Infants show pupil dilatory responses to happy and angry facial expressions

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Conflict of Interest

The work reported was completed for part fulfilment of a doctoral degree at the University of Kent, there are no conflicts of interest to declare. We can confirm that this work has not been previously published and is not under consideration for publication elsewhere, and has adhered to APA ethical standards.

Data Availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Research Highlights

- Out of the six basic emotional expressions, infants showed pupillary responses for just happy and angry facial expressions.
- Infants' responses to happy and angry persisted after adjusting for stimulus brightness.
- Greater pupillary dilation was found for dynamic compared to static expression stimuli.

Abstract

Facial expressions are one way in which infants and adults communicate emotion. Infants scan expressions similarly to adults, yet it remains unclear whether they are receptive to the affective information they convey. The current study investigates six-, nine- and twelve-month infants' (*N* = 146) pupillary responses to the six 'basic' emotional expressions (happy, sad, surprise, fear, anger, and disgust). To do this we use dynamic stimuli and gaze-contingent eye-tracking to simulate brief interactive exchanges, alongside a static control condition. Infants' arousal responses were stronger for dynamic compared to static stimuli. And for dynamic stimuli we found that, compared to neutral, infants showed dilatory responses for happy and angry expressions only. Although previous work has shown infants can *discriminate* perceptually between facial expressions, our data suggest that sensitivity to the affective content of all six basic emotional expressions may not fully emerge until later in ontogeny.

Keywords

Emotion reciprocity; pupillometry; dynamic expressions; gaze-contingent eye-tracking.

Introduction

Perceiving and sharing emotion is an important part of human social interaction (Frith, 2009), and plays a foundational role within the earliest communicative exchanges (Tomasello et al., 2005). Previous work has established that infants are able to perceptually discriminate and categorise emotional expressions (Addabbo et al., 2018; Farroni et al., 2007; Keemink et al., 2019; Kotsoni et al., 2001; Nelson et al., 1979; Ruba et al., 2017; Safar et al., 2017). Evidence from eye-tracking paradigms has also shown that infants scan facial features in a similar way to adults; looking toward regions that are 'diagnostic' for decoding expressions (Hunnius et al., 2011; Keemink et al., 2021; Prunty et al., 2021; Soussignan et al., 2017). Yet how infants *perceive* facial expressions tells us little about whether or not they are receptive to the information communicated by expressive stimuli (Nelson, 1987; Ruba et al., 2019). To determine this, one option is to measure how infants *respond* to different expressions of emotion.

Investigations of live parent-infant interactions (e.g., Haviland & Lelwica, 1987; Termine & Izard, 1988) have shown that infants as young as 10 weeks old mirror the emotions of the adult with whom they are interacting. In these experiments, infants responded to their mother's happy expressions with increased interest and smiling, while anger and sadness often induced disinterest and distress. Haviland and Lelwica (1987) report that expressions of anger occasionally triggered intense crying responses such that 21% of infants were unable to complete that condition. This work suggests that infants are not passively perceiving expressions, but that facial expressions were evoking a physiological change in their affective state, resulting their behavioural responses. Seemingly, infants are receptive to emotional content according to broad dimensions, such as valence (i.e. positive vs negative), but may not be receptive to the specific information conveyed within individual expressions (Widen, 2013; but see Ruba et al., 2019). However, relying on spontaneous behavioural responses may not be optimal for measuring changes in internal affective states. Infants' could conceivably experience an internal change in arousal, yet still not produce 'appropriate' behaviours externally (or any response at all), particularly if expressions are presented outside of their natural context (Camras & Shutter, 2010; Nelson, 1987; Walker-Andrews, 1997). The current study will address this by using pupil dilation as a physiological marker of infants' affective arousal in response to the six 'basic' emotional expressions (Ekman, 1992), presented within simulated social interactions (see Vernetti et al., 2018).

Psychologically-evoked pupillary responses have a strong functional association with the activity of the noradrenergic system's locus coeruleus (LC-NA system; Joshi, Li, Kalwani, & Gold, 2016; Murphy, O'Connell, O'Sullivan, Robertson, & Balsters, 2014; see Aston-Jones & Cohen, 2005; Laeng et al., 2012), and pupillary dilation is a correlate of a subject's state of interest, attention or arousal (Hess & Polt, 1960; Sara, 2009; Sara & Bouret, 2012). Previous work with adults has shown sexually or emotionally arousing stimuli (both visual and auditory) illicit a larger dilation relative to neutral stimuli (Attard-Johnson et al., 2016; Bradley et al., 2008; Henderson et al., 2014; Kret et al., 2013; Partala & Surakka, 2003). Given this, pupillary dilation is also a sensitive index of our receptiveness to facial expressions as perceiving emotions in others can trigger an autonomic response in the observer. For instance, adults show larger pupil dilation when viewing others' negative compared to positive emotions (Yrttiaho et al., 2017), even when the expressions are presented subliminally (Laeng et al., 2013).

Pupillary correlates of social and affective processing have also been studied in infancy. Paralleling Fantz's classic looking-time research (Fantz, 1963), Fitzgerald (1965) demonstrated that one- and four-month-old infants show greater pupillary dilation for social compared to non-social stimuli. More recent work has found that infants also show dilation in response to the emotions of others. For example, visual and auditory presentations of other infants' emotional displays produced larger dilation compared to neutral stimuli in six- and twelve-month-olds (Geangu et al., 2011), and by seven months old, infants showed larger dilation for happy compared to fearful expressions (Aktar et al., 2018; Jessen et al., 2016), regardless of whether the expression was consciously perceived (Jessen et al., 2016). Pupillometry has also been used to demonstrate that 14-month-olds' reactivity to emotional facial expressions can be modified by contextual factors such as the familiarity or gender of the actor (Gredebäck et al., 2012), or the congruency of the actor's emotions with their behaviour (Hepach & Westermann, 2013). Differential pupillary responses to emotional expressions have also been found in infants who are at high risk for developing autistic spectrum disorder (ASD) compared to low-risk controls (Wagner et al., 2016), with increased pupil sizes for emotional stimuli at 9 months being predictive of social-communicative functioning at 18 months. Current research therefore suggests that pupillary dilation is a sensitive index of an infant's affective response to the emotional expressions of others.

Nevertheless, findings from previous studies are mixed (Aktar et al., 2018; Geangu et al., 2011; Hepach & Westermann, 2013; Jessen et al., 2016), and do not neatly align according to affective valence. For instance, Geangu and colleagues (2011) reported greater pupillary dilation for negative valence videos of distressed infants, while Jessen and colleagues (2016) instead found the largest dilation in response to positive valence images of happy faces. However, direct comparisons between studies are hampered by substantial differences in methodology. Some studies have presented video stimuli (e.g., Geangu et al., 2011; Hepach & Westermann, 2013), which convey emotion through facial and verbal cues as well as behaviour (e.g., 'thumping' a stuffed animal toy to depict anger), while others have used brief (e.g., one-second) presentations of static face images (e.g., Jessen et al., 2016). To facilitate comparisons between expressions, the current study will be the first to use a standard format to record infants' pupil dilation for all six of the commonly used facial expressions (happy, sad, surprise, fear, anger and disgust; see Ekman & Friesen, 1976; Tottenham et al., 2009), which some theorists consider to be basic, universal and perhaps innate (see Ekman, 1992, 1993; Ekman et al., 1987; Izard, 1994).

To increase real-world relevance, the six 'basic' expressions will be presented within brief social exchanges simulated using dynamic stimuli and gaze-contingent eye-tracking. This paradigm has been recently used to investigate infant scanning of emotional expressions (Keemink et al., 2021; Prunty et al., 2021) and similar gaze-contingent paradigms have also been used to study infant responsiveness within simulated interactions (Keemink et al., 2019; Vernetti et al., 2018), though not yet via pupillary response. Dynamism is increasingly being considered as a critical component of naturalistic stimuli in both adult (Richoz et al., 2018; see Krumhuber et al., 2013) and infant (Addabbo et al., 2018; Godard et al., 2016; Heck et al., 2016; Libertus et al., 2017; Soussignan et al., 2017) studies. Indeed, infants demonstrate sensitivity to facial emotion at earlier ages when realistic, dynamic displays are used (Addabbo et al., 2018; Heck et al., 2016; Montague & Walker-Andrews, 2001; Soussignan et al., 2017). Contingency, however, is a component of naturalistic exchanges that is frequently overlooked. Yet infants show enhanced responsivity for contingent video stimuli and live camera feeds in comparison to pre-recorded videos (Keemink et al., 2019; Meltzoff, 1988; Nielsen et al., 2008), noting response rates (e.g., smiles and vocalisations) comparable to live interactions (e.g., Field, Goldstein, Vega-Lahr, & Porter, 1986). Dynamic, gaze-contingent interactions, even those simulated using a display screen, are therefore likely to be much closer representations of everyday interactions than static, unresponsive images.

By recording pupillary responses within this paradigm, we aim to determine if infants' evoked physiological arousal in response to expressive faces will differ from neutral faces, thus providing evidence for their reciprocating, not just perceiving, emotional states in others. Previous work (Widen & Russell, 2008) suggests that infants might only understand expressions according to broad categories such as valence (positive or negative) or arousal (high or low). According to this perspective (Widen, 2013), the formation of discrete emotion concepts shows a much more protracted development (even into the teen years) and a combination of different contextual cues (e.g., linguistic labels, situational causes, behavioural consequences etc.) are required before the affective meaning is learned (see Barrett et al., 2007; Widen, 2013). Although pupil size cannot inform about infants' *understanding* of emotions, considering the developmental trajectory of emotion concepts, we would also not expect infants to show specific physiological responses to individual expression categories. Instead, we predict that infants will show similar dilatory responses across expression boundaries, but will also demonstrate differences in affective reciprocity according to general dimensions such as emotional valence or arousal. More specifically, and considering the abovementioned evidence from previous behavioural (Haviland & Lelwica, 1987; Termine & Izard, 1988) and pupillometry studies (Aktar et al., 2018; Geangu et al., 2011; Jessen et al., 2016), and that pupillometry does not discriminate according to valence (Hepach & Westermann, 2016), we expect infants to show the strongest arousal responses for both high-arousal positive (e.g., happy) and high-arousal negative (e.g., anger, fear) expressions.

As infants' responses to facial expressions might vary across development (Kotsoni et al., 2001; Nelson et al., 1979; Ruba et al., 2017), we included three age groups: six, nine and twelve months old. Seven months is known to be a critical threshold for expression perception (Nelson et al., 1979), yet for some less familiar expressions (e.g., disgust), adult-like perception is not reached till the end of the first year (Ruba et al., 2017). Like previous work (Keemink et al., 2021), these age groups were selected to span this developmental period. We also included a static image condition to investigate the abovementioned role of dynamic-contingent displays (see Prunty et al., n.d.; Wilcox & Clayton, 1968) on pupillary responses.

In this study, we predict that infants will show stronger dilatory responses for expressive faces relative to neutral faces. We also predict that these differences will be more pronounced for high arousal positive (happiness) and negative (fear and anger) emotions, for emotions conveyed via dynamic-contingent stimuli, and for older infants.

Methods

Participants

One hundred and forty-six infants within three age groups (six, nine and twelve-months; ±14 days) were included in the final analysis (see Table 1). Twenty-two additional infants were excluded for failing to produce usable data for at least 50% of trials (*N* = 3), or for failing to complete the experiment due to fussiness (*N* = 19). Participants were assigned to either 'static' (*N* = 48) or 'dynamic' (*N* = 98) conditions. Infants with any known visual impairments were deemed ineligible and not invited for testing.

Stimuli

The stimulus set used here (see Figure 1) has been used previously to investigate infant expression scanning (Keemink et al., 2021), and include eighteen naturalistic videos with six different Caucasian actors (3 male, 3 female). Each actor appears in three videos (1 neutral, 2 expressive), with each of the six core expressions (happy, sad, surprise, fear, anger, disgust) being presented twice (by 1 male, and 1 female) and neutral six times (1 per actor). Videos (24.77˚ x 18.25˚ in visual angle) were silent and edited to three seconds in length, beginning with neutral affect and ending at peak expressive amplitude. For the neutral control stimuli, the videos captured natural head motion and blinking, but the actors maintained neutral affect. All actors wore identical black t-shirts, and appeared in front of a uniform green background. The stimuli within the static condition were stills from these videos, taken when the expression was judged to be at 'peak' amplitude (i.e. the point at which the expression reaches its highest intensity; c.f. Ekman & Friesen, 1976). Expression stimuli were validated by 51 adult observers (Prunty et al., 2021), and received high recognition accuracy scores (*M* = 84.57%, *SD* = 14.99%), and representativeness ratings (out of 5: *M* = 3.62, *SD* = .38). Discrete gaze-contingent boundaries for the eye region were defined individually for each face (all 6.8˚x 2.83˚). Stimuli were presented centrally on a 20-in. monitor (1024 x 768 pixel resolution).

As pupil size responds primarily to changes in retinal illumination (via a pupil constriction, or 'pupillary light response'; PLR), differences in ambient lighting and stimulus brightness can introduce noise within the data, particularly as pupillary responses to light are typically much larger (over 100%) than psychologically-induced changes in pupil size (approx. 20%; Beatty & Lucero-Wagoner, 2000). To ensure our results reflect infants' affective responses, and not general responses to changes in luminance, the ambient light in the room and the display monitor's brightness and background colour (black) were kept constant throughout testing and the same lighting conditions were re-created for each participant (see Hepach & Westermann, 2016). Any changes in luminance could therefore be attributed to the stimuli themselves. Given that we were interested in presenting realistic and ecologically relevant expression stimuli, we did not equate stimulus brightness across images or convert to greyscale. However, following Jackson and Sirois (2009), we calculated average stimulus brightness for each image in the static condition, and at 500ms intervals in the dynamic condition. For dynamic stimuli, brightness values showed little variation across time, and thus an average of all timepoints was taken (see Table A2 and appendix for further details). Mean values for each expression are displayed in Table 2 alongside their difference from the neutral control stimuli, and will be used to statistically control for any systematic effects of brightness.

Pupillometry

A central challenge within developmental eye-tracking is ensuring infant participants remain engaged and attentive to the presentation on the screen. However, while lack of interest might be informative for looking-time research (i.e., as an indication of disinterest or habituation), it is entirely harmful for pupillometry as each look-away and refocus on the screen will trigger light-based pupil size changes and introduce artefacts within the data. As infants look away, they also might miss crucial on-screen changes hypothesised to induce a pupillary response. Stimuli designed to minimise the confounding effects of light, such as static, silent, grey images, may not be sufficiently engaging to hold an infant's attention and thus detrimental for collecting good quality data. By presenting gaze-contingently animated and naturally engaging videos, we were able to minimise data loss, as infants are more likely to remain attentive to the screen. Time-locking the video presentation to an infants' gaze position also guaranteed that infants were fixating the stimulus at the start of the analysis time window, facilitating comparison across trials, participants, and conditions.

To measure pupil sizes, we used an SR Research Desktop-Mount EyeLink 1000+ eye tracker with a 25mm lens operating in remote mode (spatial resolution 0.01°, average gaze position error 0.25°, sampling rate 500Hz) and using an 890 nm illuminator. We also recorded eye movements and head distance using a padded target sticker placed centrally on the forehead as a reference point. Prior to the start of each experiment, a five-point calibration procedure was implemented (Experiment Builder, SR Research, Ontario, CA), using custom 'attention grabbers' (animated, noisy circles) to entice looking. These attention grabbers were also used between trials to perform a drift correction. Pupil size was recorded using the EyeLink's scale from 100 to 10000 units, with a precision of 1 unit, with noise levels of 0.2%, corresponding to a resolution of 0.01mm for a 5mm pupil.

Procedure

Infants in both conditions were presented with 18 trials in a fully randomised order (6 x neutral, 2 x happy, 2 x sad, 2 x surprise, 2 x fear, 2 x anger, 2 x disgust). For the *dynamic condition* each trial consisted of a brief contingent interaction (Keemink et al., 2019, 2021). Each interaction began with an attention-grabber located to the left or right of the screen (counterbalanced across trials), and once fixated, the first frame of the expression video (the actor, facing forward with neutral affect) appeared centrally on the screen. A fixation (minimum duration 100 msecs) upon the eye region (defined by an invisible gaze-contingent boundary) triggered the expression video to play. Infants, therefore, contingently triggered the on-screen actor to respond with one of the six basic emotional expressions (or with dynamic neutral in the control trials) by engaging them in eye contact. Trials ended after five seconds if the eye region was not fixated. If the eye region was fixated rapidly, the three-second expression videos paused on the last frame to ensure each trial reached its five-second duration. Trials within the *static condition* were not dynamic or interactive. Each trial instead presented a static image from the expression video (at peak expression) for the full five-second duration.

Data processing

Pupil size and eye movement data were processed in MATLAB (Mathworks, R2019a). Data from both eyes were first merged via averaging, then smoothed using a 4-sample rolling window returning the median. The full pupil size dataset was then converted from EyeLink arbitrary units to standard z-scores. Fixations were identified using a custom-written velocity-based algorithm that has successfully been used in recent publications (Keemink et al., 2021; Kelly et al., 2019; Prunty et al., 2020, 2021). Pupil size values that were recorded during saccades or whilst the infant was not fixating the stimulus were removed. Pupil data were then cut to a defined analysis time-window of three-seconds (i.e., the duration of the video stimulus in the dynamic condition), following the first eye-region fixation. For each trial, outliers were defined as values more than three scaled median absolute deviations (MAD) away from the median, and were removed. Trials with less than 50% of samples were discarded (470 of 2628 trials, 17.88% in total), the total number of remaining trials was 1424 (81%) for the dynamic condition, and 734 (85%) for the static condition. Trials that remained had a high number of samples on average (Dynamic M = 88%, Static M = 86%), see Table A1 in the appendix for a full breakdown by expression.

Pupil data were then baseline-corrected by subtracting the average of the first 50 samples (100ms) of the trial from each data point (see Attard-Johnson et al., 2019; Reilly et al., 2019).

Analysis plan

To analyse these data, we will first use mixed ANOVAs to investigate overall influences of participant age, stimulus type (i.e., static or dynamic), and the gender and expression of face stimuli on mean pupil size. A parallel analysis will also be conducted to investigate evoked changes in pupil sizes across time. To do this, we will use Functional Data Analysis (FDA; Ramsay & Silverman, 1997; see Sirois & Brisson, 2014), to create t-score functions that efficiently represent the difference between mean neutral and expressive stimuli across time (see appendix for further details). Finally, we will conduct a linear regression analysis to investigate the effect of expression on pupil sizes whilst controlling for any systematic effects of stimulus brightness.

Results

Infants fixated the eye region rapidly (*M* = 527ms, *SD* = 249ms), and similarly for all expressions, $F(6,810) = 1.42$, $p = .202$. The change in pupil size following the gaze-contingent onset of the expression video is depicted in Figure 2 (top panels), showing an initial pupillary constriction in response to light (PLR), followed by a period of more gradual re-dilation (see Bradley et al., 2008; Henderson et al., 2014). Further, these plots indicate that pupil dilation was larger for dynamic stimuli relative to static stimuli, but that overall, neutral (black line) showed a similar pattern across time as expressive stimuli (coloured lines).

To corroborate these observations, and to establish whether participant age or stimulus gender influenced pupillary responses, we conducted a 2 (Condition: Dynamic or

Static) x 3 (Age: 6, 9 and 12 months) x 2 (Expression: Neutral or Expressive) x 2 (Gender: Male and Female) mixed ANOVA on mean pupil sizes collapsed across time. As anticipated, we found a main effect of Condition, $F(1,269) = 25.49$, $p < .001$, $\eta_p^2 = .09$, reflecting larger pupil sizes for dynamic ($M = -0.17$, $SD = 0.26$) relative to static stimuli ($M = -0.30$, $SD = 0.22$). There was also a main effect of Expression, $F(1,269) = 4.87$, $p = .028$, $\eta_p^2 = .02$, with larger pupil sizes for expressive ($M = -0.19$, $SD = 0.17$), relative to neutral stimuli ($M = -0.24$, $SD = 0.32$). Mean pupil size, however, did not differ between age groups, $F(2, 269) = 0.55$, $p = .577$, $\eta_p^2 < .01$, or by stimulus gender, $F(2,269) = 0.09$, $p = .771$, $\eta_p^2 < .01$ and there were no interactions between factors, *Fs* < 1.0, *ps* > .33. The t-plots from the parallel FDA analysis are also presented in Figure 2 (bottom panels). The t-score curve does not reach the threshold for significance (dashed red line) at any point across the analysis time window, indicating that pupil sizes for expressive stimuli were not significantly different to neutral when analysed uncollapsed across time.

Nevertheless, from Figure 2 we can also observe that there were considerable differences *between* expressions. To investigate, we conducted a 2 (Condition) x 3 (Age) x 7 (Expression: Happy, Sad, Surprise, Fear, Anger, Disgust, Neutral) mixed ANOVA, collapsing across Gender. There was again a main effect of Condition, $F(1,114) = 20.02$, $p < .001$, $\eta_p^2 = .15$, reflecting stronger responses for dynamic expressions. There was also a main effect of Expression, $F(6,684) = 2.89$, $p = .009$, $\eta_p^2 = .03$. Planned contrasts between each expression and neutral ($M = -.24$) indicate dilatory responses for happy ($M = -.17$), $t = 2.47$, $p = .010$, and angry ($M = -.16$), $t = 3.13$, $p = .002$, expressions only, all other *ts* < 1.7, *ps* > .09. Splitting by Condition, the effect of Expression was present for dynamic, $F(6,474) = 3.18$, $p = .005$, but not static stimuli, $F(6,234) = 1.16$, $p = .331$. Consequently, and considering that there was still no effect of Age, $F(2,114) = 0.26$, $p = .773$, $\eta_p^2 = .004$, or any interactions between factors, *Fs* < 1.8, *ps* > .17, subsequent analyses will collapse across Age, and focus on dynamic expressions only (see appendix for the results for static stimuli).

To illustrate infants' differential pupillary responses for *dynamic* expressions across time, t-score functions for each expression were computed and are plotted in Figure 3 (see Figure A1 for static expressions), with Bonferroni-adjusted and unadjusted critical t values plotted in red (α = 0.05, two-tailed). A clear dilatory response relative to neutral can be seen for happiness (2232 – 2548ms) and anger (592 – 844ms), but not for the other expressions. However, there was also evidence of *reduced* pupil size compared to neutral at early timepoints for both fear (166 – 306ms) and disgust (60 – 500ms) – though fear also showed an additional period of reduced pupil size from 1194 to 1410ms. Changes in pupil size for sad and surprise did not significantly differ from dynamic neutral. These early reductions in pupil size relative to neutral are likely to be driven by pupillary responses to light, we will now investigate this possibility using a linear regression analysis.

To investigate the role of stimulus brightness on pupillary responses, we first divided trials into constriction (0 – 630ms) and dilation (632 – 3000ms) phases according to the peak PLR (i.e., the minimum average pupil size), which occurred in the dynamic condition at 630ms following trial onset (see Figure 2). We then conducted linear regression analyses for both phases, using Expression (happy, sad, surprise, fear, anger, disgust) as a predictor, with neutral as a reference level. We also included mean stimulus brightness values for each trial as a covariate (Luminance) to control for any systematic effects of light. The model for the constriction phase, $F(7,1323) = 2.01$, $p = .051$, $R^2 = .011$, indicated an effect of the covariate Luminance, $t = 2.09$, $p = .037$, but not Expression, *ts* < 1.8, *ps* > .08. However, during the dilation phase, the opposite pattern was found. The model, $F(7,1384) = 2.32$, $p = .023$, $R^2 =$

.012, indicated Luminance was not a significant predictor of pupil size, $t = 1.42$, $p = .155$, instead, there were effects of both happy, $t = 2.86$, $p = .004$, and angry expressions, $t = 2.58$, $p = .010$, relative to neutral. Although the effects of sad, $t = 0.61$, $p = .540$, surprise, $t = 0.09$, $p = .933$, fear, $t = 0.49$, $p = .627$, and disgust expressions, $t = 1.58$, $p = .115$, did not approach significance.

Discussion

Six-, nine- and twelve-month infants' evoked pupillary responses, and thus their sympathetic arousal, varied according to the facial expression of the on-screen actor. This indicates that infants can not only discriminate perceptually between expressions, but that they also show differential affective responses to the emotional expressions of others. Infants, however, only showed *dilatory* responses for happy and angry expressions; not for sad, surprise, fear, and disgust. After controlling for stimulus brightness, these effects persisted in the dilation phase, but not during the period of pupillary constriction (0 – 632ms). These results converge with investigations of infant behaviour within live parent-infant interactions, in which infants have been shown to mirror their parents' expressions of happiness and anger in their own behavioural responses (Haviland & Lelwica, 1987; Termine & Izard, 1988).

We also used Functional Data Analysis (see Sirois & Brisson, 2014) to investigate differences between expressive and neutral faces across time. Overall, expressive faces showed a similar pattern to neutral across time, but varied substantially between dynamic expressions. The FDA plots for individual expressions (Figure 3) indicated clear early and late dilation, relative to neutral, for angry and happy expressions, respectively. While surprise and sadness showed few response differences compared to neutral, fear and disgust showed the opposite trend of *reduced* pupil sizes, particularly at early timepoints. Our linear regression analysis indicated that only the dilation in response to happiness and anger during the 'dilation phase' significantly differed to neutral once pupil sizes were adjusted for differences in stimulus luminance.

Facial expressions of happiness and anger are both high-arousal emotional stimuli, but of opposite valence. Consistent with previous work in adults (Bradley et al., 2008; Partala & Surakka, 2003), we find both positive and negative emotional stimuli evoke larger pupillary dilation in infants relative to neutral. Much research has been conducted on infants' ability to perceive differences in both instances and categories of emotional expressions using behavioural methods. This prior work suggests that infants rapidly develop perceptual categories of emotion, and can categorise even highly similar facial configurations of the same valence and level of arousal (e.g., anger and disgust; Ruba et al., 2017). Infant eye-tracking also suggests that even young infants show adult-like facial scanning (Keemink et al., 2021; Prunty et al., 2021; Soussignan et al., 2017), and look toward regions diagnostic for emotion recognition (see Jack et al., 2014; Smith et al., 2005). These studies, however, are not designed to determine if infants are receptive to the emotional content of facial configurations, or whether they are merely sensitive to differences in low-level perceptual information (see Barrett et al., 2019; Nelson, 1987).

Studies that record infants' spontaneous behavioural responses to expressions of emotion (Haviland & Lelwica, 1987; Keemink et al., 2021; Serrano et al., 1995; Termine & Izard, 1988; Walker-Andrews, 1997), including those that measure how infants *use* these signals to resolve ambiguous situations (i.e. via social referencing; see Walden & Ogan, 1988), bring us closer to addressing this question. They suggest that infants can differentiate between positive and negative emotional information. For instance, if the expression is directed toward them, infants often reciprocate (Haviland & Lelwica, 1987; Keemink et al., 2019), producing congruent behavioural responses indicative of their own change in emotional state. If the expression is directed toward a third, external entity, older infants are more inclined to approach that entity if the expression is positive. However, many such studies use multiple cues to communicate the caregiver's emotion (e.g., facial movements, body gestures, vocal cues etc.), and it is conceivable, particularly in unfamiliar contexts, that infants who are receptive to emotional valence might nonetheless show incongruent behavioural responses, or none at all (see Camras & Shutter, 2010; Nelson, 1987). The present study provides convergent evidence that viewing different naturalistic expressions produces differential changes in the infants' own physiological state, with happiness and anger producing the largest sympathetic response.

Interestingly, this pattern of results does not conform to either general valence or arousal-based interpretations (see Widen & Russell, 2008), given that infants showed significantly greater dilatory responses for anger relative to other emotions of similar valence (e.g., sad, fear) and similar arousal (e.g., surprise, fear). These results instead suggest that infants do show emotion-specific responses (Ekman, 1993; Izard, 1994; Walker-Andrews, 1997). Yet before considering *how* infants differentiate between facial expressions (i.e., via broad dimensions or discrete categories), we must first determine *if* they exhibit physiological responses to all six basic emotions. Infants may indeed respond to expressions according to broad valence-based categories, but if they are unreceptive to certain facial emotions (e.g., disgust), they would produce a pattern of results that appears to be emotion-specific. Affective reciprocity for less familiar expressions, such as fear and disgust, may instead show a more protracted development (Widen, 2013; Widen & Russell, 2008). Given the socio-economic make-up of the region from which our sample was drawn (Office for

National Statistics, 2011), and the willingness and capacity of the infants' parents to participate in voluntary research, it seems reasonable to infer that the majority of these infants come from happy, stable home environments. We speculate here that infants' pattern of responses to emotional expressions might be different given a more diverse sample. We believe that this assertion warrants future empirical investigation.

The current findings also do not suggest any overall bias for negative expressions (see Vaish et al., 2008), or for fearful faces specifically (see Peltola et al., 2013). Instead, the positive emotion happiness produced the largest dilatory response, while fear produced the smallest. While pupillometry studies with adults suggest that negatively-valenced expressions produce stronger sympathetic responses (Laeng et al., 2013; Yrttiaho et al., 2017), work with children (Sepeta et al., 2012) and infants (Aktar et al., 2018; Jessen et al., 2016) have instead found greater dilation for happy compared to fear (and other negative expressions). These findings are usually attributed to the intrinsic reward value of positive social stimuli such as smiling faces (see O'Doherty et al., 2003). Interestingly, infant pupillometry studies that have reported a bias for negative expressions (e.g., Geangu et al., 2011; Hepach & Westermann, 2013) have included vivid displays of anger (e.g., vocalising and 'thumping' a stuffed toy). The current findings are therefore consistent with this literature, as infants in this study showed dilatory responses (relative to neutral) for *both* happy and angry facial expressions.

Nevertheless, as previous infant pupillometry experiments have varied in stimulus type (e.g., static and silent vs dynamic and audio-visual), duration (e.g., 1 second vs 50 seconds) and content, comparing between studies can be problematic. Here we also found a clear difference in the magnitude of pupil dilation between dynamic and static displays, with substantially larger overall pupil sizes, and reduced PLR, for dynamic expression stimuli (see

Henderson et al., 2014). This finding is consistent with previous work using facial electromyography (Sato et al., 2008) and neuroimaging (Kilts et al., 2003; Labar et al., 2003) which has found dynamic expressions illicit stronger responses compared to static expressions. Converging with previous studies investigating infant perception of dynamic and static expressions, here we also find dynamic-contingent expressions were more effective at evoking an arousal response in infants than static stimuli. Given that 'real-world' facial expressions also occur within dynamic and interactive social contexts, it is recommended that researchers move toward more naturally-engaging and ecologically-valid stimuli (Prunty et al., 2021), as long as sufficient statistical controls for luminance are implemented.

Despite presenting infants with engaging dynamic and interactive facial expression stimuli, the current study found no evidence of developmental differences in arousal response between infants six-, nine- and twelve-months old. These findings are perhaps surprising given widely-reported age-related changes in how infants perceive and attend emotional expressions (Flom & Bahrick, 2007; Nelson, 1987; Peltola et al., 2013; Quinn et al., 2011; Soussignan et al., 2017). Emotion percepts are therefore likely to have distinct developmental trajectories from emotion arousal responses, which fits with the broader evidence indicating that conceptual categories of emotion show a much more gradual development (Quinn et al., 2011; Widen & Russell, 2008). Further work is needed to explore developmental trajectories in the pupillary responses evoked by different facial emotions.

Despite its age (Fitzgerald, 1965), developmental pupillometry remains in its infancy. One reason for this is the difficulty of presenting ecologically valid stimuli, whilst also maintaining adequate controls for luminance and minimising data loss. The pupillary response is also a general response to both positive and negative arousal, and as such is subject to similar limitations as looking times, where low-level perceptual information is potentially confounding. For example, dynamic expressions naturally differ in their motion content, and thus we must consider whether differences in infants' pupillary responses are driven by the expressed emotion, or by motion information more generally. In the current study we did not measure motion in our stimuli but recognise that future studies should quantify motion to better understand its potential contribution to pupillary responses. On this occasion, it is unlikely that our results are driven by motion content alone as surprise (wide opening mouth and eyes) presented more motion than anger (subtle narrowing of eyes, furrowing of brow), but it was for anger that we recorded a pupillary response. Nevertheless, future studies will have to navigate the necessary trade-off between presenting ecologically valid stimuli and maintaining adequate experimental control.

When investigating infants' responses to emotional expressions, a further limitation to consider is the choice of an appropriate control stimulus. In the current study, we found that our baseline, a dynamic neutral face, produced larger dilatory responses than some expressive faces (e.g., fear). For infants, a *lack* of an expressive response (i.e., a neutral expression), particularly within a social interaction, may in itself be arousing, as is evident from the 'still-face' phenomenon (for a review see Adamson & Frick, 2003). This is part of a broader debate in emotion research (e.g., see Lee et al., 2008), and will need to be considered in future work.

In conclusion, investigations of infant perception tell us little about whether infants are receptive to the affective information conveyed by facial gestures. To determine this, one option is to measure infant responses to different expressions of emotion. However, within live interactions infants may not be inclined to provide 'appropriate' behavioural responses, so here we instead use pupil dilation as an implicit index of infants' physiological arousal.

Comparisons between previous investigations of infants' pupillometric responses to expressions have been hampered by substantial methodological differences. Here we presented infants with dynamic and interactive examples of the six 'basic' emotional facial expressions, finding that six-, nine- and twelve-month infants only show clear dilatory responses for happiness and anger relative to neutral. These results suggest that although infants can discriminate perceptually between facial expressions, their sensitivity to the affective content of certain expressions may show a more protracted development.

References

Adamson, L. B., & Frick, J. E. (2003). The Still Face: A History of a Shared Experimental Paradigm. *Infancy*, *4*(4), 451–473. https://doi.org/10.1207/S15327078IN0404_01

Addabbo, M., Longhi, E., Marchis, I. C., Tagliabue, P., & Turati, C. (2018). Dynamic facial expressions of emotions are discriminated at birth. *PloS One*, *13*(3), e0193868. https://doi.org/10.1371/journal.pone.0193868

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

Aston-Jones, G., & Cohen, J. D. (2005). An Integrative Theory of Locus Coeruleus-Norepinepherine Function: Adaptive Gain and Optimal Performance. *Annual Review of Neuroscience*, *28*(1), 403–450. https://doi.org/10.1146/annurev.neuro.28.061604.135709

Attard-Johnson, J., Bindemann, M., & Ó Ciardha, C. (2016). Pupillary Response as an Age-Specific Measure of Sexual Interest. *Archives of Sexual Behavior*, *45*(4), 855–870.

https://doi.org/10.1007/s10508-015-0681-3

Attard-Johnson, J., Ó Ciardha, C., & Bindemann, M. (2019). Comparing methods for the analysis of pupillary response. *Behavior Research Methods*, *51*(1), 83–95. https://doi.org/10.3758/s13428-018-1108-6

Barrett, L. F., Adolphs, R., Marsella, S., Martinez, A. M., & Pollak, S. D. (2019). Emotional expressions reconsidered: challenges to inferring emotion from human facial movements. *Psychological Science in the Public Interest*, *20*(1), 1–68. https://doi.org/10.1177/1529100619832930

Barrett, L. F., Lindquist, K. A., & Gendron, M. (2007). Language as context for the perception of emotion. *Trends in Cognitive Sciences*, *11*(8), 327–332. https://doi.org/10.1016/j.tics.2007.06.003

Beatty, J., & Lucero-Wagoner, B. (2000). The pupillary system. In *Handbook of psychophysiology* (2nd ed., pp. 142–162). Cambridge University Press.

Bradley, M. B., Miccoli, L. M., Escrig, M. a, & Lang, P. J. (2008). The pupil as a measure of emotional arousal and automatic activation (Author Manuscript). *Psychophysiology*, *45*(4), 602. https://doi.org/10.1111/j.1469-8986.2008.00654.x.The

Camras, L. A., & Shutter, J. M. (2010). Emotional facial expressions in infancy. *Emotion Review*, *2*(2), 120–129. https://doi.org/10.1177/1754073909352529

Ekman, P. (1992). An argument for basic emotions. *Cognition & Emotion*, *6*(3–4), 169–200. https://doi.org/10.1080/02699939208411068

Ekman, P. (1993). Facial expression and emotion. *The American Psychologist*, *48*(4), 384–392. https://doi.org/10.1037/0003-066X.48.4.384

Ekman, P., & Friesen, W. V. (1976). *Pictures of facial affect*. Consulting Psychologists Press.

Ekman, P., Friesen, W. V., O'Sullivan, M., Chan, A., Diacoyanni-Tarlatzis, I., Heider, K., Krause, R., LeCompte, W. A., Pitcairn, T., Ricci-Bitti, P. E., Scherer, K., & Tomita, M.

(1987). Universals and cultural differences in the judgments of facial expressions of emotion. *Journal of Personality and Social Psychology*, *53*(4), 712–717. https://doi.org/10.1037/0022-3514.53.4.712

Fantz, R. L. (1963). Pattern vision in newborn infants. *Science*, *140*(3564), 296–297. https://doi.org/10.1126/science.140.3564.296

Farroni, T., Menon, E., Rigato, S., & Johnson, M. H. (2007). The perception of facial expressions in newborns. *European Journal of Developmental Psychology*, *4*(1), 2–13. https://doi.org/10.1080/17405620601046832

Field, T. M., Goldstein, S., Vega-Lahr, N., & Porter, K. (1986). Changes in imitative behavior during early infancy. *Infant Behavior and Development*, *9*(4), 415–421. https://doi.org/10.1016/0163-6383(86)90015-9

Fitzgerald, E. (1965). Autonomic Pupillary Reflex Activity during Early Infancy and Its Relation to Social and Nonsocial Visual. *Journal of Experimental Child Psychology*, *6*(3), 470–482. https://doi.org/10.1016/0022-0965(68)90127-6

Flom, R., & Bahrick, L. E. (2007). The development of infant discrimination of affect in multimodal and unimodal stimulation: The role of intersensory redundancy. *Developmental Psychology*, *43*(1), 238–252. https://doi.org/10.1037/0012-1649.43.1.238

Frith, C. (2009). Role of facial expressions in social interactions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1535), 3453–3458. https://doi.org/10.1098/rstb.2009.0142

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

Godard, O., Baudouin, J.-Y. Y., Schaal, B., & Durand, K. (2016). Affective matching of odors and facial expressions in infants: Shifting patterns between 3 and 7 months.

Developmental Science, *19*(1), 155–163. https://doi.org/10.1111/desc.12292

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

Haviland, J. M., & Lelwica, M. (1987). The induced affect response: 10-week-old infants' responses to three emotion expressions. *Developmental Psychology*, *23*(1), 97–104. https://doi.org/10.1037/0012-1649.23.1.97

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

Henderson, R. R., Bradley, M. M., & Lang, P. J. (2014). Modulation of the initial light reflex during affective picture viewing. *Psychophysiology*, *51*(9), 815–818. https://doi.org/10.1111/psyp.12236

Hepach, R., & Westermann, G. (2013). Infants' sensitivity to the congruence of others' emotions and actions. *Journal of Experimental Child Psychology*, *115*(1), 16–29. https://doi.org/10.1016/j.jecp.2012.12.013

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

Hess, E. H., & Polt, J. M. (1960). Pupil size as related to interest value of visual stimuli. *Science (New York, N.Y.)*, *132*(3423), 349–350. https://doi.org/10.1126/science.132.3423.349

Hunnius, S., de Wit, T. C. J., Vrins, S., & von Hofsten, C. (2011). Facing threat: Infants' and adults' visual scanning of faces with neutral, happy, sad, angry, and fearful emotional

Accepted Article

expressions. *Cognition and Emotion*, *25*(2), 193–205. https://doi.org/10.1080/15298861003771189

Izard, C. E. (1994). Innate and universal facial expressions: evidence from developmental and cross-cultural research. *Psychological Bulletin*, *115*(2), 288–299. https://doi.org/10.1037/0033-2909.115.2.288

Jack, R. E., Garrod, O. G. B. B., & Schyns, P. G. (2014). Dynamic facial expressions of emotion transmit an evolving hierarchy of signals over time. *Current Biology*, *24*(2), 187–192. https://doi.org/10.1016/j.cub.2013.11.064

Jackson, I. R., & 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

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

Joshi, S., Li, Y., Kalwani, R. M., & Gold, J. I. (2016). Relationships between Pupil Diameter and Neuronal Activity in the Locus Coeruleus, Colliculi, and Cingulate Cortex. *Neuron*, *89*(1), 1–14. https://doi.org/10.1016/j.neuron.2015.11.028

Keemink, J. R., Jenner, L., Prunty, J. E., Wood, N., & Kelly, D. J. (2021). Eye movements and behavioural responses to gaze-contingent expressive faces in typically developing infants and infant siblings. *Autism Research*, *14*, 973–983. https://doi.org/10.1002/aur.2432

Keemink, J. R., Keshavarzi-Pour, M. J., & Kelly, D. J. (2019). Infants' responses to interactive gaze-contingent faces in a novel and naturalistic eye-tracking paradigm. *Developmental Psychology*, *55*(7), 1362–1371. https://doi.org/10.1037/dev0000736

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

Kilts, C. D., Egan, G., Gideon, D. A., Ely, T. D., & Hoffman, J. M. (2003). Dissociable neural pathways are involved in the recognition of emotion in static and dynamic facial expressions. *Neuroimage*, *18*(1), 156–168. https://doi.org/10.1006/nimg.2002.1323

Kotsoni, E., Haan, M. D. E., & 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. 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

Krumhuber, E. G., Kappas, A., & Manstead, A. S. R. (2013). Effects of dynamic aspects of facial expressions: A review. *Emotion Review*, *5*(1), 41–46. https://doi.org/10.1177/1754073912451349

Labar, K. S., Crupain, M. J., Voyvodic, J. T., & McCarthy, G. (2003). Dynamic perception of facial affect and facial identity in the human brain. *Cerebral Cortex*, *13*(10), 1023–1033. https://doi.org/10.1093/cercor/13.10.1023

Laeng, B., Sæther, L., Holmlund, T., Wang, C. E. A., Waterloo, K., Eisemann, M., & Halvorsen, M. (2013). Invisible emotional expressions influence social judgments and pupillary responses of both depressed and non-depressed individuals. *Frontiers in Psychology*, *4*, 291. https://doi.org/10.3389/fpsyg.2013.00291

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

Lee, E., Kang, J. I., Park, I. H., Kim, J.-J., & An, S. K. (2008). Is a neutral face really evaluated as being emotionally neutral? *Psychiatry Research*, *157*(1–3), 77–85. https://doi.org/10.1016/j.psychres.2007.02.005

Libertus, K., Landa, R. J., & Haworth, J. L. (2017). Development of attention to faces during the first 3 years: Influences of stimulus type. *Frontiers in Psychology*, *8*, 1976. https://doi.org/10.3389/fpsyg.2017.01976

Meltzoff, A. N. (1988). Imitation of televised models by infants. *Child Development*, *59*(5), 1221–1229. https://doi.org/10.2307/1130485

Montague, D. P. F., & Walker-Andrews, A. S. (2001). Peekaboo: a new look at infants' perception of emotion expressions. *Developmental Psychology*, *37*(6), 826–838. https://doi.org/10.1037/0012-1649.37.6.826

Murphy, P. R., O'Connell, R. G., O'Sullivan, M., Robertson, I. H., & Balsters, J. H. (2014). Pupil diameter covaries with BOLD activity in human locus coeruleus: Pupil Diameter and Locus Coeruleus Activity. *Human Brain Mapping*, *35*(8), 4140–4154. https://doi.org/10.1002/hbm.22466

Nelson, C. A. (1987). The Recognition of Facial Expressions in the First Two Years of Life : Mechanisms of Development. *Child Development*, *58*(4), 889–909. https://doi.org/10.2307/1130530

Nelson, C. A., Morse, P., & Leavitt, L. (1979). Recognition of facial expressions by seven-month-old infants. *Child Development*, *50*(4), 1239–1242. https://doi.org/10.2307/1129358

Nielsen, M., Simcock, G., & Jenkins, L. (2008). The effect of social engagement on 24-month-olds' imitation from live and televised models. *Developmental Science*, *11*(5), 722–731. https://doi.org/10.1111/j.1467-7687.2008.00722.x

O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D. M., Dolan, R. J., O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D. M., & Dolan, R. J. (2003). Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia*, *41*(2), 147–155. https://doi.org/10.1016/S0028-3932(02)00145-8

Office for National Statistics. (2011). *2011 Census Profile*. https://www.kent.gov.uk/about-the-council/information-and-data/Facts-and-figures-about-Kent/population-and-census#tab-4

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

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

Prunty, J. E., Jackson, K. C., Keemink, J. R., & Kelly, D. J. (2020). Caucasian infants' attentional orienting to own-and other-race faces. *Brain Sciences*, *10*(1), 53. https://doi.org/10.3390/brainsci10010053

Prunty, J. E., Keemink, J. R., & Kelly, D. J. (2021). Infants scan static and dynamic facial expressions differently. *Infancy*. https://doi.org/10.1111/infa.12426

Quinn, P. C., Anzures, G., Izard, C. E., Lee, K., Pascalis, O., Slater, A. M., & Tanaka, J. W. (2011). Looking across domains to understand infant representation of emotion. *Emotion Review*, *3*(2), 197–206. https://doi.org/10.1177/1754073910387941

Ramsay, J., & Silverman, B. (1997). *Functional data analysis*. Springer-Verlag.

Reilly, J., Kelly, A., Kim, S. H., Jett, S., & Zuckerman, B. (2019). The human task-evoked pupillary response function is linear: Implications for baseline response scaling in pupillometry. *Behavior Research Methods*, *51*(2), 865–878. https://doi.org/10.3758/s13428-018-1134-4

Richoz, A.-R., Lao, J., Pascalis, O., & Caldara, R. (2018). Tracking the recognition of static and dynamic facial expressions of emotion across the life span. *Journal of Vision*, *18*(9), 5. https://doi.org/10.1167/18.9.5

Ruba, A. L., Johnson, K. M., Harris, L. T., & Wilbourn, M. P. (2017). Developmental changes in infants' categorization of anger and disgust facial expressions. *Developmental Psychology*, *53*(10), 1826–1832. https://doi.org/10.1037/dev0000381

Ruba, A. L., Meltzoff, A. N., & Repacholi, B. M. (2019). How do you feel? Preverbal infants match negative emotions to events. *Developmental Psychology*, *55*(6), 1138–1149. https://doi.org/10.1037/dev0000711

Safar, K., Kusec, A., & Moulson, M. C. (2017). Face experience and the attentional bias for fearful expressions in 6- and 9-month-old infants. *Frontiers in Psychology*, *8*(SEP), 1–8. https://doi.org/10.3389/fpsyg.2017.01575

Sara, S. J. (2009). The locus coeruleus and noradrenergic modulation of cognition. *Nature Reviews. Neuroscience*, *10*(3), 211–223. https://doi.org/10.1038/nrn2573

Sara, S. J., & Bouret, S. (2012). Orienting and Reorienting: The Locus Coeruleus Mediates Cognition through Arousal. *Neuron*, *76*(1), 130–141. https://doi.org/10.1016/j.neuron.2012.09.011

Sato, W., Fujimura, T., & Suzuki, N. (2008). Enhanced facial EMG activity in response to dynamic facial expressions. *International Journal of Psychophysiology*, *70*(1), 70–74. https://doi.org/10.1016/j.ijpsycho.2008.06.001

Sepeta, L., Tsuchiya, N., Davies, M. S., Sigman, M., Bookheimer, S. Y., & Dapretto, M. (2012). Abnormal social reward processing in autism as indexed by pupillary responses to happy faces. *Journal of Neurodevelopmental Disorders*, *4*(1), 17. https://doi.org/10.1186/1866-1955-4-17

Serrano, J. M., Iglesias, J., & Loeches, A. (1992). Visual discrimination and recognition of facial expressions of anger, fear, and surprise in 4-to 6-month-old infants.

Developmental Psychobiology, *25*(6), 411–425. https://doi.org/10.1002/dev.420250603

Serrano, J. M., Iglesias, J., & Loeches, A. (1995). Infants' responses to adult static facial expressions. *Infant Behavior and Development*, *18*(4), 477–482. https://doi.org/10.1016/0163-6383(95)90036-5

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

Smith, M. L., Cottrell, G. W., Gosselin, F., & Schyns, P. G. (2005). Transmitting and decoding facial expressions. *Psychological Science*, *16*(3), 184–189. https://doi.org/10.1111/j.0956-7976.2005.00801.x

Soussignan, R., Dollion, N., Schaal, B., Durand, K., Reissland, N., & Baudouin, J.-Y. (2017). Mimicking emotions: how 3--12-month-old infants use the facial expressions and eyes of a model. *Cognition and Emotion*, 1–16. https://doi.org/10.1080/02699931.2017.1359015

Termine, N. T., & Izard, C. E. (1988). Infants' Responses to Their Mothers' Expressions of Joy and Sadness. *Developmental Psychology*, *24*(2), 223–229. https://doi.org/10.1037/0012-1649.24.2.223

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: the origins of cultural cognition. *The Behavioral and Brain Sciences*, *28*(5), 675–691; discussion 691-735. https://doi.org/10.1017/S0140525X05000129

Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., Marcus, D. J., Westerlund, A., Casey, B. J., & Nelson, C. (2009). The NimStim set of facial expressions: judgments from untrained research participants. *Psychiatry Research*, *168*(3), 242–249. https://doi.org/10.1016/j.psychres.2008.05.006

Vaish, A., Grossmann, T., & Woodward, A. L. (2008). Not all emotions are created equal: the negativity bias in social-emotional development. *Psychological Bulletin*, *134*(3),

Accepted Article

383–403. https://doi.org/10.1037/0033-2909.134.3.383

Vernetti, A., Senju, A., Charman, T., Johnson, M. H., Gliga, T., Team, B., & others. (2018). Simulating interaction: Using gaze-contingent eye-tracking to measure the reward value of social signals in toddlers with and without autism. *Developmental Cognitive Neuroscience*, *29*, 21–29. https://doi.org/10.1016/j.dcn.2017.08.004

Wagner, J. B., Luyster, R. J., Tager-Flusberg, H., & Nelson, C. A. (2016). Greater Pupil Size in Response to Emotional Faces as an Early Marker of Social-Communicative Difficulties in Infants at High Risk for Autism. *Infancy*, *21*(5), 560–581. https://doi.org/10.1111/infa.12128

Walden, T. A., & Ogan, T. A. (1988). The development of social referencing. *Child Development*, *59*(5), 1230–1240. https://doi.org/10.2307/1130486

Walker-Andrews, A. S. (1997). Infants' perception of expressive behaviors: Differentiation of multimodal information. *Psychological Bulletin*, *121*(3), 437–456. https://doi.org/10.1037/0033-2909.121.3.437

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

Widen, S. C., & Russell, J. A. (2008). Children acquire emotion categories gradually. *Cognitive Development*, *23*(2), 291–312. https://doi.org/10.1016/j.cogdev.2008.01.002

Wilcox, B. M., & Clayton, F. L. (1968). Infant visual fixation on motion pictures of the human face. *Journal of Experimental Child Psychology*, *6*(1), 22–32. https://doi.org/10.1016/0022-0965(68)90068-4

Yrttiaho, S., Niehaus, D., Thomas, E., & Leppänen, J. M. (2017). Mothers' pupillary responses to infant facial expressions. *Behavioral and Brain Functions*, *13*(1), 2. https://doi.org/10.1186/s12993-017-0120-9

Table 1. Participant information for both static and dynamic conditions

	Age (months)	Age M (SD) (days)	N	
			Male	Female
Static	6	192.36 (24.04)	5	6
	9	275.13 (13.24)	13	10
	12	367.57 (12.39)	7	7
Dynamic	6	192.87 (10.12)	16	17
	9	275.20 (12.80)	15	15
	12	366.23 (14.13)	17	18

Table 2. Average brightness values for dynamic and static expression stimuli, and their difference from neutral

	Dynamic		Static	
	Mean	Difference	Mean	Difference
Neutral	.5512	--	.5532	--
Happy	.5573	< .01	.5151	- .04
Sad	.5467	< .01	.5584	< .01
Surprise	.5130	- .04	.5121	- .04
Fear	.5309	- .02	.5353	- .02
Anger	.5469	< .01	.5492	< .01
Disgust	.5491	< .01	.5509	< .01

Luminance values were computed on a 0 (full black) to 1 (full white) scale

Figure Legends

Figure 1. The six 'basic' expressions. A selection of expressive stimuli used within the static condition that were created by taking stills from the dynamic expression videos at 'peak' expressive amplitude. Like classic expression stimuli (see Ekman & Friesen, 1971), the six 'basic' expressions are used (Ekman et al., 1987): happy, sad, surprise, fear, anger and disgust; from left to right respectively.

Figure 2. Infants' change in pupil size in response to dynamic and static expressive faces. Change in pupil size from a 100ms baseline (z-scores) following the first eye-region fixation and initiation of expression animation in the dynamic condition. Change in pupil size is plotted for all expressions (neutral: black/bold, happy: dark blue, sad: red, surprise: yellow, fear: purple, anger: green, disgust: light blue), divided by condition (top). Differences between expressive and neutral trials (expressive minus neutral) were converted into b-splines for each participant and used to compute t-score functions (bottom). Thresholds for significant differences are plotted in red (dynamic critical t = 1.985, static critical t = 2.012, p = .05, two-tailed).

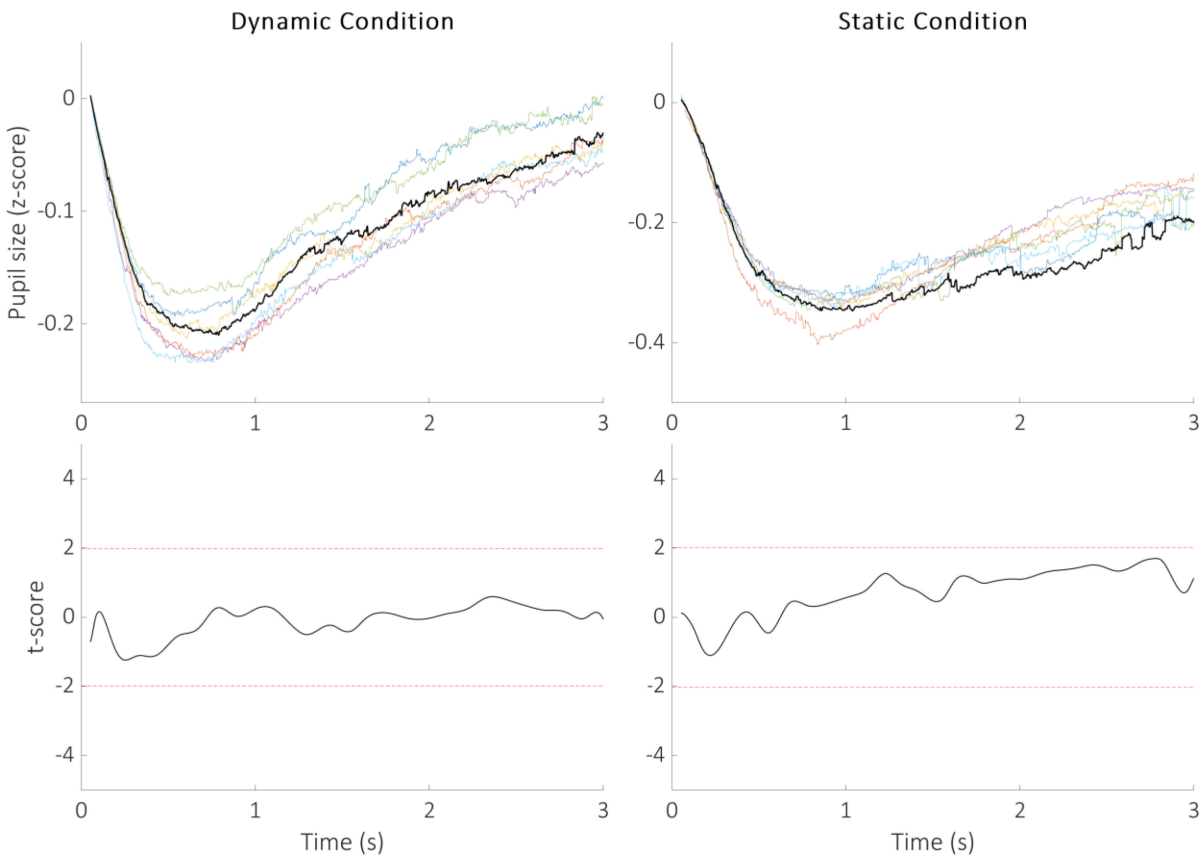

Figure 3. Infants' evoked pupillary responses for all six *dynamic* expressions. The change in pupil size for all six dynamic expressions relative to neutral are illustrated using t-score functions across time. Significance thresholds are plotted in red for both uncorrected (dashed line: critical t = 1.985, p = .05, two-tailed) and Bonferroni-corrected (solid line: critical t = 2.708, p = .008, two-tailed, six comparisons) alpha values.