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RESEARCH ARTICLE

Seven-months-old infants show increased arousal to static emotion body expressions: Evidence from pupil dilation

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Abstract

Human body postures provide perceptual cues that can be used to discriminate and recognize emotions. It was previously found that 7-months-olds' fixation patterns discriminated fear from other emotion body expressions but it is not clear whether they also process the emotional content of those expressions. The emotional content of visual stimuli can increase arousal level resulting in pupil dilations. To provide evidence that infants also process the emotional content of expressions, we analyzed variations in pupil in response to emotion stimuli. Forty-eight 7-months-old infants viewed adult body postures expressing anger, fear, happiness and neutral expressions, while their pupil size was measured. There was a significant emotion effect between 1040 and 1640 ms after image onset, when fear elicited larger pupil dilations than neutral expressions. A similar trend was found for anger expressions. Our results suggest that infants have increased arousal to negative-valence body expressions. Thus, in combination with previous fixation results, the pupil data show that infants as young as 7-months can perceptually discriminate static body expressions and process the emotional content of those expressions. The results extend information about infant processing of emotion expressions conveyed through other means (e.g., faces).

1 | INTRODUCTION

Observers often need to infer other people's emotional state for effective social interactions. It is well established that adults use a combination of perceptual cues ranging from facial, vocal and body expressions, including body temperature and odor, to perceptually discriminate and recognize other people's emotional state (Belin et al., 2011; de Gelder, 2009; de Groot & Smeets, 2017; Keltner et al., 2016; Robinson et al., 2012; Rosen et al., 2015; Salazar-López et al., 2015). The development of emotion processing is therefore an important function to investigate, particularly during the critical first 2 years of life when social communication is largely reliant on non-verbal means (e.g., Crespo-Llado, Vanderwert, & Geangu, 2018; Geangu, 2008, 2015; Lepp*ä*nen & Nelson, 2009; Miguel et al., 2019; Quadrelli et al., 2019; Zieber et al., 2014).

A prominent view for the development of emotion processing is that infants learn to extract a variety of perceptual cues from their everyday environment about people's emotions and their communicative value (Campos et al., 1994; Leppänen & Nelson, 2009; Smith et al., 2018; Walle & Lopez, 2020; Widen, 2013). Infants frequently have people in their view from the first days after birth (Jayaraman et al., 2017). There is a prevalence of faces in infants' visual experiences during the first 4 months after birth, providing them opportunities to learn perceptual cues from faces associated with different emotions. After this age, this prevalence shifts toward other body regions and parts, with a larger proportion of bodies than faces emerging between 6 and 9 months old (Fausey et al., 2016; Jayaraman et al., 2017). These changes increase infants' opportunities to extract perceptual cues from body postures associated with different emotion expressions (e.g., the extended arms for happiness or the contracted arms around the upper body for fear; Smith et al., 2018). These changes also increase the opportunities infants have to learn the relation between the emotion body expressions and the social and non-social contexts in which they occur, further contributing to the development of their ability to process the emotional content and communicative value of these expressions (Campos et al., 1994; Leppänen & Nelson, 2009; Walle & Lopez, 2020; Widen, 2013). These experiences during maturation may further lead to appropriate neuro-physiological responses associated with different emotions.

Despite the variety of perceptual cues for emotions, most infancy research focuses on faces (Bayet & Nelson, 2019; Geangu, Ichikawa, et al., 2016; van den Boomen et al., 2021). There is, however, a growing number of studies using a variety of neural and behavioral paradigms which provide evidence that infants can discriminate perceptual cues related to the emotional content of dynamic and static body expressions by 7 months old (Geangu & Vuong, 2020; Heck et al., 2018; Hock et al., 2017; Missana et al., 2014, 2015; Missana & Grossmann, 2015; Ogren et al., 2019; Zieber et al., 2014). For example, Missana et al. (2014) found larger event-related potential (ERP) responses to fear compared to happy body expressions in 8-months-old infants in an early N290 component (i.e., a negative deflection around 290 ms after stimulus onset). The differential response of the N290 to different expressions suggests that structural information relevant for emotions may be extracted relatively fast and integrated in the perceptual representations of bodies. Infant studies also found larger ERP responses to fear compared to happy body expressions in later components, such as a central negativity (Nc) component occurring around 400–800 ms after stimulus onset. This finding suggests that infants at this age allocate more attention to processing fear compared to happy body expressions (Krol et al., 2015; Missana et al., 2014; Rajhans et al., 2016). Recently, eye tracking was used to compare and contrast 7-months-old infants' visual exploration behaviors when viewing static female adult body postures expressing anger, fear, happiness and an emotionally neutral posture (Geangu & Vuong, 2020). The analyses of looking times and fixations from the eye-movement data suggest that infants at this age fixate on the upper body region for discriminating fear body expressions from the other expressions.

Collectively, neural and behavioral studies suggest that by 7 months old, infants allocate attentional resources and extract relevant perceptual cues related to different body expressions (Hock et al., 2017; Missana et al., 2014, 2015; Missana & Grossmann, 2015) but there is no clear evidence that infants process the emotional content of the body expressions. The emotional content of visual stimuli can increase arousal levels (Bradley et al., 2008). To address the gap in the literature, we analyzed the pupil data from the infants in Geangu and Vuong (2020) as dilations in pupil size generally reflect increased arousal in response to emotion stimuli and thus provide a better marker of emotion processing (Bradley et al., 2008; Geangu et al., 2011; Kret et al., 2013).

Changes to pupil size are controlled by the sympathetic and parasympathetic branches of the autonomic system which dilates or constricts the pupil, respectively. Although the primary function of the pupils is to regulate the amount of light entering the retina, their size oscillates continuously even under constant lighting conditions reflecting a homeostasis of sympathetic and parasympathetic activity. Moreover as the autonomic system is linked to the limbic system, pupillary responses has been shown to correlate with arousal induced by cognitive load or emotional stimuli (Hepach & Westermann, 2016; Sirois & Brisson, 2014; Tummeltshammer et al., 2019). These responses are tightly linked to locus coeruleus neurons which release norepinephrine (NE) that modulates arousal levels. In adults, pupils show larger dilations to emotionally arousing visual scenes and bodies, which correlate positively with other physiological measures of arousal such as heart rate, electrodermal activity (i.e., skin conductance) and facial muscle activity (Bradley et al., 2008; Kret et al., 2013). Thus, pupil data can complement eye-movement and ERP data to provide a better understanding of the developmental trajectory of different perceptual, cognitive and affective processes, such as perceptual and cognitive expectations (Jackson & Sirois, 2009; Zhang et al., 2018), human action processing (Gredebäck & Melinder, 2011; Verschoor et al., 2015), time estimation (Addyman et al., 2014), emotion recognition (Geangu et al., 2011; Upshaw et al., 2015) and threat perception (Hoehl et al., 2017).

Several infant studies have shown that pupil responses can be increased or decreased by the emotional content of facial expressions in infants as young as 6 months old (Aktar et al., 2018; Geangu et al., 2011; Jessen et al., 2016; Upshaw et al., 2015). The effect of emotion on pupil dilation can be further modulated by different factors such as the stimuli used, the presence of facial motion (i.e., dynamic vs. static expressions; Prunty et al., 2022), or the characteristics of parenting (Aktar et al., 2021; Gredebäck et al., 2012; Upshaw et al., 2015). For example, Aktar et al. (2018) showed smaller pupil dilations for static facial expressions of fear relative to neutral expressions (and to happy expressions to some extent) in 12- to 16-months-old infants. A similar finding was shown for 7-months-old infants (Jessen et al., 2016). In another study, Geangu et al. (2011) tested 6- and 12-months-old infants with more naturalistic 25-s videos containing other infants' facial and vocal expressions. The expressions in each video was either positive (happiness, laughter), neutral or negative (anger, crying). Pupil dilations were larger for positive and negative videos relative to neutral ones. It is worth noting that for both age groups there were more periods during which pupil dilations were larger to negative relative to neutral videos compared to positive relative to neutral videos. There were also periods when pupil dilations were larger to negative compared to positive videos, suggesting the presence of a negativity bias. More generally beyond social stimuli such as faces or bodies, infants as young as 6-months-old showed increased pupil dilations to perceptual cues associated with non-facial stimuli that can be (evolutionarily) fearful or threatening (e.g., snakes; Hoehl et al., 2017). Importantly the increased pupil dilations to anger and fear compared to other body expressions, and to other non-social threatening stimuli, seem to continue into adulthood (Bradley et al., 2017; Kret et al., 2013).

Despite the potential insights into the development of emotion processing provided by pupil data, to the best of our knowledge no studies to date have measured pupil dilation to investigate infants'

emotion processing of body expressions. The aim of the current study was to determine whether in 7-months-old infants, anger, fear, happy and emotionally neutral static body postures elicit different levels of arousal, by analyzing the pupil data from Geangu and Vuong (2020). We hypothesized that pupil dilations will be modulated by the emotional content of the body expressions because dilations are driven by the LC-NE system which modulates arousal levels (Hepach & Westermann, 2016; Sirois & Brisson, 2014; Tummeltshammer et al., 2019). Anger and fear expressions tend to be more emotionally arousing than happy and neutral expressions (He et al., 2018; Mondloch et al., 2013). Moreover, the LC-NE system is linked to the limbic system; thus, fearful or threatening stimuli may lead to larger pupil dilations (Bradley et al., 2017; Hoehl et al., 2017). Lastly, Geangu and Vuong's analyses of the eye-movement data showed that the infants discriminated fear (and to some extent anger) body expressions from the other expressions. Given the predominant findings in the infant and adult literature, we predicted that pupil dilations will be increased by more arousing body expressions such as fear and anger.

2 | METHOD

2.1 | Participants

Sixty 7-months-old infants (30 females; $M = 227$ days, $SD = 8$ days) were tested. They were recruited from urban and semi-urban areas in the North of England. In this study, we analyzed pupil data from the same 48 infants as in Geangu and Vuong (2020). These infants had more than 30% of their proportion of fixations on bodies, at least 2 out of 5 trials per emotion, and at least 10 trials in total. The present study was conducted according to guidelines laid down in the Declaration of Helsinki, with written informed consent obtained from a parent or guardian for each child before any assessment or data collection. All procedures involving human participants in this study were approved by the University Ethics Committee at Lancaster University.

2.2 | Stimuli

The stimuli consisted of images of female body postures expressing anger, fear, happiness and an emotionally-neutral state from de Gelder and van den Stock (2011). There were 5 stimuli for each emotion (20 stimuli in total). The body stimuli were presented as greyscale images and roughly centered on a uniform gray background (gray level = 128) with the estimated location of the belly button at the center of the screen. The entire body stimulus occupied ~6% of the image on average and had a mean stimulus luminance between 45 and 73 (out of 255). See Supplementary Materials for more information (adapted from Geangu & Vuong, 2020).

2.3 | Apparatus

A Tobii X120 system (Tobii Technology) was used to binocularly track infants' eye movements and pupil dilations. Gaze position and pupil dilation were sampled at 60 Hz, with a spatial resolution of $0.5°$ and a drift of $< 0.3°$. Infants sat on their parent's lap in a cubicle which had thick black curtains to either side to minimize environmental distractions. There was approximately 60–70 cm between the infant head and the monitor screen (1920 × 1080 pixel resolution). An infant-specific 5-points calibration procedure was used. All infants were tested with normal lighting conditions.
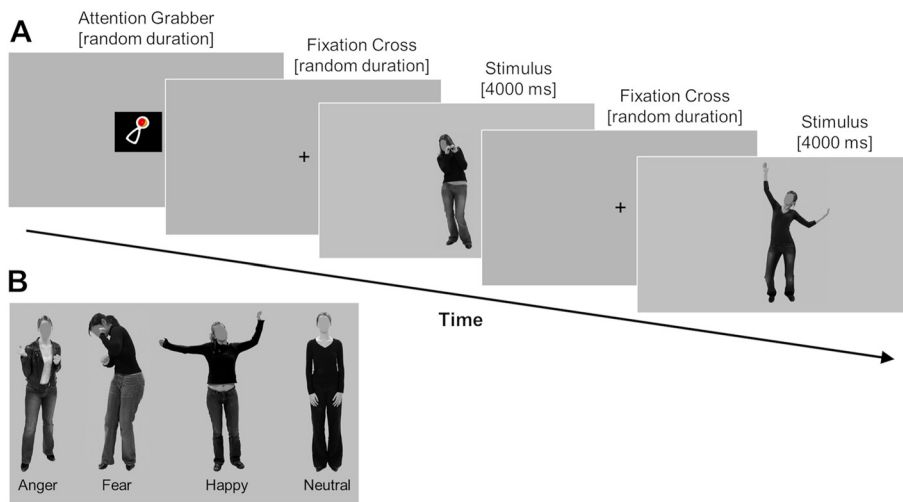
FIGURE 1   (a) The sequence of events during the experiment. An attention grabber could be used to attract infants' attention to the screen. Once infants fixated on the cross, the experimenter pressed the space bar to present the next stimulus. If infants looked away from the screen, the experimenter presented the attention grabber again. (b) An example of each of the four static body expressions.

2.4 | Design and procedure

Figure 1 illustrates the sequence of events across trials and an example body image for each expression. At the beginning of each trial, an attention grabber could be used to attract infants' attention if they were not looking at the screen. This attention grabber consisted of a colorful moving shape presented at the center of a gray screen, along with a pleasant sound. Once the infant fixated on the attention grabber, the experimenter pressed the space bar to present a black cross at the center of a gray screen. The experimenter pressed the space bar again when the infant fixated on the cross. This procedure ensured that infants began the body exploration from the same location. Following this, a body stimulus was presented for 4 s. The body's belly button was aligned with the fixation cross. The body stimulus was then replaced by a fixation cross (or an attention grabber if infants were not looking at the screen). The next trial began when the infant fixated on the cross; thus the inter-trial duration varied within and between infants. Infants were presented with all 20 body stimuli on separate trials. The stimuli were presented in four randomized orders, and infants were randomly assigned to one of these orders.

2.5 | Pupil data pre-processing

For each infant and trial, we used Tobii Studio (version 3.3.1; Tobii Technology) to extract the left and right eye pupil size (in mm) at each time point from 1000 ms before the onset of the body stimulus to the offset of the body stimulus (5000 ms total). The 1000-ms pre-onset time points included the presentation of the fixation cross (see Figure 1). All time points marked as invalid by Tobii Studio were removed. We then used the *pupil size* Matlab toolbox to pre-process the pupil size time series to remove invalid time points due to blinks and other artifacts to generate a smooth time series for further analyses (Kret & Sjak-Shie, 2019). For each eye, dilation speed outliers and edge artifacts, trend-line deviation outliers, and temporally isolated samples were removed using

the toolbox's default parameter values. Next, missing time points in one eye were replaced with data from corresponding time points from the other eye if present, and the time points were then averaged across the two eyes. Lastly, the mean time series were up-sampled to 1000 Hz and smoothed using a zero-phase low-pass filter with a 4-Hz cut-off frequency using the toolbox's default parameter values.

We next averaged the pre-processed time series for each infant across trials from the same emotional body expression, and down-sampled the trial-averaged time series to 50 Hz. Trial averaging helped to address cases when valid samples were missing from both eyes on any individual trial. Any gaps in the trial-averaged data were interpolated as follows: first, gaps were replaced with the mean pupil size for that body expression; then the time series was smoothed with a moving median (10 time point window = 200 ms); and lastly the smoothed time series was convolved with a 100-ms kernel of uniform weight. The trial-averaged time series were clipped to 900 ms before stimulus onset to 3900-ms to remove artifacts at the beginning and end of the time series due to the interpolation. We then computed the median pupil size during the 900-ms baseline period to correct for trial-by-trial variations in pupil size and subtracted this median value from each time point of the trial-averaged time series, resulting in a baseline-corrected pupil-size change time series.

The resampling and interpolation steps during pre-processing reduce variance in the data which can increase Type I errors (i.e., false positives). This reduction is illustrated in the Supplementary Materials. It is important to bear this in mind, particularly for infant data, as different eye trackers have different sampling rates and different pupil-analysis packages may be optimized for different sampling rates (typically for high sampling).

2.6 | Functional data analysis

The pupil-size change time series per emotion body expression across the 48 infants were submitted to a functional data analysis (FDA; Geangu et al., 2011; Jackson & Sirois, 2009; Ramsay & Silverman, 1997). Within the FDA framework, we conducted a functional analysis of variance (ANOVA) with emotion body expression as a within-subjects factors. The F-value time series was calculated, and any time points which exceeded a critical F-value were considered significant. We conducted 2-tailed post-hoc functional t-tests to compare possible pairs of body expressions (6 possible pairs) for significant time points from the functional ANOVA. The t-value time series for each pair was calculated, and compared to the uncorrected critical t-value and the Bonferroni-corrected critical t-value (for 6 pairs). An alpha level of 0.05 was used for all statistical tests.

2.7 | Additional analyses

The FDA represents our primary analysis to test our hypotheses. We also carried out additional analyses to better understand the relationship between pupil dilation and eye movements, and between pupil dilation and low-level image properties. First as an exploratory analysis, we tested whether there was a correlation between pupil dilation and the fixation parameters reported in the earlier analyses (Geangu & Vuong, 2020). Second, we conducted an analysis of covariance (ANCOVA) to determine the extent to which any emotion effect were accounted for by low-level image properties, that is, stimulus luminance and visual saliency (Geangu et al., 2011; Geangu & Vuong, 2020). See Supplementary Materials for more information.

3 | RESULTS

3.1 | Pupil size changes

Figure 2a shows the mean pupil size change over time as a function of emotional body expression, averaged across infants. Figure 2b shows the F-value at each time point computed from the functional ANOVA. We found a main effect of body expression between 1040 and 1640 ms after image onset, critical $F(3,141) = 2.67$, $p < 0.05$ (dashed horizontal line). Given the main effect of body expression, we conducted post-hoc t-tests comparing difference between the time series for pairs of emotional body expressions. Figure 2c shows the t-value at each time point computed from the functional t-tests. The pair-wise comparisons showed that during the period between 1040 and 1640 ms (gray region), only fear body expressions elicited significantly larger pupil dilation than neutral expressions, corrected critical $t(47) = 2.75$, $p < 0.05$ (dashed horizontal line). There was a trend for anger body expressions to elicit larger dilation than neutral expressions, uncorrected critical $t(47) = 2.01$, $p < 0.05$ (solid horizontal line). No differences were found between happy and neutral expressions during this period. Figure 2d presents the mean pupil size within the significant time period identified by the functional ANOVA. To help with data interpretation and future research, we also calculated Cohen's d for paired samples as a measure of effect size. This calculation was carried out for the mean pupil size reported in Figure 2d and are as follows for the 6 pairs: $d_{A-F} = 0.04$, $d_{A-H} = 0.30$, $d_{A-N} = 0.36$, $d_{F-H} = 0.33$, $d_{F-N} = 0.39$ and $d_{H-N} = 0.06$. There was small to moderate effect sizes for negative body expressions (anger, fear) compared to happy (positive) and neutral expressions.
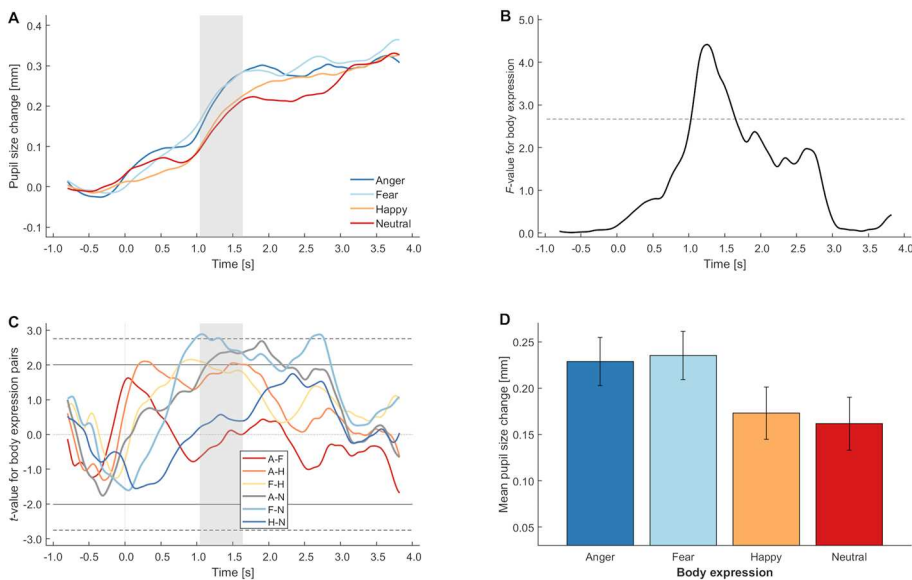

FIGURE 2 (a) Baseline-corrected pupil size changes (mm) as a function of emotional body expression and time from stimulus onset (at 0 s). The shaded gray region represents the significant time points from the functional analysis of variance (ANOVA). (b) Functional F-test with body expression as a within-subjects factor. The dashed line reflect the critical F-value. (c) Functional post-hoc t-tests to compare body-expression pairs. The dashed lines reflect the Bonferroni-corrected critical t-value and the solid horizontal lines reflect the uncorrected critical t-value. The shaded gray region represents the significant time points from the functional ANOVA. A = anger, F = fear; H = happy; N = neutral. (d) The mean pupil size change as a function of body expression averaged across significant time points (shaded gray region) from the functional ANOVA.

TABLE 1 Correlation (Pearson *r*) of difference scores (Emotion—Neutral) between pupil dilation and each fixation parameter on the upper body region as a function of emotion. *Prop fix* = proportion of fixation; *prop look* = proportion of looking times; *fix dur* = mean fixation duration; *# fix* = number of fixations.

		Pupil dilation		
Fixation parameter		**Anger**	**Fear**	**Happy**
prop fix	Anger	−0.204	−0.104	−0.016
	Fear	−0.163	−0.363**	−0.090
	Happy	0.041	−0.096	−0.084
prop look	Anger	0.037	−0.054	−0.008
	Fear	−0.181	−0.369**	−0.145
	Happy	0.007	−0.127	−0.131
fix dur	Anger	0.107	−0.051	0.189
	Fear	−0.075	−0.190	0.026
	Happy	0.058	−0.185	0.092
# fix	Anger	−0.215	−0.089	−0.006
	Fear	−0.178	−0.338**	−0.071
	Happy	0.000	−0.116	−0.073

**p < 0.019.

3.2 | Correlation between pupil dilation and fixation parameters

As an exploratory analysis, we tested whether there was a correlation between pupil dilation within the significant time period (Figure 2d) and the four fixation parameters reported in the earlier analyses (Geangu & Vuong, 2020). These parameters included: (1) proportion fixations; (2) proportion looking time for the 4-s stimulus presentation; (3) fixation duration for fixations; and (4) number of fixations (see Geangu & Vuong, 2020, for full details). We calculated a difference score between each of the expressive body postures (anger, fear and happiness) and neutral body posture for the four fixation parameters and the pupil dilation (i.e., emotion—neutral). We then calculated the Pearson correlation between the difference score for the fixation parameters and the mean pupil size during the significant time period. This analysis was conducted for fixations on the upper body region, which included the arms and hands, and excluded the head region. The motivation for this approach is that 7-months-old infants were found to fixate on the upper body region for discriminating fear body expressions from the other expressions (Geangu & Vuong, 2020). Table 1 presents the Pearson *r* for these analyses. As this was an exploratory analysis, we report uncorrected *p*-values. There were significant negative correlations between pupil dilation to fear body expressions and proportion fixation, $r(46) = -0.363$, $p = 0.011$, proportion looking time, $r(46) = -0.369$, $p = 0.010$, and number of fixations, $r(46) = -0.338$, $p = 0.019$ to fear expressions.

3.3 | Stimulus luminance and visual saliency

Following Geangu et al. (2011), we conducted two by-item analyses of covariance (ANCOVAs) to separately rule out the influence of luminance (i.e., greyscale value) and saliency on infants' pupil responses. The mean luminance was calculated for each of the 20 body images at each time point during the stimulus presentation as follows. First for each infant, we calculated the average greyscale

value across all pixels within a circle (radius = 20 pixels) centered on the infant's fixation at each time point. The mean greyscale value was then averaged across all infants at each time point for each of the 20 body images. For saliency, we first calculated visual saliency of each of the 20 body images (Itti et al., 1998; see Geangu & Vuong, 2020, for more details about calculating visual saliency). The saliency at each pixel was based on luminance (at 8 image scales) and orientation (at 4 orientations), normalized to a value between 0 and 1 (Harel et al., 2006; Itti et al., 1998). The mean saliency for each image at each time point was calculated using the same method as for mean luminance. For each image measurement, we submitted the pupil size at each time point for each of the 20 body image, with emotional body expression as the independent variable and the measurement as a covariate. The Supplementary Materials provide the mean pupil size, luminance and saliency averaged across the 5 body images per expression.

For the ANCOVA with mean luminance as the covariate, there were main effects of body expression, $F(3, 3912) = 517.533$, $p < 0.001$, and luminance, $F(1, 3912) = 324.517$, $p < 0.001$. Although there was a main effect of luminance, it had a smaller effect size, $\eta_p^2 = 0.077$, than body expression, $\eta_p^2 = 0.284$. There was also an interaction between the two factors, $F(3, 3912) = 510.474$, $p < 0.001$, $\eta_p^2 = 0.280$, suggesting that the influence of luminance varied across body expression (see also Geangu et al., 2011). Similarly for the ANCOVA with saliency as the covariate, there were main effects of both body expression, $F(3, 3912) = 62.854$, $p < 0.001$; and saliency, $F(1, 3912) = 158.600$, $p < 0.001$. Body expression had a larger effect size, $\eta_p^2 = 0.046$, than saliency, $\eta_p^2 = 0.039$, although both effect sizes were small. There was also an interaction between the two factors, $F(3, 3912) = 77.655$, $p < 0.001$, $\eta_p^2 = 0.056$, suggesting that the influence of saliency varied across body expression.

4 | DISCUSSION

In Geangu and Vuong's (2020) eye-tracking study, 7-months-old infants viewed body postures of adult females expressing anger, fear and happiness, as well as an emotionally neutral posture. The faces were blurred to remove their potential influence on the emotion expressed by the body posture (Hock et al., 2017). It was found by Geangu and Vuong that infants' fixation patterns discriminated fear from other body expressions. In particular, infants spent a larger proportion of their looking times and had longer fixation durations on the upper body for fear relative to the other expressions. There was also a higher proportion of fixations on anger and fear body expressions compared to happy expressions. These findings demonstrate that infants at this age can *perceptually discriminate* body expressions but there was no clear evidence that they processed the emotional content of those expressions (Ke et al., 2022; Ross & Atkinson, 2020). To address this, we analyzed the pupil data from the same infants, as pupil dilations reflect increased arousal induced by the emotional content of visual stimuli. These dilations are driven by the LC-NE system which modulates arousal induced by emotional stimuli (Hepach & Westermann, 2016; Sirois & Brisson, 2014; Tummeltshammer et al., 2019). We therefore predicted that arousing body expressions would increase pupil dilation. Fear and anger tend to be more arousing than happy body expressions (Hoehl et al., 2017; Kret et al., 2013; Mondloch et al., 2013). Consistent with this, we found that fear body expressions elicited larger dilations than neutral expressions around 1 s after the onset of the body image and for about 600 ms. There was also a trend for anger body expressions to elicit larger dilations than neutral expressions during this time period.

This is the first study to provide evidence that infants as young as 7 months old process the emotional content of static body postures. Infants explored fear body expressions more than neutral expressions (Geangu & Vuong, 2020) *and* showed increased arousal to fear expressions (and anger expressions

to some extent). Similar pupillary responses to anger and fear body expressions relative to happy or neutral expressions have been reported in adults (Kret et al., 2013). The responses in adults further show a strong positive correlation with other physiological measures of arousal to emotional stimuli (Bradley et al., 2008, 2017; Kret et al., 2013).

We also found negative correlations between pupil dilation to fear body expressions and visual exploration behaviors of fear expressions (i.e., proportion of fixations, proportion of looking times and number of fixations on the upper body). This finding suggests a possible emotional reactivity of avoidance (e.g., Crespo-Llado et al., 2018a,b), with infants *looking less* at fear expressions if they were *more aroused* by the expression (i.e., increased dilation to fear compared to neutral expressions). In line with this possibility, Hoehl et al. (2017) found that 6-months-old infants showed increased pupil dilations to perceptual cues associated with non-social stimuli that can be (evolutionarily) threatening (e.g., spiders and snakes, compared to flowers and fishes). Although the correlation analyses are exploratory, they provide a basis for future work to investigate how this reactivity may change with age, or factors that may affect reactivity to fear stimuli such as infant temperament or parental stress (Aktar et al., 2021; Crespo-Llado et al., 2018a, 2018b; Gredebäck et al., 2012; Hoehl, 2014; Hoehl et al., 2017; Ke et al., 2022; Upshaw et al., 2015).

Our findings extend previous studies showing that infants from as young as 6-months-old can process the emotional content from facial and vocal cues (Aktar et al., 2018, 2021; Geangu et al., 2011; Gredebäck et al., 2012; Jessen et al., 2016; Prunty et al., 2022). These studies showed that the magnitude of pupil dilation was affected by the emotional content of a variety of face stimuli. The researchers used different face sets, and used both static (Aktar et al., 2018; Gredebäck et al., 2012; Jessen et al., 2016); and dynamic (Aktar et al., 2021; Geangu et al., 2011; Prunty et al., 2022; Upshaw et al., 2015) facial expressions. Pupil dilations were also affected by emotion even if the face stimuli were presented subliminally (Jessen et al., 2016). Geangu et al. (2011) showed strong emotion effects on pupil dilation using more naturalistic and socially-relevant extended videos of other infants' facial and vocal expressions. Although this diversity of stimuli helps to increase the generality of these findings, it will be important to systematically investigate how these different factors contribute to the magnitude and direction of pupil dilation in response to perceptual cues to emotions during early development.

There were differences between our results with body expressions and some of the findings from studies with facial expressions. First, studies using static facial expressions found that fear expressions elicited smaller pupil dilations than happy and/or neutral facial expressions (Aktar et al., 2018; Jessen et al., 2016). Second, other studies showed an emotion effect on pupil dilation for dynamic but not static expressions (Prunty et al., 2022). Third, the effect of the emotional content of the facial expression were opposite for fixation duration compared to pupil dilation. For example, Aktar et al. (2018) showed *longer* fixation durations to fear expressions compared to neutral expressions but the pupil dilation was *smaller* for fear expressions. These differences may be related to the number and type of stimuli used. For example, Geangu et al. (2011) found larger pupil dilations for negative (e.g., angry) compared neutral and positive (e.g., happy) expressions using videos that presented both facial and vocal cues to emotion. Moreover, some face studies used only a single female face expressing the different emotions (Aktar et al., 2018) or did not statistically compare to an emotionally neutral control (Jessen et al., 2016), which is often suggested for pupil-data research (Hepach & Westermann, 2016). The differences may also relate to the extent to which image properties such as stimulus luminance or visual saliency can be controlled. Our ANCOVAs showed that these properties contributed to pupil dilation but it is important to note that there was still a significant emotion effect when factoring out these covariates (see also Aktar et al., 2018; Geangu et al., 2011; Jackson & Sirois, 2009; Prunty et al., 2022).

Lastly and importantly, the current results are consistent with neural measures related to emotion processing in infants. The analysis of infants' electrical cortical responses to body images indicate the

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involvement of several processes in computing emotionally-relevant information (Missana et al., 2014, 2015; Missana & Grossmann, 2015). For example, Missana et al. (2014) showed an increased amplitude of the early N290 ERP component to fear compared to happy body expressions in 8- but not 4-months-old infants, suggesting that structural information relevant to expressing emotions may be extracted faster with development. This component is a negative deflection as early as 290 ms after stimulus onset and corresponds to the N170 in adults, which is an early index of face perception (Gillmeister et al., 2019). Missana et al. (2014) also found an increased amplitude of the late Nc component to fear compared to happy body expression in 8-months-old infants, suggesting that older but not younger infants also allocated more attentional resources to processing fearful bodies compared to happy ones (Rajhans et al., 2016). The developmental change towards increased attention to bodies expressing fear is similar to the increased attention to negative facial expressions (Crespo-Llado et al., 2018a, 2018b; Geangu, Ichikawa, et al., 2016; Hoehl, 2014; Hoehl et al., 2017; Ke et al., 2022; Leppänen & Nelson, 2009; Poyo Solanas et al., 2020b). This developmental change was hypothesized to be related to the emergence of adaptive processes that orient and allocate attention to threat-related information around 5–7 months of age (e.g., Campos et al., 1994; Leppänen & Nelson, 2009). We note that the ERP studies using body stimuli tested only fear and happy expressions, and did not include emotionally-neutral control stimuli (Hepach & Westermann, 2016), which may limit the evidence they provide for emotion processing per se. Because pupil-dilation responses are driven by arousal induced by the emotional content of visual stimuli, our analysis of the pupil data from Geangu and Vuong (2020)—taken in conjunction with previous behavioral and neural studies—provide evidence that 7-months-old infants can *perceptually discriminate* body expressions and *process* their emotional content.

4.1 | Limitations and future work

Although our findings provide evidence that infants process the emotional content of body expressions rather than only perceptually discriminate them, there are a number of limitations that should be considered. First, different dependent variables from the same sample were analyzed across Geangu and Vuong (2020) and this paper (fixation and pupil variables), which inflates Type I experiment-wise error rates. Although we corrected for multiple comparisons for our main pupil analysis (Figure 2), correcting for eye-movement and pupil analyses (at the experiment level) may be too conservative and lead to Type II errors. The resampling and interpolation for infant pupil data could also increase Type I errors (see Supplementary Materials). As we discuss below, our pupil findings will provide a basis for future work. Second although infants were tested in the same constant room lighting, the luminance of the room and monitor screen were not equated. There is therefore the possibility that when infants look away from the screen their pupil size may have been modulated by potential differences in luminance between the room and the stimuli, independent of the underlying emotion processing of the body stimuli. It is thus important to consider this luminance differences when interpreting pupil dilation data, and particularly in relation to visual exploration behaviors. We cannot rule out this light-based alternative explanation in the current study. Future work should try to equate the room and screen luminance.

Third, we used static body postures that lack people's natural movements that may provide rich dynamic cues that can facilitate emotion processing (e.g., Ke et al., 2022; Poulin-Dubois et al., 2018). We also did not test other negative expressions such as disgust or sadness, or other potentially more arousing positive expressions such as surprise. These limitations may partly be due to the availability of video databases of body expressions and to practical constraints of infant studies. There are validated databases that use naturalistic visually-degraded stimuli (e.g., point-light displays, Volkova

et al., 2014) or focus on predominantly the upper body (e.g., Bänziger et al., 2012). Young infants have limited attention span so Geangu and Vuong (2020) focused on a few negative and positive expressions that have been used in most infant studies on emotion perception for both faces and bodies (i.e., anger, fear and happy). This focus allowed for better comparison to the existing literature.

Fourth, although we took into account image properties (i.e., stimulus luminance and visual saliency) that are known to drive pupil dilation independently of emotion (Hepach & Westermann, 2016; Sirois & Brisson, 2014; Tummeltshammer et al., 2019), there may be other factors that were more difficult to control. For example, happy body expressions have extended arms (see Supplementary Materials) compared to anger, fear and neutral expressions which have contracted arms close to the body. Moreover, anger and fear body expressions may occur less frequently than happy and neutral expressions in the infants' environment; these negative expressions may thus be less familiar (i.e., more novel) and thereby elicit larger pupil dilations (e.g., Chen & Westermann, 2018). Fourth, we have not considered the environmental and parental factors that may affect the frequency of different body expressions or the context in which they occur (Aktar et al., 2021; Gredebäck et al., 2012; Hoehl, 2014; Hoehl et al., 2017; Smith et al., 2018; Upshaw et al., 2015). Finally, Geangu and Vuong's (2020) study only tested a single age group.

Despite these limitations, the eye-movement and pupil-dilation analyses of Geangu and Vuong's (2020) data set provide a good basis and point to potential future studies. Future work can test different age groups from infancy to adults, combine different measures (e.g., pupil dilation, muscle activity, ERPs and EEG) and use naturalistic dynamic multi-sensory perceptual cues associated with emotions to better understand the developmental trajectory for emotion processing (e.g., Geangu et al., 2011, 2016b; Ke et al., 2022; Poulin-Dubois et al., 2018; Quadrelli et al., 2019). This integrative approach points to a need for a validated open-science video database of whole-body naturalistic body expressions (Bänziger et al., 2012; Volkova et al., 2014; see also Kret et al., 2011; Poyo Solanas et al., 2020a). Given some of the different pupil-dilation findings in infant studies (e.g., for facial expressions), it will also be important in future work to develop a standardized paradigm and stimulus set. Another important future direction is to consider the maturing infants' visual experiences, for example, the frequency of different facial and body expressions, parenting behaviors, and the context in which emotion expressions occur in the infants' environment (Fausey et al., 2016; Jayaraman et al., 2017; Smith et al., 2018). Lastly, it will be important for future work to test infants longitudinally to map out more precisely the developmental trajectory for emotion processing of body expressions for comparison with faces and other modalities of expressing emotions.

5 | CONCLUSIONS

Taken collectively, there is a large body of behavioral and neural evidence that infants as young as 7 months old can preferentially fixate on body regions and parts which are the most relevant for different social tasks (e.g., Falck-Ytter et al., 2006; Geangu, 2008; Geangu et al., 2015; Kochukhova & Gredebäck, 2010), including tasks related to processing emotion expressions by others (Geangu et al., 2011; Geangu & Vuong, 2020; Heck et al., 2018; Hock et al., 2017; Missana et al., 2014, 2015; Missana & Grossmann, 2015; Ogren et al., 2019; Zieber et al., 2014). Our results contribute to this growing body, providing evidence from pupillary responses related to the physiological arousal induced by the emotional content of body expressions. They also suggest that the emergence of body emotion processing coincide with the period when infants' visual experiences shift from faces towards body regions and parts. The body is one of many perceptual cues for ultimately recognizing emotions in others for the maturing infants, and future work should combine behavioral, physiological and

neural markers of emotion processing of naturalistic emotional facial, vocal and body stimuli during the critical first 2-years of life.

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REFERENCES

Addyman, C., Rocha, S., & Mareschal, D. (2014). Mapping the origins of time: Scalar errors in infant time estimation. *Developmental Psychology*, *50*(8), 2030–2035. https://doi.org/10.1037/a0037108

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., Nimphy, C. A., Kret, M. E., Pérez-Edgar, K., Bögels, S. M., & Raijmakers, M. E. (2021). Pupil responses to dynamic negative facial expressions of emotion in infants and parents. *Developmental Psychobiology*, *63*(7), e22190. https://doi.org/10.1002/dev.22190

Bänziger, T., Mortillaro, M., & Scherer, K. R. (2012). Introducing the Geneva Multimodal Expression corpus for experimental research on emotion perception. *Emotion*, *12*(5), 1161–1179. https://doi.org/10.1037/a0025827

Bayet, L., & Nelson, C. A. (2019). The perception of facial emotion in typical and atypical development, et al. (Eds.). In *Handbook of emotional development* (pp. 105–138). Springer.

Belin, P., Bestelmeyer, P. E. G., Latinus, M., & Watson, R. (2011). Understanding voice perception. *British Journal of Psychology*, *102*(4), 711–725. https://doi.org/10.1111/j.2044-8295.2011.02041.x

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*(4), 602–607. https://doi.org/10.1111/j.1469-8986.2008.00654.x

Bradley, M. M., Sapigao, R. G., & Lang, P. J. (2017). Sympathetic ANS modulation of pupil diameter in emotional scene perception: Effects of hedonic content, brightness, and contrast. *Psychophysiology*, *54*(10), 1419–1435. https://doi.org/10.1111/psyp.12890

Campos, J. J., Mumme, D. L., Kermoian, R., & Campos, R. G. (1994). A functionalist perspective on the nature of emotion. *Monographs of the Society for Research in Child Development*, *59*(2–3), 284-303, https://doi.org/10.1111/j.1540-5834.1994.tb01289.x

Chen, Y., & Westermann, G. (2018). Different novelties revealed by infants' pupillary responses. *Scientific Reports*, *8*(1), 9533. https://doi.org/10.1038/s41598-018-27736-z

Crespo-Llado, M. M., Vanderwert, R., Roberti, E., & Geangu, E. (2018b). Eight-month-old infants' behavioral responses to peers' emotions as related to the asymmetric frontal cortex activity.*Scientific Reports*, *8*(1), 1-11, https://doi.org/10.1038/s41598-018-35219-4

Crespo-Llado, M. M., Vanderwert, R. E., & Geangu, E. (2018). Individual differences in infants' neural responses to their peers' cry and laughter. *Biological Psychology*, *135*, 117–127. https://doi.org/10.1016/j.biopsycho.2018.03.008

de Gelder, B. (2009). Why bodies? Twelve reasons for including bodily expressions in affective neuroscience. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1535), 3475–3484. https://doi.org/10.1098/rstb.2009.0190

de Gelder, B., & van den Stock, J. (2011). The bodily expressive action stimulus test (BEAST). Construction and validation of a stimulus basis for measuring perception of whole body expression of emotions. *Frontiers in Psychology*, *2*, 181.

de Groot, J. H., & Smeets, M. A. (2017). Human fear chemosignaling: Evidence from a meta-analysis. *Chemical Senses*, *42*(8), 663–673. https://doi.org/10.1093/chemse/bjx049

Falck-Ytter, T., Gredebäck, G., & Von Hofsten, C. (2006). Infants predict other people's action goals. *Nature Neuroscience*, *9*(7), 878–879. https://doi.org/10.1038/nn1729

Fausey, C. M., Jayaraman, S., & Smith, L. B. (2016). From faces to hands: Changing visual input in the first two years. *Cognition*, *152*, 101–107. https://doi.org/10.1016/j.cognition.2016.03.005

Geangu, E. (2008). Notes on self-awareness development in infancy. *Cognitie, Creier, Comportament/Cognition, Brain, and Behavior*, *12*, 1.

Geangu, E. (2015). Development of empathy during childhood across cultures. In J. D. Wright (Ed.), *International Encyclopedia of the social and behavioral sciences* (pp. 549–553). Elsevier.

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

Geangu, E., Ichikawa, H., Lao, J., Kanazawa, S., Yamaguchi, M. K., Caldara, R., & Turati, C. (2016). Culture shapes 7-month-olds' perceptual strategies in discriminating facial expressions of emotion. *Current Biology*, *26*(14), R663–R664. https://doi.org/10.1016/j.cub.2016.05.072

Geangu, E., Quadrelli, E., Conte, S., Croci, E., & Turati, C. (2016b). Three-year-olds' rapid facial electromyographic responses to emotional facial expressions and body postures. *Journal of Experimental Child Psychology*, *144*, 1–14. https://doi.org/10.1016/j.jecp.2015.11.001

Geangu, E., Senna, I., Croci, E., & Turati, C. (2015). The effect of biomechanical properties of motion on infants' perception of goal-directed grasping actions. *Journal of Experimental Child Psychology*, *129*, 55–67. https://doi.org/10.1016/j.jecp.2014.08.005

Geangu, E., & Vuong, Q. C. (2020). Look up to the body: An eye-tracking investigation of 7-months-old infants' visual exploration of emotional body expressions. *Infant Behavior and Development*, *60*, 101473. https://doi.org/10.1016/j.infbeh.2020.101473

Gillmeister, H., Stets, M., Grigorova, M., & Rigato, S. (2019). How do bodies become special? Electrophysiological evidence for the emergence of body-related cortical processing in the first 14 months of life. *Developmental Psychology*, *55*(10), 2025–2038. https://doi.org/10.1037/dev0000762

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

Gredebäck, G., & Melinder, A. (2011). Teleological reasoning in 4-month-old infants: Pupil dilations and contextual constraints. *PLoS One*, *6*(10), e26487. https://doi.org/10.1371/journal.pone.0026487

Harel, J., Koch, C., & Perona, P. (2006). *Graph-based visual saliency* (pp. 1–8). NIPS.

He, Z., Liu, Z., Wang, J., & Zhang, D. (2018). Gender differences in processing fearful and angry body expressions. *Frontiers in Behavioral Neuroscience*, *12*, 164. https://doi.org/10.3389/fnbeh.2018.00164

Heck, A., Chroust, A., White, H., Jubran, R., & Bhatt, R. S. (2018). Development of body emotion perception in infancy: From discrimination to recognition. *Infant Behavior and Development*, *50*, 42–51. https://doi.org/10.1016/j.infbeh.2017.10.007

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

Hock, A., Oberst, L., Jubran, R., White, H., Heck, A., & Bhatt, R. S. (2017). Integrated emotion processing in infancy: Matching of faces and bodies. *Infancy*, *22*(5), 608–625. https://doi.org/10.1111/infa.12177

Hoehl, S. (2014). Emotion processing in infancy. In *Children and Emotion*. (Vol. 26, pp. 1–12). Karger Publishers.

Hoehl, S., Hellmer, K., Johansson, M., & Gredebäck, G. (2017). Itsy bitsy spider…: Infants react with increased arousal to spiders and snakes. *Frontiers in Psychology*, *8*, 1710.

Itti, L., Koch, C., & Niebur, E. (1998). A model of saliency-based visual attention for rapid scene analysis. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, *20*(11), 1254–1259. https://doi.org/10.1109/34.730558

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

Jayaraman, S., Fausey, C. M., & Smith, L. B. (2017). Why are faces denser in the visual experiences of younger than older infants? *Developmental Psychology*, *53*(1), 38–49. https://doi.org/10.1037/dev0000230

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

Ke, H., Vuong, Q. C., & Geangu, E. (2022). Three- and six-year-old children are sensitive to natural body expressions of emotion: An ERP emotional priming study. *Journal of Experimental Child Psychology*, *224*, 105497. https://doi.org/10.1016/j.jecp.2022.105497

Keltner, D., Tracy, J., Sauter, D. A., Cordaro, D. C., & McNeil, G. (2016). Expression of emotion. *Handbook of Emotions*, 467–482.

Kochukhova, O., & Gredebäck, G. (2010). Preverbal infants anticipate that food will be brought to the mouth: An eye tracking study of manual feeding and flying spoons. *Child Development*, *81*(6), 1729–1738. https://doi.org/10.1111/j.1467-8624.2010.01506.x

Kret, M. E., Pichon, S., Grèzes, J., & de Gelder, B. (2011). Similarities and differences in perceiving threat from dynamic faces and bodies. An fMRI study. *NeuroImage*, *54*(2), 1755–1762. https://doi.org/10.1016/j.neuroimage.2010.08.012

Kret, M. E., Roelofs, K., Stekelenburg, J., & de Gelder, B. (2013). 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. E., & Sjak-Shie, E. E. (2019). Preprocessing pupil size data: Guidelines and code. *Behavior Research Methods*, *51*(3), 1336–1342. https://doi.org/10.3758/s13428-018-1075-y

Krol, K. M., Rajhans, P., Missana, M., & Grossmann, T. (2015). Duration of exclusive breastfeeding is associated with differences in infants' brain responses to emotional body expressions. *Frontiers in Behavioral Neuroscience*, *8*, 459.

Leppnen, J. M., & Nelson, C. A. (2009). Tuning the developing brain to social signals of emotion. *Nature Reviews Neuroscience*, *10*(1), 37–47. https://doi.org/10.1038/nrn2554

Miguel, H. O., Gonçalves, Ó. F., Cruz, S., & Sampaio, A. (2019). Infant brain response to affective and discriminative touch: A longitudinal study using fNIRS. *Social Neuroscience*, *14*(5), 571–582. https://doi.org/10.1080/17470919.2018.1536000

Missana, M., Atkinson, A. P., & Grossmann, T. (2015). Tuning the developing brain to emotional body expressions. *Developmental Science*, *18*(2), 243–253. https://doi.org/10.1111/desc.12209

Missana, M., & Grossmann, T. (2015). Infants' emerging sensitivity to emotional body expressions: Insights from asymmetrical frontal brain activity. *Developmental Psychology*, *51*(2), 151–160. https://doi.org/10.1037/a0038469

Missana, M., Rajhans, P., Atkinson, A. P., & Grossmann, T. (2014). Discrimination of fearful and happy body postures in 8-month-old infants: An event-related potential study. *Frontiers in Human Neuroscience*, *8*, 531. https://doi.org/10.3389/fnhum.2014.00531

Mondloch, C. J., Nelson, N. L., & Horner, M. (2013). Asymmetries of influence: Differential effects of body postures on perceptions of emotional facial expressions. *PLoS One*, *8*(9), e73605. https://doi.org/10.1371/journal.pone.0073605

Ogren, M., Kaplan, B., Peng, Y., Johnson, K. L., & Johnson, S. P. (2019). Motion or emotion: Infants discriminate emotional biological motion based on low-level visual information. *Infant Behavior and Development*, *57*, 101324. https://doi.org/10.1016/j.infbeh.2019.04.006

Poulin-Dubois, D., Hastings, P. D., Chiarella, S. S., Geangu, E., Hauf, P., Ruel, A., & Johnson, A. (2018). The eyes know it: Toddlers' visual scanning of sad faces is predicted by their theory of mind skills. *PLoS One*, *13*(12), e0208524. https://doi.org/10.1371/journal.pone.0208524

Poyo Solanas, M., Vaessen, M., & de Gelder, B. (2020a). The role of computational and subjective features in emotional body expressions. *Scientific Reports*, *10*(1), 1-13, https://doi.org/10.1038/s41598-020-63125-1

Poyo Solanas, M., Vaessen, M., & de Gelder, B. (2020b). Limb contraction drives fear perception. bioRxiv.

Prunty, J. E., Keemink, J. R., & Kelly, D. J. (2022). Infants show pupil dilatory responses to happy and angry facial expressions. *Developmental Science*, *25*(2), e13182. https://doi.org/10.1111/desc.13182

Quadrelli, E., Geangu, E., & Turati, C. (2019). Human action sounds elicit sensorimotor activation early in life. *Cortex*, *117*, 323–335. https://doi.org/10.1016/j.cortex.2019.05.009

Rajhans, P., Jessen, S., Missana, M., & Grossmann, T. (2016). Putting the face in context: Body expressions impact facial emotion processing in human infants. *Developmental Cognitive Neuroscience*, *19*, 115–121. https://doi.org/10.1016/j.dcn.2016.01.004

Ramsay, J. O., & Silverman, B. W. (1997). *Functional data analysis*. Springer.

Robinson, D. T., Clay-Warner, J., Moore, C. D., Everett, T., Watts, A., Tucker, T. N., & Thai, C. (2012). Toward an unobtrusive measure of emotion during interaction: Thermal imaging techniques. *Biosociology and Neurosociology*, 225–266. Emerald Group Publishing Limited

Rosen, J. B., Asok, A., & Chakraborty, T. (2015). The smell of fear: Innate threat of 2, 5-dihydro-2, 4, 5-trimethylthiazoline, a single molecule component of a predator odor. *Frontiers in Neuroscience*, *9*, 292. https://doi.org/10.3389/fnins.2015.00292

Ross, P., & Atkinson, A. P. (2020). Expanding simulation models of emotional understanding: The case for different modalities, body-state simulation prominence, and developmental trajectories. *Frontiers in Psychology*, *11*, 309. https://doi.org/10.3389/fpsyg.2020.00309

Salazar-López, E., Domínguez, E., Ramos, V. J., De la Fuente, J., Meins, A., Iborra, O., Gálvez, G., Rodríguez-Artacho, M. A., & Gómez-Milán, E. (2015). The mental and subjective skin: Emotion, empathy, feelings and thermography. *Consciousness and Cognition*, *34*, 149–162. https://doi.org/10.1016/j.concog.2015.04.003

Sirois, S., & Brisson, J. (2014). Pupillometry. *Wiley Interdisciplinary Reviews: Cognitive Science*, *5*(6), 679-692, https://doi.org/10.1002/wcs.1323

Smith, L. B., Jayaraman, S., Clerkin, E., & Chen, Y. (2018). The developing infant creates a curriculum for statistical learning. *Trends in Cognitive Sciences*, *22*(4), 325–336. https://doi.org/10.1016/j.tics.2018.02.004

Tummeltshammer, K., Feldman, E. C., & Amso, D. (2019). Using pupil dilation, eye-blink rate, and the value of mother to investigate reward learning mechanisms in infancy. *Developmental Cognitive Neuroscience*, *36*, 100608. https://doi.org/10.1016/j.dcn.2018.12.006

Upshaw, M. B., Kaiser, C. R., & Sommerville, J. A. (2015). Parents' empathic perspective taking and altruistic behavior predicts infants' arousal to others' emotions. *Frontiers in Psychology*, *6*, 360. https://doi.org/10.3389/fpsyg.2015.00360

van den Boomen, C., Munsters, N. M., Deković, M., & Kemner, C. (2021). Exploring emotional face processing in 5-month-olds: The relation with quality of parent–child interaction and spatial frequencies. *Infancy*, *26*(6), 811–830. https://doi.org/10.1111/infa.12420

Verschoor, S. A., Paulus, M., Spapé, M., Biro, S., & Hommel, B. (2015). The developing cognitive substrate of sequential action control in 9-to 12-month-olds: Evidence for concurrent activation models. *Cognition*, *138*, 64–78. https://doi.org/10.1016/j.cognition.2015.01.005

Volkova, E., De La Rosa, S., Bülthoff, H. H., & Mohler, B. (2014). The MPI emotional body expressions database for narrative scenarios. *PLoS One*, *9*(12), e113647. https://doi.org/10.1371/journal.pone.0113647

Walle, E. A., & Lopez, L. D. (2020). Emotion recognition and understanding in infancy and early childhood. In J. B. Benson (Ed.), *Encyclopedia of infant and early childhood development* (2nd ed., Vol. 1, pp. 537–545). Elsevier.

Widen, S. C. (2013). Children's interpretation of facial expressions: The long path from valence-based to specific discrete categories. *Emotion Review*, *5*(1), 72–77. https://doi.org/10.1177/1754073912451492

Zhang, F., Jaffe-Dax, S., Wilson, R. C., & Emberson, L. L. (2018). Prediction in infants and adults: A pupillometry study. *Developmental Science*, *22*, e12780. https://doi.org/10.1111/desc.12780

Zieber, N., Kangas, A., Hock, A., & Bhatt, R. S. (2014). Infants' perception of emotion from body movements. *Child Development*, *85*(2), 675–684. https://doi.org/10.1111/cdev.12134

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