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RESEARCH ARTICLE

Pupil responses to dynamic negative facial expressions of emotion in infants and parents

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Abstract

Observing others' emotions triggers physiological arousal in infants as well as in adults, reflected in dilated pupil sizes. This study is the first to examine parents' and infants' pupil responses to dynamic negative emotional facial expressions. Moreover, the links between pupil responses and negative emotional dispositions were explored among infants and parents. Infants' and one of their parent's pupil responses to negative versus neutral faces were measured via eye tracking in 222 infants (5- to 7-month-olds, $n = 77$, 11- to 13-month-olds, $n = 78$, and 17- to 19-month-olds, $n = 67$) and 229 parents. One parent contributed to the pupil data, whereas both parents were invited to fill in questionnaires on their own and their infant's negative emotional dispositions. Infants did not differentially respond to negative expressions, while parents showed stronger pupil responses to negative versus neutral expressions. There was a positive association between infants' and their parent's mean pupil responses and significant links between mothers' and fathers' stress levels and their infants' pupil responses. We conclude that a direct association between pupil responses in parents and offspring is observable already in infancy in typical development. Stress in parents is related to their infants' pupillary arousal to negative emotions.

KEYWORDS

infancy, negative emotion, parental stress, pupillometry, temperament

1 | PUPIL RESPONSES TO DYNAMIC NEGATIVE FACIAL EXPRESSIONS OF EMOTION IN INFANTS AND PARENTS

The ability to read and understand others' emotional expressions is an essential social skill that enhancesone's chances of survival and adaptation to the social world. This social skill is especially of paramount importance early in life, where infants solely rely on parents' (or caregivers') emotional expressions for survival and mastery of the environment (LoBue et al., 2019). Before the emergence of language and locomotion, the fulfillment of infants' basic needs depends on their ability to express emotions, as well as to respond to the emotional expressions of the caregivers. Emotional signals not only provide information on the internal state (e.g., emotions, motivations, and intentions) of others but also convey the significance of external events unfolding in the environment (Barrett & Campos, 1987;

Reid & Striano, 2007). The current study aims to investigate infants' processing of emotion in dynamic faces using pupillometry as a physiological index of arousal.

Faces, as the main seat of emotional signals, attract infants' attention from the first days of life onward. Newborns orient quicker and attend longer to faces and face-like stimuli when presented next to non-social stimuli (e.g., Johnson et al., 1991; Valenza et al., 1996). This initial bias to faces becomes more robust and stable toward the end of the first year of life (Frank et al., 2009; Leppänen, 2016). A recent study revealed that infants between 3 to 12 months of age are even able to detect faces in complex naturalistic visual scenes in less than a second (Kelly et al., 2019). These findings together suggest an advantage in face processing in early development and reveal that infants gradually develop expertise with faces during the first year of life.

Infants' first experiences with emotional expressions occur with their caregivers, in the context of everyday interactions. In addition to this bias to faces at the broader level, infants show a visual preference for their primary caregiver's face over a stranger's face as early as the fourth day of life (Bushneil et al., 1989; Pascalis et al., 1995; Sai, 2005). Similar biases to caregiver's faces were also reported at 3 months of age (Barrera & Maurer, 1981), possibly as a result of further exposure to the primary caregiver's face in early interactions. Mothers' and infants' co-regulation of emotional arousal is taking place during these interactions as both sides actively engage in keeping the arousal levels at an optimal state during the interaction using self and other-directed actions to regulate emotions (Tronick, 2007).

An initial reflexive tendency to mimic facial expressions in the first months of life (Meltzoff & Moore, 1994) is followed by an increasing capacity to actively adapt to parents' emotional expressions and arousal in these early face-to-face interactions. By 4 months of age, infants not only mimic (de Klerk et al., 2018; Isomura & Nakano, 2016) and synchronize to parents' emotional expressions (Feldman, 2003), but they are also capable of tuning in to the subtle differences in their mothers' versus fathers' facial expressions of emotion (Aktar et al., 2017). This attunement is coupled with physiological synchrony among infant–parent dyads (Feldman, 2007; Feldman et al., 2011). Taken together, these findings illustrate how exposure to the parents' facial expressions, and their attention allocation to others' emotional expressions, play a role throughout the first year of life in shaping an infant's own behavioral and physiological experience of emotion.

In addition to a bias for processing faces at a broader level, and for the caregiver's faces more specifically, infants prioritize the processing of negative emotional expressions as compared to positive and neutral expressions by the second half of the first year of life (Vaish et al., 2008). For example, behavioral studies using a variety of gaze measures to compare infants' attention to fearful and happy/neutral facial expressions (e.g., looking, fixations, and dwell time) have consistently revealed that infants start to gaze longer to fearful (vs. happy) faces between 5 and 7 months of age (De Haan et al., 2004; Heck et al., 2016; Kotsoni et al., 2001; Leppänen et al., 2010; Nakagawa & Sukigara, 2012; Nelson & Dolgin, 1985; Peltola et al., 2009). In line with the increasing popularity of a neuroscientific approach to child emotional development (Morales & Fox, 2019), there is growing interest in whether a similar negativity bias can be captured in neural and physiological markers of infants' emotion processing. A negativity bias has been reported in infants' neural (i.e., event-related potentials [ERP], De Haan, et al., 2004; Leppänen et al., 2007; Peltola et al., 2009) and physiological (e.g., heart rate variability, Leppänen et al., 2010; Peltola et al., 2013) responses.

Pupillometry has become increasingly popular in emotion processing with adults(e.g., Bradley et al., 2008; Kret et al., 2013a; Kret et al., 2013b; Partala & Surakka, 2003) and infants (Aktar et al., 2016, 2018; Geangu et al., 2011; Gredebäck et al., 2012; Hepach & Westermann, 2016; Hepach et al., 2015; Jessen et al., 2016). Under constant luminance, pupil dilation is a temporally sensitive index of arousal in response to emotional stimuli independent of valence (Laeng et al., 2012). In the current study, infants' pupillary arousal in response to dynamic negative faces versus neutral faces was used as an index of infant negativity bias. Pupil responses reflect the activity of the autonomic nervous system mediated by the locus coeruleus and associated subcortical brain structures (Aston-Jones & Cohen, 2005; Bradley et al., 2008). This automatic, unconscious response is present at birth (Laeng et al., 2012) and has been shown using eye tracking as early as in the first half-year of life. For example, it is currently known that infants between 4 and 18 months of age mimic the pupil sizes of others (Aktar et al., 2020; Fawcett et al., 2016, 2017).

Earlier findings suggest that adults show a negativity bias in their pupils: They react with more pupil dilation to negative versus neutral faces (Bradley et al., 2008; Partala & Surakka, 2003; Van Steenbergen et al., 2011). However, the results are less consistent in infants with two studies reporting more pupil dilation to fearful than neutral stimuli in 6- and 12-month-olds (Geangu et al., 2011) and 14- to 17-month-olds (Aktar et al., 2016) and one study reporting less pupil dilation to fearful than neutral faces in 12- to 16-month-old infants (Aktar et al., 2018). Another study by Gredebäck et al. (2012) reported more dilated pupils in response to others' fearful (vs. neutral) facial expressions in 14-month-old infants who are cared by both their mother and fathers and not by their mother only (Gredebäck et al., 2012). These findings reveal the need to incorporate individual differences explained by family variables into the study of infant pupil response to emotional stimuli.

To date, pupil responses to negative emotions have been explored separately in infant and adult populations, and no study has directly compared pupil responses of infants with adults, including their parents/caregivers. Thus, we do not know whether infants' pupil responses to emotion align with their caregiver's as captured by the extent and the speed at which individuals dilate in response to different negative emotions. The automatic and subcortical nature of pupil responses make this physiological measure especially suitable for a direct comparison of parents' and offspring's emotion processing in infancy (Hepach & Westermann, 2016).

Pupillary reactivity to negative emotional stimuli may also reflect individual differences in broader patterns of socioemotional functioning. For example, adults (Armstrong & Olatunji, 2012; Kret, Stekelenburg, et al., 2013) and children (Price et al., 2013) with (vs. without) anxiety respond with stronger pupil dilation to angry facial expressions. Adults with (vs. without) depression show more sustained pupil dilation in response to negative stimuli (Siegle et al., 2001), and 8- to 14-year-old children with higher levels of depression show stronger pupil dilation to sad faces (Burkhouse et al., 2015). Likewise, higher levels of post-traumatic stress disorder (PTSD) symptoms in adults were shown to be linked to stronger pupil dilation to negative stimuli (e.g., Cascardi et al., 2015; Kimble et al., 2010). There is also some preliminary evidence that negative temperamental characteristics may be linked to pupillary reactivity in infancy. For example, a study reported that 14- to 17-month-old infants with higher levels of sad (but not fearful) temperament displayed greater pupil dilation to negative and positive facial expressions (Aktar et al., 2016). Taken together, the findings suggest a significant positive relationship between individual levels of negative affect and pupil responses to negative stimuli.

In addition to within-person links to pupil responses, parental anxiety or depression was found to be related to child pupil responses to negative emotions: Children of parents with anxiety disorders show stronger pupil dilation to fearful expressions, whereas children of depressed parents show stronger pupil dilation to sad faces (Burkhouse et al., 2014). Two studies investigating this link in infancy did not replicate this finding (Aktar et al., 2016, 2018). In the first study, no significant link was detected between parents' negative affect and 14- to 17-month-olds pupil responses to negative and positive faces (Aktar et al., 2016), whereas the second study found that the association was in the opposite direction: Stronger negative emotions among mothers (but not fathers) were significantly related to less dilated pupils, thus less arousal to emotional expressions, in 12- to 16-month-old infants (Aktar et al., 2018). Taken together, the findings are mixed concerning the link between parents' negative emotions and offspring' pupil responses to negative stimuli. This link awaits to be further explored in typical development.

1.1 | Current study

In the present study, we investigated parents' and infants' pupil responses to dynamic negative facial expressions of emotion at the end of the first, second, and third half-year of life (5- to 7-month-olds, 11- to 13-month-olds, and 17- to 19-month-olds). By including parents' pupil responses in the current design, we aimed to explore similarities and differences in the timing and the intensity of pupil responses to negative emotional expressions across infants and adults. In addition, testing parents and infants in the same experiment using the same physiological indices allowed us to test whether there is an overlap in infants' and parents' patterns of emotion processing in pupillary indices.

Including three age groups in a cross-sectional design allowed us to explore infants' pupillary arousal to emotion at the three age intervals that accompany three milestones in development. The first one is the emergence of a negativity bias in infants' emotion processing between 5 and 7 months of age (Vaish et al., 2008). The second milestone marks infants' ability to learn from others' emotions at the end of the first year (social referencing, Feinman et al., 1992). The third age group at around 18 months of age aims to capture the changes in emotion processing that are related to the emergence of full locomotion and language (Campos et al., 2000; Clearfield, 2011). The current cross-sectional design allows us to have a snapshot of the developmental differences in infants' pupils throughout the first 18 months of life.

The current study is the first to directly compare pupillary responses to facial expressions of emotion in infants and their parents. Pupil responses of infants and one parent were measured with an eye tracker during computerized presentations of dynamic negative (i.e., fearful, angry, sad) versus neutral facial expressions. To our knowledge, pupil responses have not yet been tested with dynamic facial expressions, which allow for a more ecologically valid test of infants' pupillary reactions (Heck et al., 2016). Parental negative emotions and infant negative temperament were assessed using both mothers' and fathers' reports. We aimed to answer the following questions:

1. *Do pupil responses to negative (vs. neutral) facial expressions differ between infants and parents?* We expected that both infants and parents would respond with stronger pupil responses to negative (angry, fearful, and sad) versus neutral facial expressions.
2. *Is there a direct association between parents' and infants' pupil responses to negative (vs. neutral) emotional expressions?* This was the first eye-tracking study that explored this question, as such we do not have an a priori hypothesis for the relation.
3. *Are parental negative emotions and/or infant negative temperament related to infants' pupil dilation to negative (vs. neutral) emotions?* We expected that infants of parents with more negative emotions would respond with stronger pupil responses to negative (vs. neutral) emotions. In addition, we expected that higher levels of infant negative temperament would be related to more emotional arousal and thus stronger pupil dilation to negative emotions. Finally, we explored the interaction between infant negative temperament and parental negative emotions on infant emotion processing, hypothesizing that the relationship would be stronger for infants high in negative temperament who also had a parent high in negative affect.
4. *Are parental negative emotions related to parents' pupil responses to negative (vs. neutral) emotions?* Based on earlier evidence revealing more arousal in adults with higher levels of negative affect, we expected that parents with more negative emotions would show stronger pupil responses to negative emotions.

2 | METHOD

2.1 | Participants

A sample of 222 infants in three age groups: 5- to 7-month-olds ($n = 77$, *Mage* = 6.08, *SD* = 0.51, range 5.00–7.50, 36 girls), 11- to 13-month-olds ($n = 78$, *Mage* = 12.08, *SD* = 0.58, range 10.70–12.90, 44 girls), and 17- to 19-month-olds ($n = 67$, *Mage* = 17.87, *SD* = 0.64, range 16.50–19.00, 33 girls) and one parent ($n = 229$, 157 mothers) contributed to this study. The parent who visited the lab with the infant contributed to the eye-tracking data, whereas both parents of participating infants were invited to complete online questionnaires for the study. Families were recruited using invitation letters sent by the municipality of Amsterdam to families with babies. To preserve generalizability to the general population, there were no other exclusion

TABLE 1 Sociodemographic characteristics of parents

	Mother	Father
Age *M* (*SD*, range)	34.14 (4.21, 22–45)	36.08 (5.18, 25–62)
Dutch origin	74.41%	79.21%
Educational level % (frequency)		
Highest level of completed education:		
Primary or secondary education	11.37 (24)	18.54 (33)
Higher professional education	23.22 (49)	26.40 (47)
Scientific education	64.93 (137)	54.49 (97)
Professional level % (*N*)		
Never worked	0 (0)	0.56 (1)
Predominantly manual labor or principal/main work requiring vocational training	3.32 (7)	5.06 (9)
Independent entrepreneur	13.74 (29)	14.05 (25)
Salaried at LBO, MBO, or HBO level	43.13 (91)	41.01 (73)
Salaried employment requiring scientific training	39.81 (84)	39.33 (70)
Monthly income *M* (*SD*, range)		
< 1000 euro	11.85 (25)	4.49 (8)
1000–1999 euro	18.96 (40)	8.99 (16)
2000–2999 euro	24.17 (51)	19.10 (34)
3000 euro or more	37.44 (79)	61.80 (110)

Notes. The table summarizes the characteristics of the mothers and fathers of the 222 infants who contributed to the dataset, HBO = hoger beroepsonderwijs (senior general secondary education), LBO = lager beroepsonderwijs (preparatory secondary vocational education), M = mean, MBO = middelbaar beroepsonderwijs (vocational education), N = sample size, SD = standard deviation.

criteria. Eye-tracking data were missing from 12 infants from the initial sample of 251 families visiting the lab for this study due to child fussiness/fatigue, tracking problems, software/equipment failure, or experimenter errors. Parent testing did not proceed in cases ($n = 14$) where the child got fussy during or following testing. Data from an additional 17 infants and eight parents were removed during data reduction (see below). Non-completer infants did not differ from completers in age, $p = .456$, gender, $p = .256$, or negative temperament, $p = .857$. The sociodemographic characteristics of participating families are presented in Table 1. The study was approved by the Ethics Review Board of the Faculty of Social and Behavioral Sciences, University of Amsterdam. Parents gave written informed consent for participation.

2.2 | Materials and procedure

2.2.1 | Stimuli

The stimuli were colored dynamic videos (on 1280 × 1024 pixels screen) of two male and two female North European models from Amsterdam Dynamic Facial Expression Set (ADFES) (Van der Schalk et al., 2011) expressing neutral, happy, fearful, sad, angry faces. Each emotional expression started neutral (500 ms) and was followed by the dynamic unfolding of the emotional expression that reached the apex in 500 ms, and stayed at the apex for another 5 s.

2.2.2 | Procedure

Infants' and parents' pupillary reactions were measured via an EyeLink® eye tracker (sampling rate was 500 Hz) in a dimly illuminated room that remained unchanged during testing. Gaze was calibrated and validated with a 5-point procedure for all participants before the experiment. Infants were placed in a car seat 60 cm away from the screen. During infant testing, the parent was seated on the side of the infant and was instructed to not intervene unless the infant sought attention or became fussy. Following the infant, the parent sat in front of the eye-tracking screen to complete the same task.

Five dynamic expressions from four models were repeated twice, resulting in 40 trials. Each block started with the neutral expression in the first trial, followed by the four trials with the dynamic emotional expressions of the same model. In the absence of earlier studies measuring infants' pupil response to dynamic negative faces, we chose to start each block with the baseline neutral condition for eventual carryover effects of negative videos in infants' overall arousal levels indexed by pupil size. All models were presented before a given model was repeated. The order of the emotions from a given model within each block following the neutral expression, and the order of the models in each block, was randomly determined. The trial order generated for the infants was repeated identically with the parent. Each trial started with a 500 ms attention-getter followed by 1000 ms of a blank screen, continued with 1500 ms presentation of a blurred face matching to the

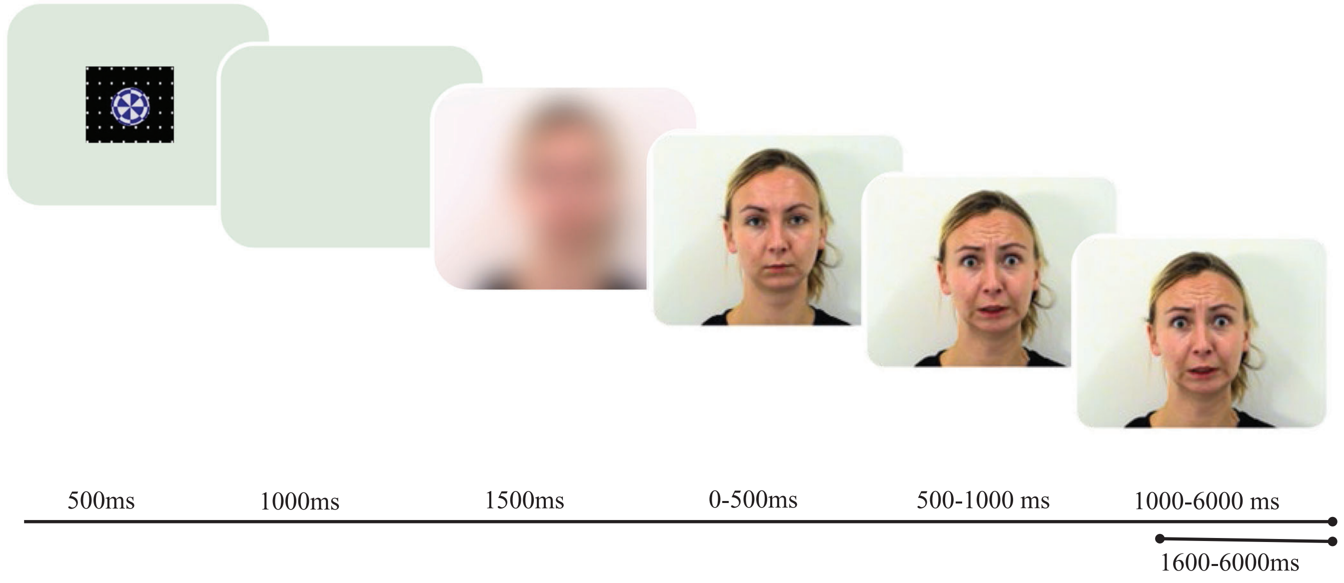

FIGURE 1 Time flow of the trials in the current experiment

luminance of the stimuli (aiming to adjust participants' eyes to the stimulus luminance), and ended with the dynamic stimuli (starting with a neutral expression for 500 ms, followed by the movement toward the apex in 500 ms and stayed at the apex of that emotion for 5000 ms; see Figure 1). The presentation of the attention-getters (e.g., a circle expanding and contracting) was repeated if necessary, before the onset of each trial.

2.2.3 | Questionnaires

Parents' negative emotions

Both parents filled in the Depression Anxiety Stress Scales (DASS; Lovibond & Lovibond, 1995). The DASS is a 42-item questionnaire consisting of three 14-item subscales for depression, anxiety, and stress symptoms rated on a 4-point scale. The mean anxiety, depression, and stress scores were obtained from those subscales. The depression subscale measures the lack of positive affect along with the negative affect dimensions characterizing depressed mood states (e.g., helplessness, Brown et al., 1997). The anxiety subscale captures the autonomic arousal/fearfulness dimensions, whereas the stress subscale measures negative affect states characterizing generalized anxiety (such as tension and irritability). The reliability (Cronbach's α) was .78 for mothers and .70 for fathers for the anxiety subscales, .85 for mothers and .87 for fathers for the depression, and .88 for mothers and .90 for fathers for the stress subscale. For each parent, the mean scores on these three subscales were averaged into a mean score of negative emotion. The descriptives and the correlations between mothers' and fathers' negative emotion scores appear in Table 2. The mean scores of mothers' and fathers' negative emotions were significantly correlated r (176) = .37, $p < .001$. Additionally, the intercorrelations between parents' mean scores on the subscales of depression, anxiety, and stress subscales are presented in Table S1.

TABLE 2 Descriptives and correlations between maternal and paternal negative emotion dispositions and infant negative temperament

	N	*M*	*SD*	2	3
1. *Mother Negative Emotion*	211	0.23	0.22	.37***	.24***
2. *Father Negative Emotion*	178	0.26	0.24	–	.14
3. *Infant Negative Temperament*	213	2.75	0.56	–	–

Note: *N* = sample size, *M* = mean, *SD* = standard deviation, 1 = *Mother Negative Emotion*, 2 = *Father Negative Emotion*, 3 = *Infant Negative Temperament*.
***$p \leq .001$.

Infant negative temperament

Both parents completed the shortened version of the Infant Behavior Questionnaire-Revised (IBQ-R; Gartstein & Rothbart, 2003). The current study focused on temperamental dimensions that relate to the following negative emotions: fear, sadness, and distress to limitations. Parents rated the frequency of infants' expressions of fear, sadness, and anger proneness on a 7-point scale. Cronbach's αs for these subscales were .79, .84, .81 for mothers' and .78, .85, .81 for fathers' ratings, respectively. Mothers' and fathers' ratings were averaged on these three dimensions, which were aggregated into a single mean score of negative temperament. The descriptives and the correlations between infants' negative temperament and parents' negative emotion scores appear in Table 2 (also see Table S1).

2.3 | Data reduction

The current study focused on changes in pupil size to emotional expressions as a physiological index of emotional arousal. Pupil data from parents and infants were extracted using EyeLink® Data Viewer (SR Research Ltd). All available data from infants and parents were entered in the analyses and were processed in the same way to allow comparison.

Outlying scores (> |3| *SD*) were removed from each participant's distribution of pupil scores. Next, blinks (missing observations that are shorter than 500 ms) were replaced via linear interpolation (see Jackson & Sirois, 2009). Missing sequences that took longer than 500 ms were considered as "looking away" and therefore not interpolated. Following the interpolation, the pupil data were first averaged to 120 observation points with 50-ms intervals in the 6 s presentation of dynamic stimuli where each emotional expression started neutral (500 ms) and was followed by the dynamic unfolding of the emotional expression that reached the apex in 500 ms and stayed at the apex for another 5 s. Participants' pupil responses to emotional expressions were baselined (via division) to the mean pupil size obtained during the 500-ms presentation of the neutral expression preceding the unfolding of emotion in each trial. This allowed us to control for the differences in the luminance across different models. Baseline-corrected pupil size was the outcome measure in the analyses and analyzed in the last 4.5 s of 6 s video presentation (i.e., starting from 500 ms after the emotion reaches the apex, 45 observation points of 100 ms time interval were used for analysis). Trials in which the data were available for at least 1 s within the total 6 s presentation time (trials where the data was missing less than 83.33% of the time) were included in the analyses (seven infants and four parents excluded at this stage).

Infants and parents who contributed less than 10 trials were removed from the analyses ($n = 10$ infants and four parents excluded at this stage). The pupil data were available at this stage on average for 33 trials ($SD = 7.67$, range: 10–40) from infants and 39 trials ($SD = 3.37$, range: 15–40) from parents. The percentage of missing observations within trials was 25.12% in the 6-month-olds, 25.86% in the 12-month-olds, 20.26% in the 18-month-olds groups, and 5.49% for parents in the final dataset.

2.4 | Statistical analyses

The current data structure consists of repeated observations of infants' and parents' pupil responses to negative emotion over time within trials and across emotion. Multi-level models were used to account for the repeated structure of the dataset. These models can accommodate the current nested structure, in addition to random and non-random sources of missingness. The sample size at the top of this hierarchical dataset ($N = 451$, 222 infants and 229 parents) allows sufficient power to detect potential differences between infants' and parents' pupil responses (Maas & Hox, 2005). The intercept, trial number, and models (model number) were randomized in all models and retained in the models when significant. All other predictors including *Negative* (vs.) *Neutral* emotions were treated as fixed effects. Baselined pupil scores were the outcome measure in the analyses. Thus, the findings in pupil responses should be interpreted as a relative change in pupil size from baseline. We used maximum likelihood for estimation and an auto-regressive covariance structure for repeated effects of time for all models. The initial models contained the theoretically relevant interactions (specified per model below). The non-significant interactions were excluded one-by-one starting from higher-order interactions, and higher *p*-value, to attain the most concise final models. The decisions on the inclusion/exclusion of initially tested interactions were based on the significance of the *F*-scores. Neutral expression was used as the reference in all pupil models. In the infant analyses, the 6-month-olds were the reference age group. Given that pupil responses reflect general arousal rather than differentially responding to positive versus negative valence, and our current focus was on negative emotions and negative emotional dispositions, we constrained the analysis to negative (angry, fearful, sad) versus neutral facial expressions. Parents' negative emotion scores and infant negative temperament were entered as continuous variables in the models. All continuous predictor and outcome variables were standardized. Inspection of the distributions for the scores on negative temperament and parents' negative emotions indicated sufficient normality (skewness and kurtosis were $< |2.6|$) except for maternal negative emotions. We, therefore, inspected the distribution of residuals for the models that included negative emotion scores from the mothers (i.e., questions 3 and 4), and these indicated sufficient normality (both skewness and kurtosis $< |2|$).

The multi-level regression models generate both *F*-scores and β estimates for fixed effects. The *F*-scores allow the testing of overall group differences for fixed categorical variables (such as *Negative* (vs. *Neutral*) *Faces*, and *Parent/Infant*), whereas β estimates allow pairwise comparisons between each of the negative expressions (i.e., angry, fearful, sad) with the neutral reference. In the current analyses, we used the *F*-scores for testing the overall differences between categorical variables, whereas fixed effects of dichotomous categorical variables and continuous variables were interpreted using β estimates.

3 | RESULTS

1. Do pupillary reactions to negative (vs. neutral) facial expressions differ between infants and parents?

We compared infants' and parents' pupil responses in a multi-level regression model ($N = 451$, 222 infants and 229 parents) consisting of the main effects of *Negative* (vs. *Neutral*) *Faces*, and *Parent/Infant* (*Parent* vs. *Infant*), and the two-way interaction between *Negative* (vs. *Neutral*) *Faces* and Parent/Infant. The final model is presented in Table 3. The two-way interaction between *Negative* (vs. *Neutral*) *Faces* and *Parent/Infant* was significant, F (3, 263073.46) = 96.25, $p < .001$. The inspection of infants' and parents' pupillary responses to negative versus neutral expressions averaged over stimulus time, presented in Figure 2, suggests that the differences in infant versus parent emotion processing were related to a differential responding of parents and infants to neutral faces. Parents, but not infants, differentially reacted to negative versus neutral emotional expressions. We further confirmed these differences by separately testing emotion effects in the parent and infant samples. Infants' pupil responses did not differ

TABLE 3 Multi-level regression of pupil responses on family member (parent vs. infant), and negative versus neutral faces

	Numerator df	*Denominator df*	*F*	*p*			
Intercept	1	239.20	0.01	.913			
Negative versus Neutral Faces	3	14318.81	14.35	<.001			
Parent/Infant (Parent vs. Infant)	1	296,494.28	209.84	<.001			
*Negative versus Neutral Faces * Parent/Infant*	3	263,073.46	96.25	<.001			
Estimates of fixed effects							
						95% Confidence intervals	
Parameter	*ß*	*SE*	*df*	*t*	*p*	**Lower bound**	**Upper bound**
Intercept	–.16	0.02	483.47	−7.54	<.001	−0.20	−0.12
Angry (vs. Neutral)	.13	0.02	15,758.43	6.82	<.001	0.09	0.16
Fearful (vs. Neutral)	.16	0.02	15,761.82	8.63	<.001	0.12	0.20
Sad (vs. Neutral)	.19	0.02	15,808.33	10.30	<.001	0.16	0.23
Parent/Infant	.24	0.01	279,069.67	21.00	<.001	0.22	0.26
*Angry * Parent/Infant*	–.19	0.02	266,162.03	−11.69	<.001	−0.22	−0.16
*Fearful * Parent/Infant*	–.27	0.02	266,250.94	−16.43	<.001	−0.30	−0.24
Sad Parent/Infant*	–.16	0.02	265,776.15	−9.99	<.001	−0.20	−0.13
		Estimate	*SE*	*Wald Z*	*p*	**Lower bound**	**Upper bound**
Repeated measures	AR1 diagonal	0.96	0.01	135.62	<.001	0.95	0.97
	AR1 rho	0.93	<0.01	1917.33	<.001	0.93	0.94
Intercept [subject = ID]	Variance	0.06	0.01	8.39	<.001	0.05	0.08
Trial ID	Variance	0.01	0.00	5.52	<.001	0.01	0.02
Model Number	Variance	0.03	0.00	8.44	<.001	0.02	0.04

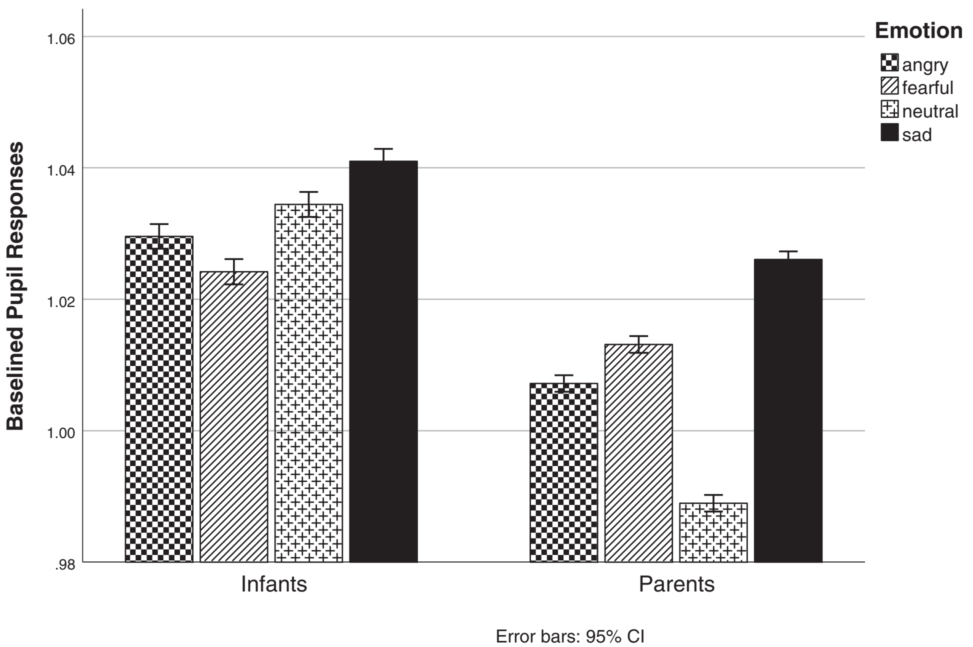

FIGURE 2 Observed mean baselined pupil responses per emotion category for infants (on the left) and parents (on the right)

TABLE 4 Multi-level regression of infant pupil responses on negative versus neutral faces and parents' pupil responses

	Numerator df	*Denominator df*	*F*	*p*			
Intercept	1	202.09	0.03	.860			
Negative versus Neutral Faces	3	422.63	2.44	.064			
Age Group (12 and 18 vs. 6-month-olds)	2	202.21	4.59	.011			
Parental Pupil Response	1	808.03	4.35	.037			
Estimates of fixed effects							
						95% Confidence intervals	
Parameter	*ß*	*SE*	*df*	*t*	*p*	**Lower bound**	**Upper bound**
Intercept	−.18	0.10	304.09	−1.72	.087	−0.38	0.03
Angry (vs. Neutral)	−.13	0.07	477.95	−1.78	.076	−0.27	0.01
Fearful (vs. Neutral)	−.09	0.07	471.71	−1.20	.230	−0.23	0.06
Sad (vs. Neutral)	.04	0.07	487.01	.56	.574	−0.10	0.19
Age Group 12 months	.36	0.13	202.74	2.74	.007	0.10	0.61
Age Group 18 months	.33	0.13	202.28	2.46	.015	0.07	0.59
Parental Pupil Response	.07	0.04	808.03	2.08	.037	0.00	0.14
		Estimate	***SE***	***Wald Z***	***p***	**Lower bound**	**Upper bound**
Repeated Measures	AR1 diagonal	0.51	0.03	15.24	<.001	0.45	0.58
	AR1 rho	−0.02	0.07	−0.32	.746	−0.15	0.11
Intercept [subject = ID]	Variance	0.48	0.06	7.58	<.001	0.37	0.62

Note: df = degrees of freedom, *F* = *F*-value, *p* = significance level, *ß* = beta, *SE* = standard error, *t* = *t*-value.

between *Negative* versus *Neutral Faces* ($N = 222$, $p = .435$), while parents showed stronger pupil responses to the *Negative* as compared to *Neutral Faces*, $N = 229$, F (3, 10241.90) = 38.19, $p < .001$ (*ß*' s were .11 for angry, .15 for happy, and .20 for sad faces, $SE = 0.02$, *ps* < .001).

In additional analyses, we have shown that infants' pupil responses across the three age groups did not differ as a function of negative emotion in the current sample (for a comparison of the temporal dynamics of the pupil response across parents and infants, see Supplement section Additional Analyses on the Effect of Age on Infants' Pupillary Responses to Negative Emotion).

2. Is there a direct association between parents' and infants' pupil responses to negative (vs. neutral) emotional expressions?

In the next step, we tested the direct association between infants' and visiting parents' mean pupil responses to negative versus neutral faces (averaged across time within and between trials with fearful, angry, and sad vs. neutral faces). This set of multi-level analyses had infant pupil responses as the outcome variable, and included the main effect of *Negative* (angry, fearful, sad) versus *Neutral Faces*, *Age Group* (12 and 18 vs. 6-month-olds), parents' pupil responses, in addition to all the two-way and three-way interactions between these three variables as fixed predictors. The intercept was randomized.

None of the tested interactions were significant in this model ($N = 210$) (*ps* ≥ .194), reducing the final model to the main effects. The final model presented in Table 4 revealed a direct positive association between parents' and infants' pupil responses to negative (vs. neutral) emotions, $F(1, 808.03) = 4.35$, $p = .037$. The findings show a direct relation in the way parents' and infants' pupils respond to dynamic facial expressions independent of *Age Group*, such that infants of parents with stronger pupillary reactions to facial expressions display stronger pupil reactions to facial expressions. This effect was on general pupillary responses and thus did not differ as a function of negative (vs.) neutral emotion.

3. Are parental negative emotions and/or infant negative temperament related to infants' pupil responses to negative (vs. neutral) emotions?

Next, we investigated the impact of individual differences on infants' pupil responses. Specifically, we examined the impact of infant negative temperament and parents' negative emotions. This model included the main effects of *Age Group*, *Negative* versus *Neutral Faces*, mothers' and fathers' negative emotions, and infant negative temperament, along with the two and three-way interactions between *Negative* versus *Neutral Faces*, parental negative emotions, and infant negative temperament.

Among tested interactions ($N = 176$), there was a significant two-way interaction between *Negative* versus *Neutral Faces* and mothers' negative emotions F (3, 3987.70) = 3.44, $p = .016$ and a trending interaction between emotion and fathers' negative emotions,

TABLE 5 Multi-level regression of infant pupil responses on negative versus neutral faces and parental and infant negative emotion dispositions

	Numerator df	*Denominator df*	*F*	*p*			
Intercept	1	175.91	0.08	.778			
Age Group	2	175.24	4.96	.008			
Negative versus Neutral Faces	3	3900.42	0.89	.444			
Maternal Negative Emotions	1	174.76	0.81	.369			
Paternal Negative Emotions	1	179.43	0.63	.428			
Infant Negative Temperament	1	177.25	0.72	.399			
*Negative versus Neutral Faces * Maternal Negative Emotions*	3	3987.70	3.44	.016			
*Negative versus Neutral Faces * Paternal Negative Emotions*	3	3998.94	2.46	.061			
Estimates of fixed effects							
						95% Confidence intervals	
Parameter	***ß***	***SE***	***df***	***t***	***p***	**Lower bound**	**Upper bound**
Intercept	−.12	0.06	214.00	−2.01	.045	−0.24	0.00
12-month-olds (vs. 6-month-olds)	.22	0.08	178.39	2.70	.008	0.06	0.39
18-month-olds (vs. 6-month-olds)	.23	0.08	171.77	2.79	.006	0.07	0.40
Angry (vs. Neutral)	−.04	0.03	3905.84	−1.34	.179	−0.11	0.02
Fearful (vs. Neutral)	−.03	0.03	3899.49	−1.06	.288	−0.10	0.03
Sad (vs. Neutral)	.00	0.03	3906.35	−0.13	.895	−0.07	0.06
Maternal Negative Emotions	−.03	0.04	307.95	−0.77	.444	−0.12	0.05
Paternal Negative Emotions	.01	0.04	326.15	0.19	.848	−0.07	0.09
Infant Negative Temperament	.03	0.04	177.25	0.85	.399	−0.04	0.10
*Angry * Maternal Negative Emotions*	.10	0.04	3953.25	2.77	.006	0.03	0.18
*Fearful * Maternal Negative Emotions*	.10	0.04	3935.42	2.77	.006	0.03	0.17
*Sad * Maternal Negative Emotions*	.07	0.04	4025.49	1.83	.068	−0.01	0.14
*Angry * Paternal Negative Emotions*	−.09	0.04	4033.59	−2.57	.010	−0.16	−0.02
*Fearful * Paternal Negative Emotions*	−.03	0.03	4006.77	−0.99	.322	−0.10	0.03
*Sad * Paternal Negative Emotions*	−.02	0.04	3991.36	−0.49	.622	−0.09	0.05
		Estimate	***SE***	***Wald Z***	***p***	**Lower bound**	**Upper bound**
Repeated Measures	AR1 diagonal	0.84	0.01	63.14	<.001	0.82	0.87
	AR1 rho	0.95	<0.01	1279.41	<.001	0.95	0.96
Intercept [subject = ID]	Variance	0.15	0.02	7.39	<.001	0.11	0.19
Trial ID	Variance	0.04	0.01	5.04	<.001	0.24	0.52
Model Number	Variance	0.05	0.01	4.96	<.001	0.03	0.07

Note: df = degrees of freedom, *F* = *F*-value, *p* = significance level, *ß* = beta, *SE* = standard error, *t* = *t*-value.

F (3, 3998.94) = 2.46, p = .061. These were retained in the final model presented in Table 5. Infants of mothers with higher levels of negative emotions reacted more strongly to angry, p = .006, and to fearful, p = .006, versus neutral expressions, whereas there was a similar marginal trend for sad expressions (p = .068). In contrast, infants of fathers with higher levels of negative emotions reacted with smaller pupil responses to angry (vs. neutral) faces, p = .010, whereas they did not differ in their pupil responses to fearful, p = .322, or sad, p = .622 faces. Infant temperament did not predict infant pupil responses, neither alone in the final model (p = .399) nor in interaction with *Negative* versus *Neutral Faces* or parental negative emotions ($ps > .215$ in the initial model). We conclude that parents', especially mothers' negative emotions, rather than infants' negative temperament explain variance in infants' pupillary arousal to negative (vs. neutral) facial expressions.

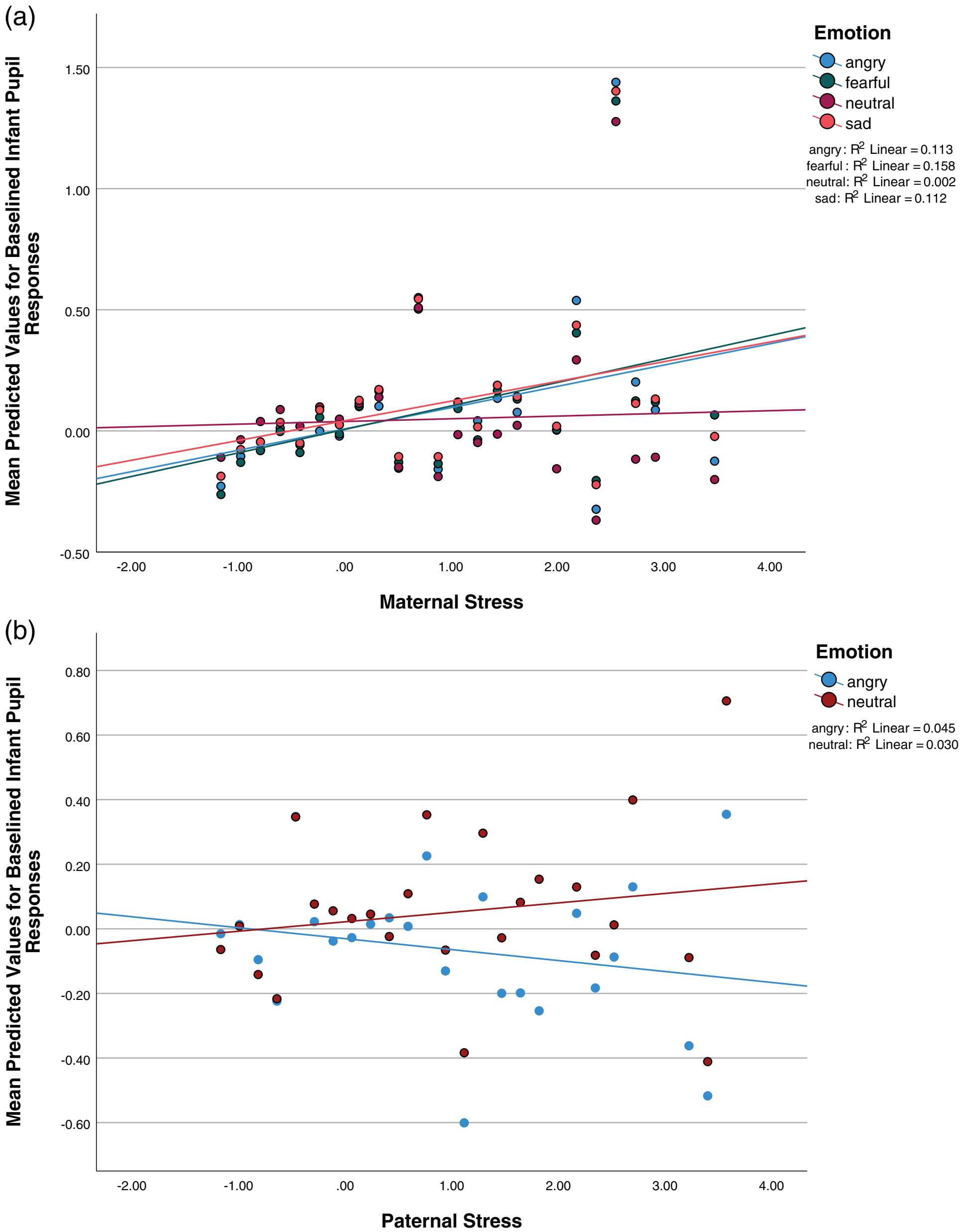

FIGURE 3 (a) The scatter plot of the interaction between *Negative* versus *Neutral Faces* (in separate lines) and *Paternal Stress* (on the x-axis) predicting *Infant Mean Pupil Responses* (on the y-axis). (b) The scatter plot of the interaction between *Angry* versus *Neutral Faces* (in separate lines) and *Paternal Stress* (on the x-axis) predicting *Infant Mean Pupil Responses* (on the y-axis)

3.1 | Post hoc exploratory analyses on infants' pupil responses

The results revealed differential pupil responses to negative emotions in infants of mothers and fathers with higher levels of negative emotions. In an additional step, we further explored what specific aspect of parents' negative emotional disposition may account for these findings, repeating the same multi-level model as above, by separately including parents' depression, anxiety, and stress as predictors in three separate models (N = 176), in place of the averaged measure of mothers' and fathers' negative emotions. The two-way interactions between *Negative* versus *Neutral Faces* and mothers' (p = .224) or fathers' (p = .371) depression were not significant. Likewise, the two-way interactions between *Negative* versus *Neutral Faces* and mothers' (p = .119) or fathers' (p = .360) anxiety were not significant. In turn, in the model with parents' stress, the two-way interactions between *Negative* versus *Neutral Faces* and maternal F (3, 3967.72) = 3.41, p = .017, and paternal F (3, 3950.50) = 3.35, p = .018, stress were both significant in the final model presented in Table 6. Infants of mothers with higher levels of stress showed more pronounced pupil responses to angry (p = .004), fearful (p = .012), and sad (p = .025) faces. The plot of the interaction, presented in Figure 3a, reveals a non-significant link between infants' pupil responses to neutral faces and maternal stress, whereas a positive link is noted between higher stress levels in mothers and

TABLE 6 Multi-level regression of infant pupil responses on negative versus neutral faces, infant negative emotion dispositions, and parental stress

	Numerator df	*Denominator df*	*F*	*p*			
Intercept	1	175.25	0.09	.762			
Age Group	2	174.39	5.10	.007			
Negative versus Neutral Faces	3	3900.72	0.94	.422			
Maternal Stress	1	177.62	2.38	.125			
Paternal Stress	1	178.72	0.28	.597			
Infant Negative Temperament	1	177.50	0.39	.534			
*Negative versus Neutral Faces * Maternal Stress*	3	3967.72	3.41	.017			
*Negative versus Neutral Faces * Paternal Stress*	3	3950.50	3.35	.018			
Estimates of fixed effects							
						95% Confidence intervals	
Parameter	*ß*	*SE*	*df*	*t*	*p*	**Lower bound**	**Upper bound**
Intercept	–.12	0.06	213.08	–2.04	.042	–0.24	0.00
12-month-olds (vs. 6-month-olds)	.23	0.08	177.55	2.76	.006	0.07	0.39
18-month-olds (vs. 6-month-olds)	.23	0.08	171.09	2.81	.006	0.07	0.40
Angry (vs. Neutral)	–.04	0.03	3906.10	–1.37	.171	–0.11	0.02
Fearful (vs. Neutral)	–.03	0.03	3899.83	–1.05	.295	–0.10	0.03
Sad (vs. Neutral)	.00	0.03	3904.22	–0.09	.928	–0.07	0.06
Maternal Stress	–.01	0.04	316.36	–0.27	.785	–0.10	0.07
Paternal Stress	.01	0.04	329.75	0.24	.810	–0.07	0.09
Infant Negative Temperament	.02	0.04	177.50	0.62	.534	–0.05	0.10
*Angry * Maternal Stress*	.11	0.04	3931.53	2.88	.004	0.03	0.18
*Fearful * Maternal Stress*	.09	0.04	3928.88	2.52	.012	0.02	0.17
*Sad * Maternal Stress*	.08	0.04	3983.08	2.24	.025	0.01	0.16
*Angry * Paternal Stress*	–.09	0.03	3997.47	–2.72	.007	–0.16	–0.03
*Fearful * Paternal Stress*	.00	0.03	3941.32	0.01	.995	–0.07	0.07
*Sad * Paternal Stress*	–.02	0.03	3967.12	–0.54	.591	–0.08	0.05
		Estimate	***SE***	***Wald Z***	***p***	**Lower bound**	**Upper bound**
Repeated Measures	AR1 diagonal	0.84	0.01	63.15	<.001	0.82	0.87
	AR1 rho	0.95	<0.01	1278.27	<.001	0.95	0.96
Intercept [subject = ID]	Variance	0.15	0.02	7.35	<.001	0.11	0.19
Trial ID	Variance	0.04	0.01	5.06	<.001	0.02	0.05
Model Number	Variance	0.05	0.01	4.99	<.001	0.03	0.07

stronger pupil responses to negative expressions in infants. In turn, infants of fathers with high levels of stress showed less pronounced pupil responses to angry versus neutral faces only ($\beta = -.09$, $SE = 0.03$, $p = .007$). The plot of the interaction is presented in Figure 3b.

4. Are parental negative emotions related to parental pupil responses to negative (vs. neutral) emotions?

To investigate individual differences in parents' pupil responses explained by parents' negative emotions, we conducted additional models with parental pupil responses as the outcome and *Negative* versus *Neutral Faces*, and parental negative emotions as predictors. We also tested the two-way interaction between *Negative* versus *Neutral Faces* and parental negative emotions in these models ($N = 217$). Neither the main effect of parental negative emotions ($p = .386$) nor the two-way interaction with *Negative* versus *Neutral Faces* ($p = .119$) was significant.

4 | DISCUSSION

The current study was the first to investigate pupil responses to negative versus neutral facial expressions in parent–infant dyads, exploring similarities and differences in parents' and infants' pupil responses to emotion. In addition to the direct link between infants' and parents' mean pupillary arousal, we explored the links between parents' negative emotions and parents' pupillary arousal and between parents' negative emotion, infant negative temperament, and infants' pupillary arousal in response to negative faces. At a glance, the findings reveal significant differences in parents' and infants' pupil responses to negative versus neutral faces. Despite these differences, there was a direct relationship between parents' and infants' mean pupil responses to facial expressions across the three age groups. Thus, infants who overall responded with stronger pupil responses to negative and neutral faces had parents who also show stronger pupillary responses to these faces. With respect to individual differences, findings suggest associations between parent's stress levels and their infant's pupil responses. No relation was noted between infant negative temperament and infant pupillary responses to negative emotion. The findings are further discussed below separately per the research question.

1. Do pupil responses to negative (vs. neutral) facial expressions differ between infants and parents?

The current data show overall significant differences between infants' and parents' emotion processing. In line with earlier evidence in adults, parents in the current study responded with more dilated pupils to negative (vs. neutral) facial expressions (Bradley et al., 2008; Van Steenbergen et al., 2011). Parents' differential pupil response to negative expressions may be partially related to the relatively reduced motion content of the neutral versus negative stimuli in the current experiment. However, given that a similar pupil dilation response was previously reported with static negative versus neutral faces (Bradley et al., 2008; Van Steenbergen et al., 2011), it is unlikely to fully account for this finding. It is also important to note that different from earlier adult studies where the order of presentation was completely randomized, the reference stimuli with the neutral expression always preceded the negative emotional expressions of a given model in the current experiment. Thus, although the reduced responding of parents' pupils to neutral expression may partially reflect order effects in addition to the emotion effects in this sample, in the light of consistent findings with earlier studies that used a randomized order, we conclude that the current findings revealing more dilated pupils to negative versus neutral faces in parents cannot be fully accounted by an order effect. In contrast, infants' pupil responses did not differ between neutral and fearful expressions, which is at odds with earlier evidence showing more pupil dilation to fearful than neutral stimuli in 6- and 12-month-olds (Geangu et al., 2011) and in 14- to 17-month-olds (Aktar et al., 2016) and less pupil dilation to fearful than neutral faces in 12- to 16-month-old infants (Aktar et al., 2018).

The differences in infant versus parent emotion processing mainly stem from differential responses to neutral faces, which was the reference in the current models (Figure 2). There may be at least two potential explanations for the lack of infants' differential responding to neutral faces. The first concerns the differences in the temporal dynamics of neutral as compared to emotional facial expressions. Dynamic expressions of neutral faces are relatively more static than emotional expressions as the movement towards the apex, and the specific muscle movements are absent, limiting the movement to eye blinks. This inherently less dynamic display of neutral faces by itself may have triggered a violation of expectations in infants, which is known to enhance infants' arousal and pupil response to neutral faces (see Krüger et al., 2019). Second, neutral expressions may have evoked enhanced pupillary arousal in infants because they are more likely to be perceived as ambiguous (Tottenham et al., 2013), especially in early development where positive facial expressions are the most prominent expression during early interactions with the caregiver. Relatively longer durations of parental neutral expressions in these interactions reflect emotionally flat interaction patterns of depressed parents (e.g., Aktar et al., 2017; Cohn et al., 1990; Murray et al., 2010). In fact, experimental studies investigating the causal effects of parents' depressed interaction patterns in typically developing infants focus on infants' reactions to the sudden change in parent's interaction, from predominantly positive to neutral expressions (i.e., the still-face effect, Mesman et al., 2009). This sensitivity to neutral faces may explain diminished differential responding to negative as compared to neutral facial expressions observed in the current study.

In additional exploratory analyses (presented in the section Additional Analyses on the Effect of Age on Infants' Pupillary Responses to Negative Emotion of the supplement), we found that infants' pupil responses across the three age groups did not differ as a function of negative emotion in the current sample. There was a significant effect of age, independent of emotion, revealing an increase in infants' pupillary arousal to faces through the first 18 months of life. This age-related increase was also reported in an earlier study on infants' pupil mimicry (Aktar et al., 2020). The current cross-sectional evidence suggests that emotion processing at the pupillary level is stable through the first 18 months. Future longitudinal studies investigating pupil response to negative emotion from infancy to toddlerhood and into early childhood will be essential to shed light on the developmental trajectories of pupillary arousal to negative stimuli.

2. Is there a direct association between parents' and infants' pupil responses to negative (vs. neutral) emotional expressions?

In the current study, we explored the direct association between infants' and parents' pupil responses to negative emotional expressions (after accounting for temporal differences summarized above). A positive association between infants' and parents' mean pupil responses to negative (vs. neutral) faces was evident despite the temporal differences in infants' and parents' pupil responses. Based on these findings, we conclude that the direct association in parents' and infants' physiological arousal may be already captured in the pupil responses to negative emotion as early as the first 18 months of life. Thus, the findings provide the first preliminary support for the argument that parents who show stronger and more vigilant pupil responses to negative and neutral emotions may have children who are also more vigilant toward negative and neutral emotions. It remains to be discovered whether this overlap is accounted for by genetic, or environmental influences in the familial transmission, in samples including clinical and subclinical populations of parents with young infants.

3. Are parental negative emotions and/or infant negative temperament related to infants' pupil responses to negative (vs. neutral) emotions?

In contrast to earlier evidence that revealed a link between higher levels of negative temperament and stronger pupil responses to negative faces in 14- to 17-month-olds (Aktar et al., 2016), infant temperament was not significantly related to pupil responses to negative emotional facial expressions in the current study. This finding is consistent with earlier evidence revealing no significant direct link between infants' temperamental negative affect and their pupil responses to static positive and negative emotions in 12- to 16-month-olds (Aktar et al., 2018). We conclude that temperamental dispositions may not be directly related to pupillary indices of arousal to negative emotion in typically developing infants.

The current findings suggest that infants' pupillary arousal was related to parents' negative emotion rather than their own temperamental characteristics, possibly reflecting environmental influences related to infants' exposure to parental negative emotion. With regard to the link between maternal negative emotion and infants' pupil responses to negative emotion, the results suggest positive associations between maternal negative emotions and infants' pupil responses to negative emotion. This effect was driven by the specific link between parents' stress and infants' pupil sizes in the current sample. This finding further adds to the inconsistencies in the earlier studies, which had revealed no significant link (Aktar et al., 2016) or a reverse association between more negative emotion in mothers and *less* pupil dilation to facial expressions of emotion (Aktar et al., 2018). It is important to note that parental stress was not included in the operationalization of parental negative emotion in the earlier studies that measured parents' negative affect, and/or depression, and anxiety in relation to infant pupils (Aktar et al., 2016; 2018). The findings from the post hoc exploratory analyses of the current study, however, reveal that this link is mainly driven by individual differences in parents' stress rather than anxiety or depression levels. In other words, it was parents' negative affect states characterizing generalized anxiety rather than depression or fearfulness/arousal that explained variance in infants' pupils (Brown et al., 1997). Thus, in addition to the differences in the choice of emotional stimuli, the inconsistencies between these earlier and current findings may be related to the fact that this positive association was mainly driven by parental stress in the current study.

The positive association between mothers' stress and infant pupillary responses to threat hints at an increased vigilance or emphasis toward negative faces as a result of maternal stress. In contrast, our findings show a marginally significant negative association between fathers' negative emotions and infants' pupil responses to angry faces, which are considered to be a direct signal for threat (as opposed to the indirect value of fearful faces that indicate danger in the environment, e.g., see Marsh et al., 2005). Earlier evidence that revealed no direct link between infants' pupillary responses and fathers' negative emotions may have not captured this link because parental stress was not part of the parental negative emotions measured in this earlier study (Aktar et al., 2016, 2018). Overall, it was clear that the father effects were smaller, and harder to detect, partially because they were specific to anger. The current findings highlight the importance of including fathers' negative emotions, especially stress in infant studies of emotion processing, and suggest that exposure to fathers' negative emotions may be related to a reduced vigilance in pupil responses of infants to angry faces.

The differential link of maternal and paternal negative emotions to infants' pupillary arousal may be related to the differences in the extent and content of exposure to the two parents' emotions in the first years of life. With respect to the extent of exposure, Gredebäck aet al. (2012) found that infants' pupillary arousal in response to negative emotional faces is influenced by how much time the infant spends with the parent. The differential associations of parents' stress levels with infants' pupillary arousal to negative faces in the current study may be related to a predominant exposure to mothers in early development. As a result, children may be more familiar with, and more attuned to, mothers' expressions. With respect to the content of exposure, studies examining infants' face-to-face interactions with their mothers and fathers find that the positive faces are more common when mothers versus fathers are interacting with the child, whereas neutral faces are more common with fathers (e.g., Aktar et al., 2017). The current study illustrates the value of incorporating both parents' negative emotions along with infant temperament in the study of infants' emotion processing.

The current associations between parental negative affect and infant pupil responses were specific to stress rather than depression or anxiety levels of the mothers and fathers. Thus, it seems that the variation in mothers' and fathers' experience of stress may specifically impact an infants' physiological responses to threat-relevant negative emotions in community samples. Note however that the relatively little variance observed in the depression and anxiety scores (see Table S1) may have limited our ability to detect an eventual association in this community sample. Stress, conceptualized as negative mood states linked to generalized anxiety levels (Brown et al., 1997), is not an uncommon experience in the early years of parenthood, reflecting parents' ability to adapt to new challenges of parenting. Current findings suggest that typically developing infants may be susceptible to exposure to those experiences of their parents. The findings highlight the importance of including parental stress in studies of infant emotion processing, especially in typical development, along with parental depression and anxiety measures (Aktar & Bögels, 2017).

4. Are parental negative emotions related to parents' pupil responses to negative (vs. neutral) emotions?

Finally, the current study investigated the associations between parents' negative emotions (depression, anxiety, and stress levels) and parents' pupil responses to negative (vs. neutral) emotions. No significant association was found between parents' negative emotions and pupillary arousal to negative faces. This finding is at odds with earlier evidence revealing a link between more negative affect and stronger pupillary responses to negative faces in adults (e.g., Bradley et al., 2008; Kret et al., 2013) and children (e.g., Burkhouse et al., 2015; Price et al., 2013). The lack of significant associations between parental negative emotions and pupillary responses may be related to the characteristics of this community sample, as the majority of the participating parents had little to mild levels of anxiety/depression/stress symptoms. Findings reveal the need to further specify the exact nature and potential moderators of the association between one's experience of negative emotions and their pupil responses to dynamic negative facial expressions.

4.1 | Limitations and future directions

The current study is the first to directly test and compare infants' and parents' pupillary arousal in a sample of infants and parents, and to include fathers in a study assessing the link between parental negative emotion and infant pupillary arousal. The following limitations should be considered while interpreting the current findings. First, it is important to note that reported associations of child and parent negative emotions with pupillary responses were cross-sectional and correlational and cannot directly address causal mechanisms. The only variable experimentally manipulated in the current design was emotion displayed in the task. The design, therefore, precludes any prospective or causal inferences on the effect of parental negative emotion and infant temperament on infants' pupillary arousal to negative facial expressions.

Second, the current study did not include direct observations of parents' negative emotions or infants' temperament. Parents' negative emotions and infant negative temperament were measured using questionnaires. Although questionnaires are widely used to measure negative emotional traits, parents' reports of infant temperament may be biased due to their psychopathology (Najman et al., 2000). This may at least partially explain the significant positive associations observed between parents' reports of their own negative emotions and their infants' negative temperament. Future studies should consider measuring the nature and the extent of infants' direct exposure to both parents' negative emotions and infant temperament using naturalistic observations along with self-report measures.

Third, although parents' emotion processing was incorporated in the current design, the pupil data were only available from one of the parents, the parent who visited the lab. Both parents, however, completed the questionnaires measuring their negative emotions and child temperament. Future investigations should consider incorporating both parents' pupillary responses for a more complete picture of environmental influences within the family.

Finally, it is important to highlight the limitations coming from the use of a physiological response that reflects general arousal rather than specific negative valence. Because the current study uses pupil responses, the reported associations between parental negative emotions and infant pupil responses may not be specific to negative faces but may extend to infants' pupil responses to positive (vs. neutral) expressions and parents' positive emotions. Future studies using pupillometry should consider investigating the specificity of these associations both on the positive and negative affect dimensions. On a related note, as briefly addressed above, our choice of neutral as reference for the pupillary responses to negative emotion comes with the limitation of reduced motion content in the reference stimuli, which may partially explain parents' differential pupillary responding to negative faces.

Despite these limitations, the findings of the current study expand our understanding of pupil responses in infants and parents and its links to mothers' and fathers' negative emotions. The current study reveals, for the first time that parents who show stronger pupil responses to negative and neutral stimuli have infants who also show stronger pupil responses to those stimuli. Moreover, the findings suggesting links of parents' stress levels with their own and their infants' pupillary responses to negative emotion reveal that everyday stress experiences of parents may shape their offspring's processing of emotion in the early years of parenthood.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTION

Evin Aktar designed the study, conducted the statistical analyses, and wrote the first draft of this manuscript under the guidance of Maartje E. J. Raaijmakers, Susan M. Bögels, and Mariska E. Kret, who all contributed to the refining of this initial design. Mariska E. Kret provided guidance on the statistical approach. Cosima A. Nimphy contributed to the data processing and statistical analyses and authored parts of the current manuscript. Koraly Pérez- authored parts of the discussion, provided guidance on the theoretical approach, and feedback on the earlier versions of the manuscript.

CODE AVAILABILITY

All codes used during data processing will be stored online within one month after publication to DataverseNL, available upon request from the corresponding author.

DATA AVAILABILITY STATEMENT

All raw data and materials and codes will be stored online within 1 month after publication to DataverseNL, available upon request from the corresponding author.

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REFERENCES

Aktar, E., & Bögels, S. (2017). Exposure to parents' negative emotions as a developmental pathway to the family aggregation of depression and anxiety in the first year of life. *Clinical Child and Family Psychology Review*, *20*, 369–390. https://doi.org/10.1007/s10567-017-0240-7

Aktar, E., Colonnesi, C., de Vente, W., Majdandžić, M., & Bögels, S. M. (2017). How do parents' depression and anxiety, and infants' negative temperament relate to parent–infant face-to-face interactions? *Development and Psychopathology*, *29*(3), 697–710. https://doi.org/10.1017/S0954579416000390

Aktar, E., Mandell, D. J., de Vente, W., Majdandžić, M., Oort, F. J., van Renswoude, D. R., Raijmakers, M. E. J., & Bögels, S. M. (2018). Parental negative emotions are related to behavioral and pupillary correlates of infants' attention to facial expressions of emotion. *Infant Behavior and Development*, *53*, 101–111. https://doi.org/10.1016/j.infbeh.2018.07.004

Aktar, E., Mandell, D. J., de Vente, W., Majdandžić, M., Raijmakers, M. E., & Bögels, S. M. (2016). Infants' temperament and mothers', and fathers' depression predict infants' attention to objects paired with emotional faces. *Journal of Abnormal Child Psychology*, *44*, 975–990. https://doi.org/10.1007/s10802-015-0085-9

Aktar, E., Raijmakers, M. E., & Kret, M. E. (2020). Pupil mimicry in infants and parents. *Cognition and Emotion*, *34*, 1160–1170. https://doi.org/10.1080/02699931.2020.1732875

Armstrong, T., & Olatunji, B. O. (2012). Eye tracking of attention in the affective disorders: A meta-analytic review and synthesis. *Clinical Psychology Review*, *32*(8), 704–723. https://doi.org/10.1016/j.cpr.2012.09.004

Aston-Jones, G., & Cohen, J. D. (2005). An integrative theory of locus coeruleus-norepinephrine function: Adaptive gain and optimal performance. *Annual Review of Neuroscience*, *28*(1), 403–450. https://doi.org/10.1146/annurev.neuro.28.061604.135709

Barrera, M. E., & Maurer, D. (1981). Recognition of mother's photographed face by the three-month-old infant. *Child Development*, *52*, 714–716. https://doi.org/10.2307/1129196

Barrett, K. C., & Campos, J. J. (1987). Perspectives on emotional development II: A functionalist approach to emotions. In J. D. Osofsky, & J. D. Osofsky (Eds.), *Handbook of infant development. 2* (pp. 555–578). John Wiley & Sons.

Bradley, M. M., Miccoli, L., Escrig, M. A., & Lang, P. J. (2008). The pupil as a measure of emotional arousal and autonomic activation. *Psychophysiology*, *45*, 602–607. https://doi.org/10.1111/j.1469-8986.2008.00654.x

Brown, T. A., Chorpita, B. F., Korotitsch, W., & Barlow, D. H. (1997). Psychometric properties of the Depression Anxiety Stress Scales (DASS) in clinical samples. *Behaviour Research and Therapy*, *35*(1), 79–89. https://doi.org/10.1016/S0005-7967(96)00068-X

Burkhouse, K. L., Siegle, G. J., & Gibb, B. E. (2014). Pupillary reactivity to emotional stimuli in children of depressed and anxious mothers. *Journal of Child Psychology and Psychiatry*, *55*(9), 1009–1016. https://doi.org/10.1111/jcpp.12225

Burkhouse, K. L., Siegle, G. J., Woody, M. L., Kudinova, A. Y., & Gibb, B. E. (2015). Pupillary reactivity to sad stimuli as a biomarker of depression risk: Evidence from a prospective study of children. *Journal of Abnormal Psychology*, *124*(3), 498–506. https://doi.org/10.1037/abn0000072

Bushneil, I. W. R., Sai, F., & Mullin, J. T. (1989). Neonatal recognition of the mother's face. *British Journal of Developmental Psychology*, *7*(1), 3–15. https://doi.org/10.1111/j.2044-835X.1989.tb00784.x

Campos, J. J., Anderson, D. I., Barbu-Roth, M. A., Hubbard, E. M., Hertenstein, M. J., & Witherington, D. (2000). Travel broadens the mind. *Infancy*, *1*(2), 149–219. https://doi.org/10.1207/S15327078IN0102_1

Cascardi, M., Armstrong, D., Chung, L., & Paré, D. (2015). Pupil response to threat in trauma-exposed individuals with or without PTSD. *Journal of Traumatic Stress*, *28*(4), 370–374. https://doi.org/10.1002/jts.22022

Clearfield, M. W. (2011). Learning to walk changes infants' social interactions. *Infant Behavior and Development*, *34*(1), 15–25. https://doi.org/10.1016/j.infbeh.2010.04.008

Cohn, J. F., Campbell, S. B., Matias, R., & Hopkins, J. (1990). Face-to-face interactions of postpartum depressed and nondepressed mother-infant pairs at 2 months. *Developmental Psychology*, *26*, 15–23. https://doi.org/10.1037/0012-1649.26.1.15

De Haan, M., Belsky, J., Reid, V., Volein, A., & Johnson, M. H. (2004). Maternal personality and infants' neural and visual responsivity to facial expressions of emotion. *Journal of Child Psychology and Psychiatry*, *45*, 1209–1218. https://doi.org/10.1111/j.1469-7610.2004.00320.x

De Klerk, C. C., Hamilton, A. F. D. C., & Southgate, V. (2018). Eye contact modulates facial mimicry in 4-month-old infants: An EMG and fNIRS study. *Cortex: A Journal Devoted to the Study of the Nervous System and Behavior*, *106*, 93–103. https://doi.org/10.1016/j.cortex.2018.05.002

Fawcett, C., Arslan, M., Falck-Ytter, T., Roeyers, H., & Gredebäck, G. (2017). Human eyes with dilated pupils induce pupillary contagion in infants. *Scientific Reports*, *7*, 9601. https://doi.org/10.1038/s41598-017-08223-3

Fawcett, C., Wesevich, V., & Gredebäck, G. (2016). Pupillary contagion in infancy: Evidence for spontaneous transfer of arousal. *Psychological Science*, *27*, 997–1003. https://doi.org/10.1177/0956797616643924

Feinman, S., Roberts, D., Hsieh, K., Sawyer, D., & Swanson, D. (1992). A critical review of social referencing in infancy. In S. Feinman (Ed.), *Social referencing and the social construction of reality in infancy* (pp. 4–15). Plenum Press. https://doi.org/10.1007/978-1-4899-2462-9_2

Feldman, R., Magori-Cohen, R., Galili, G., Singer, M., & Louzoun, Y. (2011). Mother and infant coordinate heart rhythms through episodes of interaction synchrony. *Infant Behavior and Development*, *34*(4), 569–577. https://doi.org/10.1016/j.infbeh.2011.06.008

Feldman, R. (2003). Infant–mother and infant–father synchrony: The coregulation of positive arousal. *Infant Mental Health Journal: Official Publication of The World Association for Infant Mental Health*, *24*(1), 1–23. https://doi.org/10.1002/imhj.10041

Feldman, R. (2007). Parent–infant synchrony and the construction of shared timing; physiological precursors, developmental outcomes, and risk conditions. *Journal of Child Psychology and Psychiatry*, *48*(3-4), 329–354. https://doi.org/10.1111/j.1469-7610.2006.01701.x

Frank, M. C., Vul, E., & Johnson, S. P. (2009). Development of infants' attention to faces during the first year. *Cognition*, *110*(2), 160–170. https://doi.org/10.1016/j.cognition.2008.11.010

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

Geangu, E., Hauf, P., Bhardwaj, R., & Bentz, W. (2011). Infant pupil diameter changes in response to others' positive and negative emotions. *PLoS One*, *6*(11), e27132. https://doi.org/10.1371/journal.pone.0027132

Gredebäck, G., Eriksson, M., Schmitow, C., Laeng, B., & Stenberg, G. (2012). Individual differences in face processing: Infants' scanning patterns and pupil dilations are influenced by the distribution of parental leave. *Infancy*, *17*(1), 79–101. https://doi.org/10.1111/j.1532-7078.2011.00091.x

Heck, A., Hock, A., White, H., Jubran, R., & Bhatt, R. S. (2016). The development of attention to dynamic facial emotions. *Journal of Experimental Child Psychology*, *147*, 100–110. https://doi.org/10.1016/j.jecp.2016.03.005

Hepach, R., Vaish, A., & Tomasello, M. (2015). Novel paradigms to measure variability of behavior in early childhood: Posture, gaze, and pupil dilation. *Frontiers in Psychology*, *6*, 858. https://doi.org/10.3389/fpsyg.2015.00858

Hepach, R., & Westermann, G. (2016). Pupillometry in Infancy Research. *Journal of Cognition and Development*, *17*(3), 359–377. https://doi.org/10.1080/15248372.2015.1135801

Isomura, T., & Nakano, T. (2016). Automatic facial mimicry in response to dynamic emotional stimuli in five-month-old infants. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1844), 20161948. https://doi.org/10.1098/rspb.2016.1948

Jessen, S., Altvater-Mackensen, N., & Grossmann, T. (2016). Pupillary responses reveal infants' discrimination of facial emotions independent of conscious perception. *Cognition*, *150*, 163–169. https://doi.org/10.1016/j.cognition.2016.02.010

Jackson, I., & Sirois, S. (2009). Infant cognition: Going full factorial with pupil dilation. *Developmental Science*, *12*(4), 670–679. https://doi.org/10.1111/j.1467-7687.2008.00805.x

Johnson, M. H., Dziurawiec, S., Ellis, H., & Morton, J. (1991). Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition*, *40*(1–2), 1–19. https://doi.org/10.1016/00100277(91)90045-6

Kelly, D. J., Duarte, S., Meary, D., Bindemann, M., & Pascalis, O. (2019). Infants rapidly detect human faces in complex naturalistic visual scenes. *Developmental Science*, *22*, e12829. https://doi.org/10.1111/desc.12829

Kimble, M., Fleming, K., Bandy, C., Kim, J., & Zambetti, A. (2010). Eye tracking and visual attention to threating stimuli in veterans of the Iraq war. *Journal of Anxiety Disorders*, *24*(3), 293–299. https://doi.org/10.1016/j.janxdis.2009.12.006

Kotsoni, E., de Haan, M., & Johnson, M. H. (2001). Categorical perception of facial expressions by 7-month-old infants. *Perception*, *30*(9), 1115–1125. https://doi.org/10.1068/p3155

Kret, M. E., Roelofs, K., Stekelenburg, J., & de Gelder, B. (2013a). Emotional signals from faces, bodies and scenes influence observers' face expressions, fixations and pupil-size. *Frontiers in Human Neuroscience*, *7*, 810. https://doi.org/10.3389/fnhum.2013.00810

Kret, M., Stekelenburg, J., Roelofs, K., & De Gelder, B. (2013b). Perception of face and body expressions using electromyography, pupillometry and gaze measures. *Frontiers in Psychology*, *4*, 28. https://doi.org/10.3389/fpsyg.2013.00028

Krüger, M., Bartels, W., & Krist, H. (2019). Illuminating the dark ages: Pupil dilation as a measure of expectancy violation across the life span. *Child Development*, *91*(6), 2221–2236. https://doi.org/10.1111/cdev.13354

Laeng, B., Sirois, S., & Gredebäck, G. (2012). Pupillometry: A window to the preconscious? *Perspectives on Psychological Science*, *7*(1), 18–27. https://doi.org/10.1177/1745691611427305

Leppänen, J. M. (2016). Using eye tracking to understand infants' attentional bias for faces. *Child Development Perspectives*, *10*(3), 161–165. https://doi.org/10.1111/cdep.12180

Leppänen, J. M., Moulson, M. C., Vogel-Farley, V. K., & Nelson, C. A. (2007). An ERP study of emotional face processing in the adult and infant brain. *Child Development*, *78*, 232–245. https://doi.org/10.1111/j.1467-8624.2007.00994.x

Leppänen, J., Peltola, M. J., Mäntymaa, M., Koivuluoma, M., Salminen, A., & Puura, K. (2010). Cardiac and behavioral evidence for emotional influences on attention in 7-month-old infants. *International Journal of Behavioral Development*, *34*(6), 547–553. https://doi.org/10.1177/0165025410365804

LoBue, V., Pérez-Edgar, K., & Buss, K. A. (Eds.). (2019). *Handbook of emotional development*. Springer.

Lovibond, P. F., & Lovibond, S. H. (1995). The structure of negative emotional states: Comparison of the Depression Anxiety Stress Scales (DASS) with the Beck Depression and Anxiety Inventories. *Behaviour Research and Therapy*, *33*, 335–343. https://doi.org/10.1016/0005-7967(94)00075-U

Maas, C., & Hox, J. (2005). Sufficient sample sizes for multilevel modeling. *Methodology: European Journal of Research Methods for the Behavioral and Social Sciences*, *1*(3), 86–92. https://doi.org/10.1027/1614-2241.1.3.86

Marsh, A. A., Ambady, N., & Kleck, R. E. (2005). The effects of fear and anger facial expressions on approach-and avoidance-related behaviors. *Emotion (Washington, D.C.)*, *5*(1), 119–124. https://doi.org/10.1037/1528-3542.5.1.119

Meltzoff, A. N., & Moore, M. K. (1994). Imitation, memory, and the representation of persons. *Infant Behavior and Development*, *17*(1), 83–99. https://doi.org/10.1016/0163-6383(94)90024-8

Mesman, J., van IJzendoorn, M., & Bakermans-Kranenburg, M. (2009). The many faces of the Still-Face Paradigm: A review and meta-analysis. *Developmental Review*, *29*(2), 120–162. https://doi.org/10.1016/j.dr.2009.02.001

Morales, S., & Fox, N. A. (2019). A neuroscience perspective on emotional development. In V. LoBue, K. Pérez-Edgar, & K. Buss (Eds.), *Handbook of emotional development*. (pp. 57–81). Springer.

Murray, L., Halligan, S., & Cooper, P. (2010). Effects of postnatal depression on mother–infant interactions and child development. In J. G. Bremner, & T. D. Wachs (Eds.), *The Wiley-Blackwell handbook of infant development* (Vol. 2, 2nd ed., pp. 192–220). Wiley-Blackwell.

Najman, J. M., Williams, G. M., Nikles, J., Spence, S., Bor, W., O'Callaghan, M., Le Brocque, R., & Andersen, M. J. (2000). Mothers' mental illness and child behavior problems: Cause-effect association or observation bias? *Journal of the American Academy of Child & Adolescent Psychiatry*, *39*, 592–602. https://doi.org/10.1097/00004583-200005000-00013

Nakagawa, A., & Sukigara, M. (2012). Difficulty in disengaging from threat and temperamental negative affectivity in early life: A longitudinal study of infants aged 12–36 months. *Behavioral and Brain Functions*, *8*(1), 40. https://doi.org/10.1186/1744-9081-8-40

Nelson, C. A., & Dolgin, K. G. (1985). The generalized discrimination of facial expressions by seven-month-old infants. *Child Development*, *56*, 58–61. https://doi.org/10.2307/1130173

Partala, T., & Surakka, V. (2003). Pupil size variation as an indication of affective processing. *International Journal of Human-computer Studies*, *59*(1-2), 185–198. https://doi.org/10.1016/S1071-5819(03)00017-X

Pascalis, O., de Schonen, S., Morton, J., Deruelle, C., & Fabre-Grenet, M. (1995). Mother's face recognition by neonates: A replication and an extension. *Infant Behavior and Development*, *18*(1), 79–85. https://doi.org/10.1016/0163-6383(95)90009-8

Peltola, M. J., Hietanen, J. K., Forssman, L., & Leppänen, J. M. (2013). The emergence and stability of the attentional bias to fearful faces in infancy. *Infancy*, *18*(6), 905–926. https://doi.org/10.1111/infa.12013

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

Price, R. B., Siegle, G. J., Silk, J. S., Ladouceur, C., McFarland, A., Dahl, R. E., & Ryan, N. D. (2013). Sustained neural alterations in anxious youth performing an attentional bias task: A pupilometry study. *Depression and Anxiety*, *30*(1), 22–30. https://doi.org/10.1002/da.21966

Reid, V. M., & Striano, T. (2007). The directed attention model of infant social cognition. *European Journal of Developmental Psychology*, *4*(1), 100–110. https://doi.org/10.1080/17405620601005648

Sai, F. Z. (2005). The role of the mother's voice in developing mother's face preference: Evidence for intermodal perception at birth. *Infant and Child Development*, *14*(1), 29–50. https://doi.org/10.1002/icd.376

Siegle, G., Granholm, E., Ingram, R., & Matt, G. (2001). Pupillary and reaction time measures of sustained processing of negative information in depression. *Biological Psychiatry*, *49*(7), 624–636. https://doi.org/10.1016/S0006-3223(00)01024-6

Tottenham, N., Phuong, J., Flannery, J., Gabard-Durnam, L., & Goff, B. (2013). A negativity bias for ambiguous facial-expression valence during childhood: Converging evidence from behavior and facial corrugator muscle responses. *Emotion (Washington, D.C.)*, *13*(1), 92–103. https://doi.org/10.1037/a0029431

Tronick, E. Z. (2007). *The neurobehavioral and social-emotional development of infants and children*. Norton. https://doi.org/10.1002/imhj.21533

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

Valenza, E., Simion, F., Cassia, V. M., & Umiltà, C. (1996). Face preference at birth. *Journal of Experimental Psychology: Human Perception and Performance*, *22*(4), 892–903. https://doi.org/10.1037/0096-1523.22.4.892

van der Schalk, J., Hawk, S. T., Fischer, A. H., & Doosje, B. (2011). Moving faces, looking places: Validation of the Amsterdam Dynamic Facial Expression Set (ADFES). *Emotion (Washington, D.C.)*, *11*(4), 907–920. https://doi.org/10.1037/a0023853

Van Steenbergen, H., Band, G. P., & Hommel, B. (2011). Threat but not arousal narrows attention: Evidence from pupil dilation and saccade control. *Frontiers in Psychology*, *2*, 281. https://doi.org/10.3389/fpsyg.2011.00281

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