
- Holtfrerich, S.K.C., Pfister, R., El Gammal, A.T., Bellon, E., Diekhof, E.K., 2018. Endogenous testosterone and exogenous oxytocin influence the response to baby schema in the female brain. Sci. Rep. 8, 1–10. https://doi.org/10.1038/s41598-018-2600.4
- Hrdy, Sarah Blaffer, 2007. Evolutionary context of human development: The cooperative breeding model. In: Ahnert, L., Grossmann, K.E., Hrdy, S.B., Lamb, M.E., Porges, S. W., Sachser, N. (Eds.), Carter, C.S. Oxford University PressNew York, Family Relationships, pp. 39–68. https://doi.org/10.1093/acprof:oso/ 9780195320510.003.0003.
- Huffmeijer, R., Eilander, J., Mileva-Seitz, V.R., Rippe, R.C.A., 2018. Changes in face-specific neural processing explain reduced cuteness and approachability of infants with cleft lip. Soc. Neurosci. 13, 439–450. https://doi.org/10.1080/17470919.2017.1340336.
- Kim, P., Rigo, P., Mayes, L.C., Feldman, R., Leckman, J.F., Swain, J.E., 2014. Neural plasticity in fathers of human infants. Soc. Neurosci. 9, 522–535. https://doi.org/ 10.1080/17470919.2014.933713.

- Kraaijenvanger, E.J., Hofman, D., Bos, P.A., 2017. A neuroendocrine account of facial mimicry and its dynamic modulation. Neurosci. Biobehav. Rev. 77, 98–106. https:// doi.org/10.1016/j.neubiorev.2017.03.006.
- Kraaijenvanger, E.J., He, Y., Spencer, H., Smith, A.K., Bos, P.A., Boks, M.P.M., 2019. Epigenetic variability in the human oxytocin receptor (OXTR) gene: a possible pathway from early life experiences to psychopathologies. Neurosci. Biobehav. Rev. 96, 127–142. https://doi.org/10.1016/j.neubiorev.2018.11.016.
- Kringelbach, M.L., Stark, E.A., Alexander, C., Bornstein, M.H., Stein, A., 2016. On cuteness: unlocking the parental brain and beyond. Trends Cogn. Sci. 20, 545–558. https://doi.org/10.1016/j.tics.2016.05.003.
- Krol, K.M., Puglia, M.H., Morris, J.P., Connelly, J.J., Grossmann, T., 2019. Epigenetic modification of the oxytocin receptor gene is associated with emotion processing in the infant brain. Dev. Cogn. Neurosci. 37, 100648 https://doi.org/10.1016/j. dcn.2019.100648.
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. Imer test package: tests in linear mixed effects models. J. Stat. Softw. 82 (13), 1–26. https://doi.org/10.18637/ jss.v082.i13.
- Lang, P.J., Greenwald, M.K., Bradley, M.M., Hamm, A.O., 1993. Looking at pictures: affective, facial, visceral, and behavioral reactions. Psychophysiology 30, 261–273. https://doi.org/10.1111/j.1469-8986.1993.tb03352.x.
- Langlois, J.H., Ritter, J.M., Casey, R.J., Sawin, D.B., 1995. Infant attractiveness predicts maternal behaviors and attitudes. Dev. Psychol. 31, 464–472. https://doi.org/ 10.1037/0012-1649.31.3.464.
- Lee, S., Lee, D.K., 2018. What is the proper way to apply the multiple comparison test? Korean. J. Anesthesiol. 71, 353–360. https://doi.org/10.4097/kja.d.18.00242.
- Lenth, R.V., 2023. emmeans: Estimated Marginal Means, aka Least-Squares Means. In: R package version 1.8.5. https://rylenth.github.io/emmeans/.
- Lorenz, K., 1943. Die angeborenen Formen möglicher Erfahrung. Z. Tierpsychol. 5, 235–409. https://doi.org/10.1111/j.1439-0310.1943.tb00655.x.
- Löwenbrück, F., Hess, U., 2021. Not all "caregivers" are created equal: liking, caring and facial expression responses to the baby schema as a function of parenthood and testosterone. Biol. Psychol. 163 https://doi.org/10.1016/j.biopsycho.2021.108120.
- Nittono, H., Ihara, N., 2017. Psychophysiological responses to kawaii pictures with or without baby Schema. SAGE Open 7, 1–2. https://doi.org/10.1177/
- Parianen Lesemann, F.H., Spencer, H., Montoya, E.R., Kraaijenvanger, E.J., He, Y., Branje, S., Boks, M.P., Bos, P.A., 2020. Methylation of oxytocin related genes and early life trauma together shape the N170 response to human faces. Eur. Neuropsychopharmacol. 39, 19–28. https://doi.org/10.1016/j. euroneuro.2020.08.008.
- Parsons, C.E., Young, K.S., Bhandari, R., van Ijzendoorn, M.H., Bakermans-Kranenburg, M.J., Stein, A., Kringelbach, M.L., 2014. The bonnie baby: experimentally manipulated temperament affects perceived cuteness and motivation to view infant faces. Dev. Sci. 17, 257–269. https://doi.org/10.1111/desc.12112.
- Parsons, C.E., Young, K.S., Petersen, M.V., Jegindoe Elmholdt, E.-M., Vuust, P., Stein, A., Kringelbach, M.L., 2017. Duration of motherhood has incremental effects on mothers' neural processing of infant vocal cues: a neuroimaging study of women. Sci. Rep. 7, 1727. https://doi.org/10.1038/s41598-017-01776-3.
- Perkeybile, A.M., Carter, C.S.S., Wroblewski, K.L., Puglia, M.H., Kenkel, W.M., Lillard, T. S., Karaoli, T., Gregory, S.G., Mohammadi, N., Epstein, L., Bales, K.L., Connelly, J.J., 2019. Early nurture epigenetically tunes the oxytocin receptor. Psychoneuroendocrinology 99, 128–136. https://doi.org/10.1016/j.psynguen.2018.08.037.
- Puglia, M.H., Lillard, T.S.T., Morris, J., Connelly, J., Posner, M.I., 2015. Epigenetic modification of the oxytocin receptor gene influences the perception of anger and fear in the human brain. Proc. Natl. Acad. Sci. U. S. A. 112, 3308–3313. https://doi. org/10.1073/pnas.1422096112.
- Puglia, M.H., Krol, K.M., Missana, M., Williams, C.L., Lillard, T.S., Morris, J.P., Connelly, J.J., Grossmann, T., 2020. Epigenetic tuning of brain signal entropy in emergent human social behavior. BMC Med. 18, 244. https://doi.org/10.1186/ s12916-020-01683-x.
- Quintana, D.S., Lischke, A., Grace, S., Scheele, D., Ma, Y., Becker, B., 2021. Advances in the field of intranasal oxytocin research: lessons learned and future directions for clinical research. Mol. Psychiatry 26, 80–91. https://doi.org/10.1038/s41380-020-00864-7
- Riem, M.M.E., Bakermans-Kranenburg, M.J., Pieper, S., Tops, M., Boksem, M.A.S., Vermeiren, R.R.J.M., van IJzendoorn, M.H., Rombouts, S.A.R.B., 2011. Oxytocin modulates amygdala, insula, and inferior frontal gyrus responses to infant crying: a randomized controlled trial. Biol. Psychiatry 70, 291–297. doi:https://doi.org/10 .1016/j.biopsych.2011.02.006.
- Rijlaarsdam, J., van IJzendoorn, M.H., Verhulst, F.C., Jaddoe, V.W., Felix, J.F.,
  Tiemeier, H., Bakermans-Kranenburg, M.J., 2017. Prenatal stress exposure, oxytocin
  receptor gene (OXTR) methylation, and child autistic traits: the moderating role of
  OXTR rs53576 genotype. Autism Res. 10, 430–438. https://doi.org/10.1002/
- Schindler, S., Bublatzky, F., 2020. Attention and emotion: an integrative review of emotional face processing as a function of attention. Cortex 130, 362–386. https:// doi.org/10.1016/j.cortex.2020.06.010.
- Schweinberger, S.R., Neumann, M.F., 2016. Repetition effects in human ERPs to faces. Cortex 80, 141–153. https://doi.org/10.1016/j.cortex.2015.11.001.
- Sherman, G.D., Haidt, J., Iyer, R., Coan, J.A., 2013. Individual differences in the physical embodiment of care: Prosocially oriented women respond to cuteness by becoming more physically careful. Emotion 13, 151–158. https://doi.org/10.1037/a0029259.
- Sims, T.B., Van Reekum, C.M., Johnstone, T., Chakrabarti, B., 2012. How reward modulates mimicry: EMG evidence of greater facial mimicry of more rewarding

- happy faces. Psychophysiology 49, 998–1004. https://doi.org/10.1111/j.1469-8086.2012.01377.x
- Smith, A.K., Kilaru, V., Klengel, T., Mercer, K.B., Bradley, B., Conneely, K.N., Ressler, K. J., Binder, E.B., 2015. DNA extracted from saliva for methylation studies of psychiatric traits: evidence tissue specificity and relatedness to brain. Am. J. Med. Genet. Part B Neuropsychiatr. Genet. 168, 36–44. https://doi.org/10.1002/ajmg. b 32278
- Spencer, H., Parianen Lesemann, F.H., Kraaijenvanger, E.J., Overbeek, G., Montoya, E.R., Branje, S., Boks, M.P.M., Bos, P.A., 2022. Oxytocin system gene methylation is associated with empathic responses towards children. Psychoneuroendocrinology 137, 105629. https://doi.org/10.1016/j.psyneuen.2021.105629.
- Sprengelmeyer, R., Perrett, D.I., Fagan, E.C., Cornwell, R.E., Lobmaier, J.S., Sprengelmeyer, A., Aasheim, H.B.M.M., Black, I.M., Cameron, L.M., Crow, S., Milne, N., Rhodes, E.C., Young, A.W., 2009. The cutest little baby face: a hormonal link to sensitivity to cuteness in infant faces. Psychol. Sci. 20, 149–154. https://doi. org/10.1111/j.1467-9280.2009.02272.x.
- Sternglanz, S.H., Gray, J.L., Murakami, M., 1977. Adult preferences for infantile facial features: an ethological approach. Anim. Behav. 25, 108–115. https://doi.org/ 10.1016/0003-3472(77)90072-0.
- Strathearn, L., Fonagy, P., Amico, J., Read Montague, P., 2009. Adult attachment predicts maternal brain and oxytocin response to infant cues. Neuropsychopharmacology 34, 2655–2666. https://doi.org/10.1038/ npp.2009.103.

- Szyf, M., Bick, J., 2013. DNA methylation: a mechanism for embedding early life experiences in the genome. Child Dev. 84, 49–57. https://doi.org/10.1111/j.1467-8624.2012.01793.x.
- Tassinary, L.G., Cacioppo, J.T., 1992. Unobservable facial actions and emotion. Psychol. Sci. 3, 28–33. https://doi.org/10.1111/j.1467-9280.1992.tb00252.x.
- van Boxtel, A., 2010. Facial EMG as a tool for inferring affective states. Proc. Meas. Behav. 2010, 104–108.
- Volpert-Esmond, H.I., Page-Gould, E., Bartholow, B.D., 2021. Using multilevel models for the analysis of event-related potentials. Int. J. Psychophysiol. 162, 145–156. https:// doi.org/10.1016/j.ijpsycho.2021.02.006.
- Vuoriainen, E., Bakermans-Kranenburg, M.J., Huffmeijer, R., van IJzendoorn, M.H., Peltola, M.J., 2022. Processing children's faces in the parental brain: a meta-analysis of ERP studies. Neurosci. Biobehav. Rev. 136, 104604 https://doi.org/10.1016/j. neubjorev.2022.104604.
- Wang, A.L., Lowen, S.B., Elman, I., Shi, Z., Fairchild, V.P., Bouril, A., Gur, R.C., Langleben, D.D., 2018. Sustained opioid antagonism modulates striatal sensitivity to baby schema in opioid use disorder. J. Subst. Abuse Treat. 85, 70–77. https://doi. org/10.1016/j.jsat.2017.10.007.
- Wojdacz, T.K., Dobrovic, A., 2007. Methylation-sensitive high resolution melting (MS-HRM): a new approach for sensitive and high-throughput assessment of methylation. Nucleic Acids Res. 35 (6), e41. https://doi.org/10.1093/nar/gkm013.