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Pupillary responses reveal infants' discrimination of facial emotions independent of conscious perception

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ABSTRACT

Sensitive responding to others' emotions is essential during social interactions among humans. There is evidence for the existence of subcortically mediated emotion discrimination processes that occur independent of conscious perception in adults. However, only recently work has begun to examine the development of automatic emotion processing systems during infancy. In particular, it is unclear whether emotional expressions impact infants' autonomic nervous system regardless of conscious perception. We examined this question by measuring pupillary responses while subliminally and supraliminally presenting 7-month-old infants with happy and fearful faces. Our results show greater pupil dilation, indexing enhanced autonomic arousal, in response to happy compared to fearful faces regardless of conscious perception. Our findings suggest that, early in ontogeny, emotion discrimination occurs independent of conscious perception and is associated with differential autonomic responses. This provides evidence for the view that automatic emotion processing systems are an early-developing building block of human social functioning.

1. Introduction

Emotional communication is an essential aspect of human social encounters (Frith, 2009). Perceiving emotional expressions in others triggers automatic physiological responses in the observer that are regulated by the autonomic nervous system such as changes in heart rate, skin conductance, and pupil dilation (Bradley, Miccoli, Escrig, & Lang, 2008; Ramachandra, Depalma, & Lisiewski, 2009). These responses reflect changes in activation or suppression of the sympathetic and parasympathetic parts of the autonomic nervous system and are thought to facilitate evolutionary adaptive responding to relevant information (Porges, 2003). Specifically, viewing facial emotional expressions has been shown to elicit changes in pupil dilation that occurred regardless of conscious perception of the face in adults (see Laeng, Sirois, & Gredeback, 2012, for review). Increased pupil dilation reflects greater activation of the sympathetic nervous system or a suppression of the parasympathetic nervous system, mediated by the locus coeruleus (Bradley et al., 2008; Laeng et al., 2012). The locus coeruleus has strong connections to other subcortical brain structures such as the amygdala (Van Bockstaele, Colago, & Valentino, 1998) and this is argued to support a close coupling between changes in pupil size and affective processing (Laeng et al., 2012). In particular, one can distinguish between phasic and tonic activation of the locus coeruleus; while the former characterizes responses to specific events, the latter is related to changes in task or a person's overall attentional state (Laeng et al., 2012).

Measuring pupillary responses to emotional stimuli has become an established method to examine subcortically mediated autonomic responses (sympathetic arousal) in adults (Bradley et al., 2008). Increased pupil dilation has typically been observed in response to emotionally arousing stimuli irrespective of valence (Bradley et al., 2008; Partala & Surakka, 2003). However, for facial expressions adults tend to show an increased pupil dilation in response to negative, especially fearful, compared to happy facial expressions (Laeng et al., 2013). The sympathetic arousal (pupil dilation) seen to fearful expressions has been argued to reflect a response that may prepare the body to flee (e.g., Porges, 2003). While most prior work has focused on consciously perceived emotions, changes in pupil size have also been observed in response to emotional stimuli that are not perceived consciously but were presented subliminally. As for supraliminal stimuli, an increase in pupil size in adults occurs in response to masked fearful facial expressions, which are not consciously perceived (Laeng et al., 2013). Along these lines, it has been shown that patients suffering from unilateral cortical blindness show a comparable increase in

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pupillary size to fearful stimuli presented in their blind or intact visual field (Tamietto et al., 2009). Taken together, prior work shows that fearful facial expressions automatically evoke increased pupil dilation in adults, indexing subcortically mediated greater sympathetic arousal.

Only recently research has begun to examine the developmental and brain origins of such automatic facial emotion processing systems during infancy. Prior behavioral and event-related brain potential (ERP) work has established face visibility thresholds in infants of various ages, serving as an important basis for the investigation of subliminal and supraliminal emotional face processing in infants (Gelskov & Kouider, 2010; Kouider et al., 2013). In a series of ERP studies (Jessen & Grossmann, 2014, 2015), it has been shown that 7-month-old infants discriminate between fearful and happy facial expressions regardless of whether facial emotional cues were presented subliminally or supraliminally. This suggests that, similar to what is known about adults (Smith, 2012), infants' facial emotion detection does not require conscious perception of visual emotional cues and is reflected in cortical processes measured by ERP. However, it is unclear whether processing others' emotional facial expressions is mediated by subcortical processes and impacts infants' autonomic responses, especially pupil dilation, independent of conscious perception.

Pupillometry has received increased attention in developmental research concerned with the early development of social perception and cognition in recent years, because it allows for the noninvasive investigation of autonomic responses, providing an important window into the social mind of preverbal infants (Hepach, Vaish, & Tomasello, 2012; Jackson & Sirois, 2009). With respect to emotion perception during infancy, using audio-visual displays, 6- and 12-month-old infants have been found to show largest pupil dilation in response to other infants in distress when compared to a neutral condition, but pupil dilation was also increased in response to other infants expressing happiness (Geangu, Hauf, Bhardwaj, & Bentz, 2011). Infant pupillary responses to adult emotional facial expressions appear to depend on several contextual factors. For example, 14-month-old infants' pupil dilation responses to fearful facial expressions depend on whether they view their parent or a stranger and also on whether their primary caregiver is their mother or their father (Gredeback, Eriksson, Schmitow, Laeng, & Stenberg, 2012). Furthermore, 14-month-old infants, but not 10-month-old infants, show increased pupil dilation when the emotion expressed by an adult mismatched the action carried out by the adult (Hepach & Westermann, 2013). This suggests that pupil dilation is a sensitive measure of infants' emerging sensitivity to emotions in others and that, at least in older infants, contextual factors contribute to pupil dilation responses to emotions. Critically, it remains to be seen how younger infants respond to fearful and happy facial expressions displayed by adults and whether pupil dilation to emotional facial expressions occurs independent of conscious perception.

In the current study, we therefore investigated pupillary responses in 7-month-old infants to fearful and happy facial expressions presented subliminally and supraliminally. This age group was chosen because 7-month-old infants have been shown to be able to discriminate between fearful and happy facial expressions (Peltola, Leppänen, Mäki, & Hietanen, 2009). Based on prior ERP work (Jessen & Grossmann, 2014, 2015), we hypothesized that infants are able to discriminate between emotional facial expressions regardless of conscious perception. More specifically, we examined whether infants' pupil dilation will be greater to fearful when compared to happy facial expressions, as previously shown in adults (Laeng et al., 2013). While our main analysis was focused on pupil dilation, in addition, we examined infants' looking patterns using eyetracking as this has also been shown to vary as a function of others' emotional expression (Hunnius, de Wit, Vrins, & von Hofsten, 2011). We hypothesized that looking patterns (face scanning) in infants will provide additional evidence for emotion discrimination independent of conscious perception. Furthermore, measuring pupil dilation and looking patterns allowed us to examine the relationship between the two measures.

2. Methods

2.1. Participants

Thirty infants were invited to participate in the study. The infants were seven months of age (mean: 205 days, range 196–225 days, 16 female). For one infant, no eye tracking data could be obtained, as the infant was too fussy. Infants were included in the analysis of pupil size and the analysis of fixation duration according to different inclusion criteria (see below). Twenty infants (10 female, mean age: 204 days) were included in the analysis of pupil size, and 22 infants (11 female, mean age: 204 days) were included in the analysis of fixation duration.

All infants were born full-term (38–42 weeks gestational age), had a birth weight of at least 2800 g and no known visual impairments. The parents gave written informed consent. The study was approved by the local ethics committee, and conducted according to the declaration of Helsinki.

2.2. Stimuli

The basic stimulus material consisted of happy, fearful, and neutral facial expressions portrayed by six young actresses from the FACES database (age 19–30, ID-numbers 54, 63, 85, 90, 115, and 173, see Ebner, Riediger, and Lindenberger, 2010). All emotional faces had been recognized with an accuracy of at least 90% by a group of young adults ($N = 52$, age 20–31 years, see Ebner et al., 2010). These photographs were cropped so that only the face and a minimum of hair was visible in an oval shape. To compare luminance between the conditions, pictures were converted to grayscale (while preserving luminance), the sum of all pixels was computed, and these values were entered into an ANOVA. Stimuli from the different emotions did not differ in luminance ($p = .28$). Additionally, we created scrambled masks from neutral facial expressions that were presented after each subliminal stimulus. The faces were presented with a height of 21.5 cm and a width of 16 cm.

One feature with respect to which happy and fearful faces might differ is the visibility of teeth, since happy faces are more likely to be characterized by an open mouth (laughing). However, this is unlikely to account for differences observed across emotions in the current study because teeth were not only visible in the happy facial expressions but also in four out of the six fearful facial expressions presented.

To keep the infants' attention focused on the screen, we presented short video clips containing bubbles moving in front of a blue background after each trial (Hepach et al., 2012).

Besides the stimuli included in the analyses, four additional types of stimuli were presented but not analyzed for the present manuscript. In these pictures, only the sclera of the eyes of happy and fearful facial expressions was visible, either showing a white sclera with a black pupil or a black sclera with a white pupil.

2.3. Design

Happy and fearful facial expressions were presented either supra- or subliminally, resulting in a 2×2 design with the factors Emotion (happy, fear) and Presentation Condition (supraliminal, subliminal). Each trial started with a single bubble that was

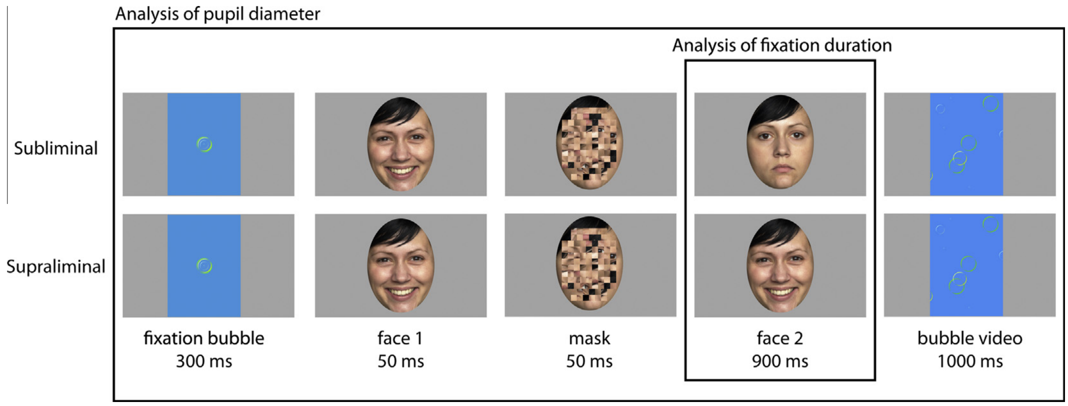

Fig. 1. Trial structure and stimuli. Depicted are two example trials, one in the subliminal happy condition (top row), the other in the supraliminal happy condition (bottom row). The trial structure is identical except for face 2, which is a neutral face in the subliminal condition and a face depicting the same emotion as face 1 in the supraliminal condition. (Note that in the actual experiment, the identity of face 1 and face 2 always differed. However, the depicted actress is the only one allowed to be shown in publications, and hence is used for illustration purposes.) The analysis of the pupil diameter was computed over the entire duration of a trial, while the analysis of the fixation duration was only computed during the presentation of face 2.

presented for 300 ms at the center of the screen in front of a blue background in order to direct the infant's attention to the center of the screen (Fig. 1). This fixation bubble was followed by either a happy or a fearful facial expression (face 1) presented for 50 ms, that is, below the infants' perceptual threshold (Gelskov & Kouider, 2010). Next, a scrambled neutral face was presented as a mask for another 50 ms. In the supraliminal conditions, this mask was followed for 900 ms by a second face (face 2), expressing the same emotion as face 1, but by a different actress. In the subliminal conditions, a neutral facial expression by a different actress was shown for 900 ms (face 2). The trial ended with the presentation of a video with bubbles for 1 s.

While these four conditions were the main conditions of interest, we also included a neutral condition, in which both, face 1 and face 2, showed a neutral facial expression (from different actresses). Results of this condition were not included in the final statistical analyses, but are shown for comparison in Fig. 2 on a descriptive level.

Besides these five conditions, four additional conditions were presented. In these conditions, pictures of sclerae as described above were shown instead of face 1. However, these conditions were not analyzed for the present manuscript.

Five trials of the same condition were shown in a row, constituting one miniblock. After a set of 18 such miniblocks (two per condition), a short break was made. If the infant was still attentive, a second and third set of 18 miniblocks was presented. Therefore, infants saw a maximum of 6 miniblocks per condition, yielding 30 trials in total (5 per miniblock). Miniblocks were presented in a pseudorandomized order that avoided repetitions of the same condition while ensuring that 2 miniblocks per condition were presented within each set of 18 miniblocks. The stimulus presentation was controlled using Tobii Studio (Tobii Technology, Stockholm, Sweden).

2.4. Procedure

The eyetracking recording was performed using a Tobii X2-60 Mobile Eye Tracker (Tobii Technology, Stockholm, Sweden) with a sampling rate of 60 Hz. The eyetracker was attached below the screen of a Dell Precision M6800 laptop with a 17.3 in. screen, a screen resolution of 1920×1080 pixel, and a refresh rate of 60 Hz. To ensure an equal luminance during all recordings, the experiment was performed in a room without daylight and the artificial lighting was identical for all participants.

After arriving in the lab, parents and infant were familiarized with the environment, and parents were informed about the procedure and signed a consent form. During the experiment, the infant was seated on his/her parent's lap approximately 60 cm in front of the screen and the parent wore opaque glasses to avoid any experimental influence via the parent. Parents were instructed not to interact with their child during the experiment.

The calibration of the eyetracker was performed using a child-friendly 5-point-calibration procedure, during which the picture of a little duck accompanied by a sound appeared at all four corners as well as the center of the screen. If calibration was successful, the experiment started. Otherwise, the calibration procedure was repeated. An experimenter monitored the infant via a video camera and started each trial manually when the infant attended to the screen.

2.5. Data analysis (Pupil diameter)

The data was exported from Tobii Studio and analyzed in Matlab (Version 7.14, R2012a). Pupil diameter was recorded for both eyes separately, and if data was available for both eyes, the mean was computed. If a value was only available for one eye, this value was considered for further analysis (on average 15% of the data points). For analyzing the pupil size, the entire duration of one trial (i.e. 2300 ms) was considered (Fig. 1). A trial was excluded from further analysis if a value was recorded for less than 50% of the sampling points during this time. Additionally, a trial was excluded if the infant did not look at the section of the screen where the subliminal stimulus (face 1) was presented in the subliminal conditions to ensure that infants were able to process the stimuli (on an unconscious level). Only infants with at least one trial per condition following these criteria were included in the final analysis. In the final sample, infants contributed on average 9.7 trials per condition (SD = 3.9).

For statistical analysis, the mean pupil diameter over the entire trial duration was computed. These values were averaged separately for every participant and condition and divided by the overall mean pupil size of that participant to account for possible interindividual differences. Finally, the values were entered in a repeated measures ANOVA with the factors Emotion (happy, fearful) and Presentation Condition (supraliminal, subliminal). Effect sizes are given in partial eta-squared (η^2).

We computed the mean pupil size separately for all six fearful facial expressions (see Supplementary material) as an additional

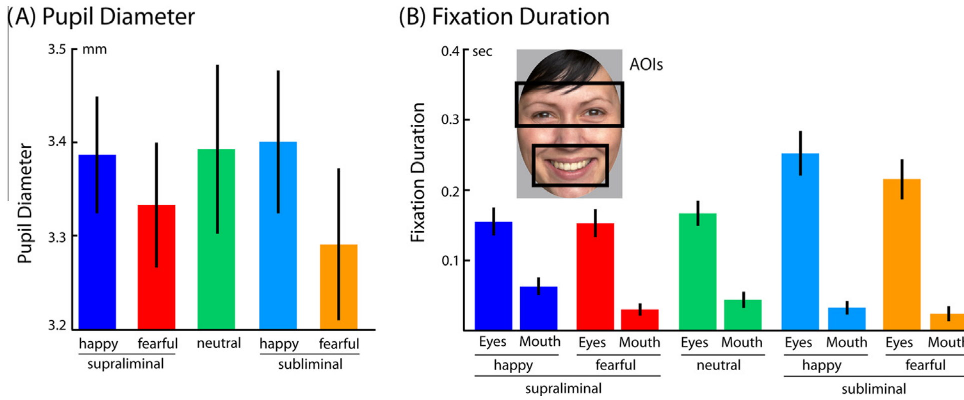

Fig. 2. Results. (A) Infants showed a larger pupil diameter in response to happy faces (in blue) compared to fearful face (in red and orange), irrespective of presentation duration. (B) Infants looked longer when happy faces (in blue) were presented compared to when fearful faces (in red and orange) were presented, irrespective of whether the emotional face was presented supraliminally or whether a neutral faces was only preceded by a subliminal emotional face. In the upper part of the figure, the areas of interest (AOIs) for eye region and mouth region are shown. In both graphs, the neutral condition (in green) is shown for comparison. Reported are mean values ± standard error. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

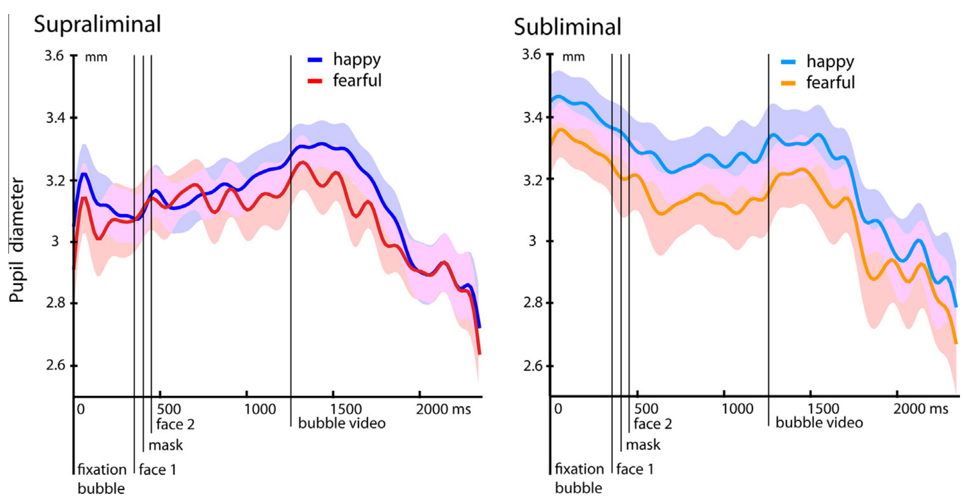

Fig. 3. Changes in Pupil Size over Time. Shown is the mean pupil size (solid line) with standard error during supraliminal (left part) and subliminal (right part) trials. The happy condition is plotted in blue, while the fearful condition is plotted in red and orange. On the *x*-axis, the different events during one trial are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

measure in order to ensure that the observed effects were not driven by the two fearful faces not displaying teeth. This additional analysis revealed that the pupil size in response to one of the two fearful faces that did not display teeth appeared smaller compared to the other five items. We therefore reran our analysis excluding all stimuli from this particular actress. Note that for this control analysis, only 17 participants were included, because with this limited set of stimuli, three participants did not fulfill the inclusion criterion of at least one trial per condition.

For illustration of the time course (Fig. 3), missing data points were interpolated and data was filtered with a 7 Hz lowpass filter.

2.6. Data analysis (Fixation duration)

A fixation was defined as a series of data points for at least 60 ms within a visual angle of 0.5°. We defined two areas of interest (AOIs), one encompassing the eyes and one encompassing the mouth (Fig. 2B). Only the time during which the supraliminal face (i.e., face 2) was presented was considered for analysis of the fixation duration (Fig. 1), and only trials in which the infant showed at least one fixation on the screen during this time were considered for further analysis. Again, we also excluded all trials in the subliminal conditions in which the infant did not look at that part of the screen where the subliminal stimulus was presented. Only infants with at least one trial per condition following these criteria were included in the final analysis. In the final sample, infants contributed on average 13.9 trials per condition (SD = 7.1).

For statistical analysis, the mean fixation duration for each AOI (eyes and mouth) was computed and entered in a repeated measures ANOVA with the factors Emotion (happy, fearful), Presentation Condition (supraliminal, subliminal), and AOI (eyes, mouth). Effect sizes are given in partial eta-squared (η^2) for ANOVAs and *r* for *t*-tests.

To investigate whether the observed effects in pupil diameter were driven by differences in fixation duration (see discussion) we additionally computed a correlation between pupil diameter and fixation duration, irrespective of condition, for both mouth AOI and eye AOI, as well as for the sum of both AOIs.

3. Results

3.1. Pupil diameter

We observed a main effect of Emotion [$F(1,19) = 6.45$, $MSE = .0039$, $p = .02$, $\eta^2 = .25$], revealing a larger pupil diameter for happy compared to fearful facial expressions irrespective of presentation condition (Figs. 2A and 3). There was no main effect of Presentation Condition [$F(1,19) = 0.40$, $MSE = .0029$, $p = .53$, $\eta^2 = .02$] and no interaction between Presentation Condition and Emotion [$F(1,19) = 1.17$, $MSE = .0011$, $p = .29$, $\eta^2 = .06$].

A control analysis excluding items from one actress displaying no teeth in the fearful condition (see Methods) and three participants yielded a similar pattern of results, although the main effect of emotion is only marginally significant in this case [$F(1,16) = 3.845$, $p = 0.068$, $\eta^2 = .19$]. The marginal effect is likely explained by reduced power because we had to exclude three additional infants from this analysis ($n = 17$ instead of $n = 20$ in the main analysis) in order to adhere to our inclusion criterion.

3.2. Fixation duration

While the main focus of the study was clearly on the analysis of pupil size, we also compared differences in fixation duration to complement this analysis.

As for pupil size, we observed a main effect of Emotion; infants showed a significantly longer fixation duration for happy compared to fearful facial expressions [$F(1,21) = 4.57$, $MSE = 0.015$, $p = .044$, $\eta^2 = .19$]. Furthermore, we found a main effect of Presentation Condition, showing that infants looked longer in the subliminal compared to the supraliminal condition [$F(1,21) = 8.57$, $MSE = 0.020$, $p = .008$, $\eta^2 = .29$] (see Fig. 2B). Note that in the subliminal conditions, a neutral face was presented during the time used for analyzing the fixation duration; hence, this effect can also be framed as a longer looking duration to neutral faces (as compared to emotional faces) preceded by subliminal emotional ones. An interaction between Presentation Condition and AOI [$F(1,21) = 20.42$, $MSE = 0.010$, $p < .001$, $\eta^2 = .49$] revealed that this was the case in particular for the eye region [$t(21) = -4.06$, $p < .001$, $r = .66$].

Furthermore, we observed a main effect of AOI [$F(1,21) = 59.05$, $MSE = 0.073$, $p < .001$, $\eta^2 = .74$], showing that infants fixated longer on the eye than on the mouth AOI.

There was no significant interaction between Emotion and Presentation Condition [$F(1,21) = 0.09$, $MSE = 0.007$, $p = .77$, $\eta^2 = .004$], AOI and Emotion [$F(1,21) = 0.004$, $MSE = 0.008$, $p = .95$, $\eta^2 = .0002$], or Emotion, Presentation Condition, and AOI [$F(1,21) = 1.76$, $MSE = 006$, $p = .20$, $\eta^2 = .077$].

3.3. Results of correlation analysis

We did not observe a significant correlation between pupil diameter and fixation duration for the sum of both AOIs ($p = .51$, $r = -.18$), for the eye AOI ($p = .31$, $r = -.27$), or for the mouth AOI ($p = .55$, $r = .16$).

4. Discussion

The current study examined 7-month-old infants' pupillary responses to supraliminally and subliminally presented fearful and happy facial expressions using eyetracking. Our results revealed that infants of this age show greater pupil dilation to happy facial expressions compared to fearful facial expressions. This effect of emotion on pupil dilation occurred independent of conscious perception of the face and indexes that happy expressions elicit enhanced sympathetic arousal in infants. Our results further revealed that infants exhibited a similar, but uncorrelated, increase in attention to happy faces when compared to fearful faces. These findings suggest that, by 7 months of age, emotion discrimination from faces occurs independent of conscious perception and is associated with differential activation of subcortically mediated autonomic responses as evident in the changes in pupil size. This critically extends prior work on unconscious emotion processing in infants (Jessen & Grossmann, 2014, 2015), demonstrating that subliminal stimuli not only affect the central but also the peripheral nervous system. The present data thereby provide evidence for the notion that automatic emotion processing systems are an essential and early-developing building block of human social functioning.

It is critical to emphasize that while previous studies reported differential ERP responses to subliminally presented emotional information in infants (Jessen & Grossmann, 2014, 2015), this is the first study to show that infant emotion discrimination, that is independent of conscious perception, extends beyond cortical activation patterns (ERP) and can be seen in peripheral responses (pupil dilation). This is in line with previous work in adults, reporting changes in pupil dilation in response to emotional facial expressions that were not consciously perceived (Laeng et al., 2013; Tamietto et al., 2009). Importantly, while we observed similar effects in both pupil dilation (greater dilation to happy faces) and looking time (enhanced looking to happy faces), there was no correlation between the two measures, suggesting that the observed pupil effect is not directly related to differences in looking.

While the exact neural processes involved in the observed pupil dilation effects remain to be studied, previous work suggests that the locus coeruleus plays a key role in pupillary responses. More specifically, recent neuroscience studies show that non-luminance related changes in pupil size are closely coupled to changes in phasic activity of the locus coeruleus and connected areas, both in humans (Murphy, O'Connell, O'Sullivan, Robertson, & Balsters, 2014) and non-human primates (Aston-Jones & Cohen, 2005; Joshi, Li, Kalwani, & Gold, 2016). In the current study, we investigated event-related, phasic changes in pupil size by comparing absolute pupil sizes closely time-locked to the presented stimuli. Nevertheless, in contrast to previous studies, which explicitly focused on phasic changes in pupil size (e.g., Geng, Blumenfeld, Tyson, & Minzenberg, 2015; Kamp & Donchin, 2015; Murphy, Robertson, Balsters, & O'Connell, 2011) we employed a block design and can therefore not exclude the possibility that the current effects are also related to longer-lasting, tonic changes in pupil size.

The current data provide support for our main hypothesis that infants are able to discriminate between emotional facial expressions regardless of conscious perception. However, contrary to our prediction based on prior work with adults (Laeng et al., 2013), in which pupil dilation was greater to fearful expressions when compared to happy facial expressions, infants showed greater pupil dilation to happy when compared to fearful faces. These differences between the current data from infants and prior data from adults suggest that a developmental change occurs beyond the age of 7 months that leads to greater pupil dilation to fearful faces. There is some work to suggest that enhanced subcortical responding to fearful faces shows protracted development in children (Thomas et al., 2001). Infants in the current study may show greater sympathetic arousal to facial expressions that are most familiar and most relevant in their daily social interactions (Campos et al., 2000) and it is happy expressions that are processed automatically.

The pattern of the current pupil dilation results are also in disagreement with previous studies with infants that had found greater pupil dilation in response to negative rather than positive emotional expressions (Gredeback et al., 2012; Hepach & Westermann, 2013). There are several possible reasons that may account for this discrepancy. Specifically, previous infant studies investigated children 10 months of age and older (Gredeback et al., 2012; Hepach & Westermann, 2013), while the participants in our study were only 7 months of age. The only study investigating emotion perception in a younger age group reported increases in pupil dilation in response to videos (audio-visual information) of infants showing distress but also in response to infants showing happiness (Geangu et al., 2011). Furthermore, this study used videos of a much longer duration (50 s as compared to less than 1 s in the current study), which makes it difficult to directly compare the results. Stimulus material (infant expressions versus adult expressions), stimulus duration (long versus short), and modality (audio-visual versus visual only) may account for the differences between the current data and the data in this prior study. Clearly, more work is needed to directly test these possibilities and to extend the use of the current paradigm to other age groups in order to trace likely developmental changes.

With respect to looking time differences in response to different facial emotional expressions, results from previous studies are mixed. While some infant studies report longer looking times for threatening faces (e.g., Peltola et al., 2009), other studies found longer looking times for non-threatening faces (e.g., Hunnius et al., 2011). Our findings of enhanced looking to happy faces when compared to fearful faces is in agreement with the latter study, showing avoidance of threat, characterized by longer looking to non-threatening compared to threatening faces, including fearful faces. Studies reporting the opposite pattern in infants, namely an increased looking time to threatening compared to non-threatening faces, typically presented two faces simultaneously (Peltola et al., 2009), which may trigger comparison processes different from freely viewing a faces that might explain the observed differences in looking time.

It is important to note that with respect to the looking analysis, similar effects of emotional expression on looking patterns were observed for supraliminally and subliminally presented faces. This is particularly striking for the subliminally presented faces, because looking patterns differed while infants in both emotion conditions were looking at the same neutral faces. In other words, infants showed enhanced looking at neutral faces subliminally primed by happy faces when compared to neutral faces primed by fearful faces. Going beyond previous ERP studies (Jessen & Grossmann, 2014, 2015), this provides first evidence for subliminal priming in infants and is in line with work showing that subliminally presented emotional stimuli affect the processing of subsequent neutral stimuli in adults (Lu, Zhang, Hu, & Luo, 2011). Relatedly, for both emotions, looking times to the eyes were longer in the subliminal condition, when infants saw a neutral face, compared to the supraliminal condition, when infants saw either a happy or a fearful face. Crucially, our analysis showed that in the neutral condition, in which infants also saw a neutral face, no prolonged looking occurred. Hence, the observed effect is likely related to the presentation of the subliminal stimulus rather than to the presentation of a neutral face. Infants may perceive the neutral facial expressions as more ambiguous due to the preceding emotional subliminal prime. They may thus spent more time looking at the potentially most diagnostic feature of the face, the eyes (Eisenbarth & Alpers, 2011), in an attempt to disambiguate the facial expression. The study of such subliminal priming effects clearly deserves further attention in future studies with infants.

In summary, the current data demonstrate that 7-month-old infants process facial emotions independent of conscious perception. These emotion discrimination processes were reflected in changes in infants' pupil diameter, indexing changes in autonomic nervous system activity potentially mediated by the locus coeruleus. This suggests that, from early in development, processes exist that enable humans to automatically respond to emotional expressions in others. These findings provided new insights into infants' developing sensitivity to others' facial emotional expressions and support the view that automatic emotion processing systems are a fundamental building block of human social functioning. Having automatic emotion processing and discrimination systems operate independent of conscious perception from early in ontogeny might serve important functions by activating and regulating physiological systems during social encounters between humans (Hari & Kujala, 2009; Schilbach et al., 2013). This is in line with developmental theories that emphasize the preparedness of humans in responding sensitively to others' emotional signals (Davidov, Zahn-Waxler, Roth-Hanania, & Knafo, 2013; Hoffman, 2001; Trevarthen & Aitken, 2001) and extends cognitive theories based on work with adults that stipulate the adaptive value of unconscious processes by highlighting its importance from early in development (Bargh & Morsella, 2008; Wilson, 2002). Furthermore, prior work has shown that changes in sympathetic arousal in response to others' needs measured through pupil dilation predict subsequent prosocial behavior (helping) towards the person in need in 2-year-old children and are thought to reflect an intrinsic motivation of toddlers to help (Hepach, Vaish, Grossmann, & Tomasello, in press; Hepach, Vaish, & Tomasello, 2013; Hepach et al., 2012). The current findings with much younger infants point towards the early emergence of social and motivational systems in the first year of life that may feed into and provide the basis for behavioral manifestations of social and cooperative tendencies seen in the second year of life. Taken together, the current study advances our understanding of social and emotional processing and its early ontogeny in humans by demonstrating the existence of subcortical emotion discrimination independent of conscious perception in 7-month-old infants.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2016.02.010.

References

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

Bargh, J. A., & Morsella, E. (2008). The unconscious mind. *Perspectives on Psychological Science, 3*(1), 73–79. http://dx.doi.org/10.1111/j.1745-6916.2008.00064.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. http://dx.doi.org/10.1111/j.1469-8986.2008.00654.x.

Campos, J. J., Anderson, D. I., Barbu-Roth, M. A., Hubbard, E. M., Hertenstein, M. J., & Witherington, D. (2000). Travel broadens the mind. *Infancy, 1*, 149–219.

Davidov, M., Zahn-Waxler, C., Roth-Hanania, R., & Knafo, A. (2013). Concern for others in the first year of life: Theory, evidence, and avenues for research. *Child Development Perspectives, 7*(2), 126–131.

Ebner, N. C., Riediger, M., & Lindenberger, U. (2010). FACES – A database of facial expressions in young, middle-aged, and older women and men: Development and validation. *Behavior Research Methods, 42*(1), 351–362. http://dx.doi.org/10.3758/BRM.42.1.351.

Eisenbarth, H., & Alpers, G. W. (2011). Happy mouth and sad eyes: Scanning emotional facial expressions. *Emotion, 11*(4), 860–865. http://dx.doi.org/10.1037/a0022758.

Frith, C. (2009). Role of facial expressions in social interactions. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 364* (1535), 3453–3458. http://dx.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. http://dx.doi.org/10.1371/journal.pone.0027132.

Gelskov, S. V., & Kouider, S. (2010). Psychophysical thresholds of face visibility during infancy. *Cognition, 114*(2), 285–292. http://dx.doi.org/10.1016/j.cognition.2009.09.012.

Geng, J. J., Blumenfeld, Z., Tyson, T. L., & Minzenberg, M. J. (2015). Pupil diameter reflects uncertainty in attentional selection during visual search. *Frontiers in Human Neuroscience, 9*, 435. http://dx.doi.org/10.3389/fnhum.2015.00435.

Gredeback, G., Eriksson, M., Schmitow, C., Laeng, B., & Stenberg, G. (2012). Individual differences in face processing: Infants' scanning patterns and pupil dilations are influences by the distribution of parental leave. *Infancy, 17*(1), 79–101.

Hari, R., & Kujala, M. V. (2009). Brain basis of human social interaction: From concepts to brain imaging. *Physiological Reviews, 89*(2), 453–479. http://dx.doi.org/10.1152/physrev.00041.2007.

Hepach, R., Vaish, A., Grossmann, T., & Tomasello, M. (in press). Young children want to see others get the help they need. *Child Development*.

Hepach, R., Vaish, A., & Tomasello, M. (2012). Young children are intrinsically motivated to see others helped. *Psychological Science, 23*(9), 967–972. http://dx.doi.org/10.1177/0956797612440571.

Hepach, R., Vaish, A., & Tomasello, M. (2013). A new look at children's prosocial motivation. *Infancy, 18*(1), 67–90.

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

Hoffman, M. L. (2001). *Empathy and moral development: Implications for caring and justice*. Cambridge: Cambridge University Press.

Hunnius, S., de Wit, T. C., Vrins, S., & von Hofsten, C. (2011). Facing threat: Infants' and adults' visual scanning of faces with neutral, happy, sad, angry, and fearful emotional expressions. *Cognition and Emotion, 25*(2), 193–205. http://dx.doi.org/10.1080/15298861003771189.

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

Jessen, S., & Grossmann, T. (2014). Unconscious discrimination of social cues from eye whites in infants. *Proceedings of the National Academy of Sciences of the United States of America, 111*(45), 16208–16213. http://dx.doi.org/10.1073/pnas.1411333111.

Jessen, S., & Grossmann, T. (2015). Neural signatures of conscious and unconscious emotional face processing in human infants. *Cortex, 64*, 260–270. http://dx.doi.org/10.1016/j.cortex.2014.11.007.

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), 221–234. http://dx.doi.org/10.1016/j.neuron.2015.11.028.

Kamp, S. M., & Donchin, E. (2015). ERP and pupil responses to deviance in an oddball paradigm. *Psychophysiology, 52*(4), 460–471. http://dx.doi.org/10.1111/psyp.12378.

Kouider, S., Stahlhut, C., Gelskov, S. V., Barbosa, L. S., Dutat, M., de Gardelle, V., ... Dehaene-Lambertz, G. (2013). A neural marker of perceptual consciousness in infants. *Science, 340*(6130), 376–380. http://dx.doi.org/10.1126/science.1232509.

Laeng, B., Saether, L., Holmlund, T., Wang, C. E., 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. http://dx.doi.org/10.3389/fpsyg.2013.00291.

Laeng, B., Sirois, S., & Gredeback, G. (2012). Pupillometry: A window to the preconscious? *Perspectives on Psychological Science, 7*(1), 18–27.

Lu, Y., Zhang, W. N., Hu, W., & Luo, Y. J. (2011). Understanding the subliminal affective priming effect of facial stimuli: An ERP study. *Neuroscience Letters, 502*(3), 182–185. http://dx.doi.org/10.1016/j.neulet.2011.07.040.

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. *Human Brain Mapping, 35*(8), 4140–4154. http://dx.doi.org/10.1002/hbm.22466.

Murphy, P. R., Robertson, I. H., Balsters, J. H., & O'Connell, R. G. (2011). Pupillometry and P3 index the locus coeruleus-noradrenergic arousal function in humans. *Psychophysiology, 48*(11), 1532–1543. http://dx.doi.org/10.1111/j.1469-8986.2011.01226.x.

Partala, T., & Surakka, V. (2003). Pupil size variation as an indication of affective processing. *International Journal of Human-Computer Studies, 59*, 185–198.

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

Porges, S. W. (2003). The Polyvagal theory: Phylogenetic contributions to social behavior. *Physiology & Behavior, 79*(3), 503–513.

Ramachandra, V., Depalma, N., & Lisiewski, S. (2009). The role of mirror neurons in processing vocal emotions: Evidence from psychophysiological data. *International Journal of Neuroscience, 119*(5), 681–690.

Schilbach, L., Timmermans, B., Reddy, V., Costall, A., Bente, G., Schlicht, T., & Vogeley, K. (2013). Toward a second-person neuroscience. *Behavioral and Brain Sciences, 36*(4), 393–414. http://dx.doi.org/10.1017/S0140525X12000660.

Smith, M. L. (2012). Rapid processing of emotional expressions without conscious awareness. *Cerebral Cortex, 22*, 1748–1760.

Tamietto, M., Castelli, L., Vighetti, S., Perozzo, P., Geminiani, G., Weiskrantz, L., & de Gelder, B. (2009). Unseen facial and bodily expressions trigger fast emotional reactions. *Proceedings of the National Academy of Sciences of the United States of America, 106*(42), 17661–17666. http://dx.doi.org/10.1073/pnas.0908994106.

Thomas, K. M., Drevets, W. C., Whalen, P. J., Eccard, C. H., Dahl, R. E., Ryan, N. D., & Casey, B. J. (2001). Amygdala response to facial expressions in children and adults. *Biological Psychiatry, 49*(4), 309–316.

Trevarthen, C., & Aitken, K. J. (2001). Infant intersubjectivity: Research, theory, and clinical applications. *Journal of Child Psychology and Psychiatry and Allied Disciplines, 42*(1), 3–48.

Van Bockstaele, E. J., Colago, E. E., & Valentino, R. J. (1998). Amygdaloid corticotropin-releasing factor targets locus coeruleus dendrites: Substrate for the co-ordination of emotional and cognitive limbs of the stress response. *Journal of Neuroendocrinology, 10*(10), 743–757.

Wilson, T. D. (2002). *Strangers to ourselves: Discovering the adaptive unconscious*. Cambridge, MA: Harvard University Press.