



Research

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Fearful but not happy expressions boost face detection in human infants

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Human adults show an attentional bias towards fearful faces, an adaptive behaviour that relies on amygdala function. This attentional bias emerges in infancy between 5 and 7 months, but the underlying developmental mechanism is unknown. To examine possible precursors, we investigated whether 3.5-, 6- and 12-month-old infants show facilitated *detection* of fearful faces in noise, compared to happy faces. Happy or fearful faces, mixed with noise, were presented to infants ($N = 192$), paired with pure noise. We applied multivariate pattern analyses to several measures of infant looking behaviour to derive a criterion-free, continuous measure of face detection evidence in each trial. Analyses of the resulting psychometric curves supported the hypothesis of a detection advantage for fearful faces compared to happy faces, from 3.5 months of age and across all age groups. Overall, our data show a readiness to detect fearful faces (compared to happy faces) in younger infants that developmentally precedes the previously documented attentional bias to fearful faces in older infants and adults.

1. Introduction

Humans from all cultures display distinct facial expressions signalling different emotions [1], a behaviour that engages complex facial musculature and is common to all mammals, particularly primates [2–4]. Perceiving these emotionally, socially and ecologically salient stimuli [5] engages a remarkably large number of subcortical and cortical pathways in the human brain [6]. Numerous disorders and atypical experiences disrupt facial emotion perception, including autism [7], neglect or abuse [8], institutional rearing [9], callous-unemotional traits [10], and psychiatric disorders [11]. Perception of fearful faces is of particular interest, characterized by enhanced attentional allocation [12], visual search [13], categorization [14] and contrast sensitivity [15], reflecting the upregulation of perceptual cortices by amygdala nuclei [6,16,17]. These crucial pathways, which underlie the perception of faces and their expressions, could be present from birth [17]. Tracking the developmental trajectories leading to adaptive facial emotion perception is critical to determine how disorders affect such capacity [18]. However, it is unknown whether fearful faces are better detected in infancy.

The ability to categorize certain facial emotions emerges in infants between 5 and 7 months [18–21], along with an attentional bias to fearful faces and eyes, i.e. a tendency for these stimuli to hold attention [18,22–27]. Infants as young as 5 months rapidly detect ecologically relevant stimuli such as angry faces or snakes [28–32], and fearful faces may be considered ecologically relevant [33]. We hypothesized that fearful faces could be preferentially *detected* in infancy, possibly before the onset of an attentional bias to fear depending on task demands and with visual inputs designed to parametrically probe the

sensitivity of the face (emotional) system. To this end, we designed a degraded face detection task with very low task demands.

We presented fearful or happy faces mixed with random noise [34,35] and paired them with pure noise in a face-versus-noise detection task to 192 infants at 3.5, 6 and 12 months of age. These three age groups represent ages before, during and after the documented developmental onset of an attentional bias to fearful faces between 5 and 7 months. We hypothesized that fearful faces would be more easily detected by infants than happy faces at the same level of signal at 6 and 12 months. In addition, we aimed to test whether 3.5-month-olds would also detect fearful faces preferentially, or conversely detect happy faces preferentially given their familiarity [36] and visual preference for this expression [37].

Global contrast and amplitude spectra were equated to prevent those cues from supporting face detection [38,39]. We used phasic noise, preserving these visual properties [34]. Eye visibility was included as a control variable, due to the critical role of the eyes in perceiving fearful expressions [16,40] and faces in general [41]. Eyes may be especially important for fearful face detection by infants who lack experience with this expression [36].

Face detection was measured by preferential looking and multivariate pattern analysis (MVPA). MVPA combines multiple variables (such as voxel activations) to classify trials according to stimulus category, target location, or other parameters [42]. MVPA is used with different data types including fMRI [43], EEG [44], fNIRS [45] and behavioural [46] data. One previous study used MVPA with infant fNIRS [45], and at least one used MVPA with infant EEG data [47]. To our knowledge, the current findings represent the first use of MVPA with infant *behavioural* data.

In the current study, we used MVPA to detect patterns of looking behaviour that differentiate between face and noise, and derived multivariate measures of face versus noise discrimination for each trial. By doing so, we quantitatively assessed how well the looking behaviour of infants differentiated between face and noise without requiring a human observer to guess the location of the face (as is the case for forced-choice preferential looking [48]), and without making an assumption on which particular aspect of looking behaviour would best capture the difference between face and noise. Preferential looking and multivariate face versus noise discrimination were used to fit psychometric curves and estimate face detection thresholds. Psychometric curves have been used in studies of children and adults to investigate perceptual development [49] or the effect of emotion on perception [15], and there are some precedents to using them in infant behavioural studies [50].

2. Method

(a) Participants

Sixty-four 3.5-month-olds (31 girls, mean age 116.9 ± 0.6 days, s.e.m.), 64 6-month-olds (31 girls, mean age 191.0 ± 0.8 days), and 64 12-month-olds (32 girls, mean age 375.6 ± 0.7 days) from a predominantly Caucasian environment were included in the study. All infants were born full term (38.8 ± 0.1 weeks of amenorrhoea). Thirty additional infants (sixteen 3.5-month-

olds, six 6-month-olds, eight 12-month-olds) were excluded due to fussiness (nine 3.5-month-olds, two 6-month-olds, eight 12-month-olds), technical failure (one 3.5-month-old, one 6-month-old), experimenter error (three 3.5-month-olds, three 6-month-olds), or side-bias on at least three of the six trials (three 3.5-month-olds). Side-bias in a given 10-s trial was defined as the infant looking to the same side of the screen more than 95% of the time. All caregivers provided written, informed consent before the experiment, which was approved by the local ethics committee (Institutional Review Board).

(b) Stimuli

Happy and fearful frontal view faces from the same 12 models (six males, six females) were selected from the Karolinska Directed Emotional Faces database [51]. Stimuli were grey-scaled, and external features were cropped. Luminance, contrast, spatial frequencies, and eye placement were matched in SHINE [52] and Psychomorph [53]. Faces subtended a visual angle of about 18 (vertically) by 12 degrees (horizontally).

Weighted mean phase noise preserving global contrast and frequency spectrum [34] was generated in MATLAB v. 7.9.0.529, and stimuli were gamma-corrected ($\gamma = 1.7286$). These stimuli were similar to those previously validated with children in an emotion labelling task [35]. Faces were mixed with 0, 20, 40, 50, 60 or 70% noise, i.e. they had 30, 40, 50, 60, 80 or 100% signal. Stimuli were generated so that half had more visible eyes than mouth (eye+), and half had less visible eyes than mouth (eye-) as measured by peak signal to noise ratio (PSNR). Signal in the eye region was significantly greater in eye+ than eye- stimuli (PSNR, $p < 0.001$; Structural SIMilarity [SSIM], $p = 0.031$; Wang *et al.* [54]; electronic supplementary material, table S1). Examples are presented in figure 1*a,b* and electronic supplementary material, figure S1; average stimuli are presented in electronic supplementary material, figure S2. There was no effect of emotion on signal quantity in the stimuli (PSNR, or SSIM in the face or eye region, as a main effect or in interaction with eye visibility, all $ps > 0.5$).

(c) Procedure

The infants sat on their caregiver's lap about 60 cm from the screen. The caregiver was instructed not to interact with the infant during the experiment. Stimuli were presented using Psychtoolbox [55]. Each infant saw six trials consisting of a face paired with matched visual noise (figure 1*a*). Trials lasted 10 s from the first look. Faces were happy or fearful, male or female, counterbalanced across participants. Each of the trials featured a different face model and signal level (30, 40, 50, 60, 80 or 100%, figure 1*b*). Faces were on the left (or right) for half of the trials. Models, signal levels and side were randomly ordered across trials. Faces were sampled so that, across participants, half of the faces in a given condition and signal level had more signal in the eye than mouth region (eye+) and vice versa (eye-).

(d) Data analysis

(i) Pre-processing

Infant looking was recorded by a camera and coded offline with 40 ms precision. A subsample was coded by a second observer with 0.98, 0.96 and 0.96 agreement in the 3.5-, 6- and 12-month-old groups, respectively (Pearson's r , 25% of the videos). Percentages of total looking time (PTLTs) to the left and right sides were derived relative to total time looking at the screen during each trial. For each condition, age group, and signal level, trials with PTLT further than 2 s.d. from the mean were considered outliers and excluded (4.17%, 2.60% and 4.43% of the trials for 3.5-, 6- and 12-month-olds, respectively).

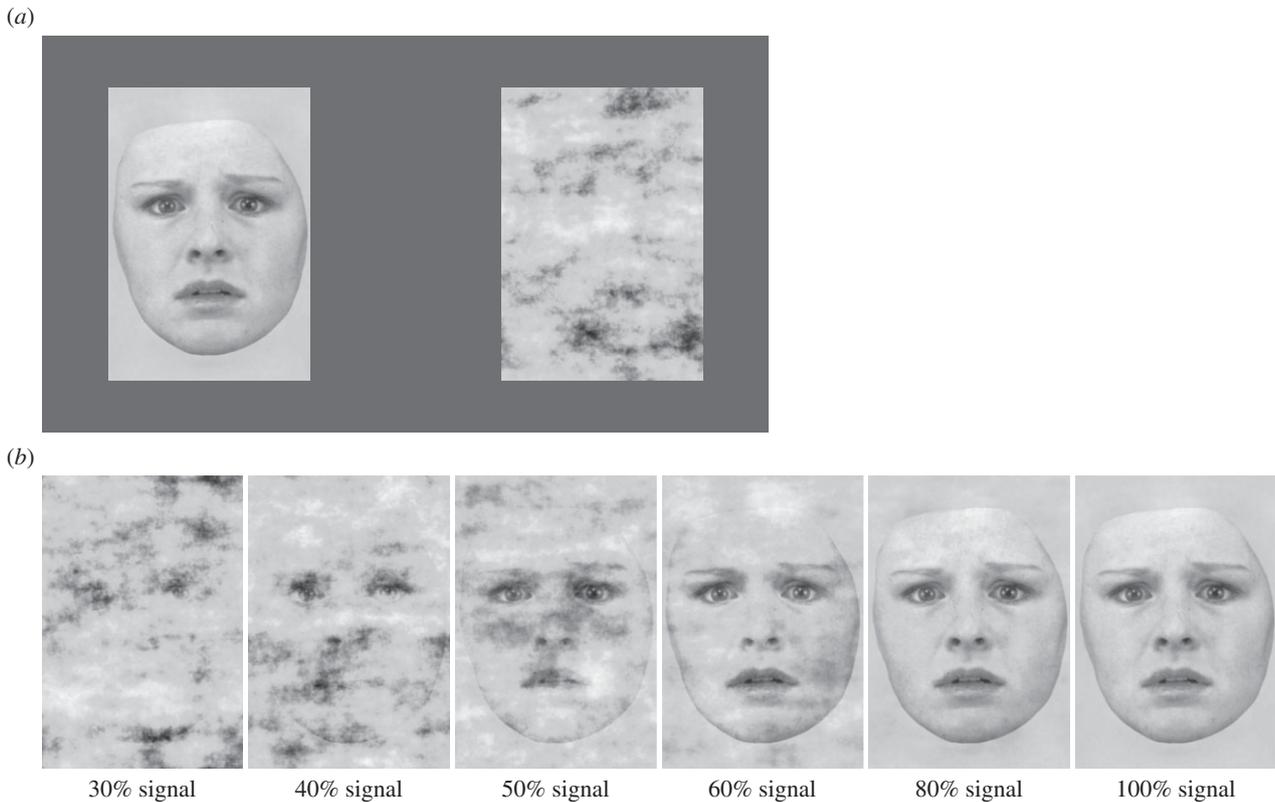


Figure 1. Stimuli. (a) Example trial featuring a fearful face at 100% signal (left) paired with matched pure noise (right). (b) Example stimulus at 30–100% signal level. Original stimulus was distributed as part of the KDEF database [51], whose copyright holder is: Karolinska Institute, Department of Clinical Neuroscience, Section of Psychology, Stockholm, Sweden.

(ii) Multivariate measure of face detection

A multivariate measure of face detection was derived by classifying trials as ‘face is on the left’ or ‘face is on the right’. The rationale for this metric is similar to the idea of ‘double psychophysics’ [48]: if one can reliably guess on which side of the screen the face was presented by looking at the infant’s behaviour, then it can be inferred that the infant is discriminating between the presence of a face or noise. We implemented this idea computationally using MVPA [42] to locate the side of presentation of the face (left or right) on each trial based on (i) PTLT to the left, (ii) number of looks to the left, (iii) number of looks to the right, (iv) duration of first look to the left, (v) duration of first look to the right, (vi) median duration of looks to the left, (vii) median duration of looks to the right, and (viii) direction of first look (left or right). Durations were log-transformed [56]. Continuous measures were z-scored within-subject. Measures were chosen *a priori* given the visual preference of infants for faces [57]. PTLT to the right is equal to 100% minus PTLT to the left, and thus did not need to be included. Trials from all participants were pooled to maximize the number of training examples, and a logistic regression algorithm (a common classifier for MVPA) was repeatedly trained on all trials except one and tested on the trial that was left-out (leave-one-out cross-validation). Forward sequential feature selection was implemented inside each cross-validation loop (see electronic supplementary material, table S2 for results on the full dataset). This procedure led to locating the face side for each trial in a way that reflects generalization. We used logistic regression because it provides log-odds, a direct, criterion-free, continuous measure of evidence for each response (‘face is on the left’ versus ‘face is on the right’)—as opposed to accuracy, a binary measure dependent on a decision criterion. Raw evidence (log-odds for the right versus left side) was pooled to derive correct evidence (log-odds for the correct versus incorrect side) as a multivariate measure of face versus noise discrimination.

(iii) Modelling of psychometric curves

Infant psychometric curves exhibited a positive asymptote well below the level of maximal response. For example, visual preferences for the face side presented an average of about 75% at the maximal level of signal (100%), even though on a given trial infants could theoretically look more than 90% of the time to the face side. This characteristic violates an assumption of usual psychometric models, where performance approaches 100% at the maximal level of signal. To obviate the need for this assumption, we used a nonlinear mixed-effects model approach with the following formula:

$$f(x, z) = Y_0 + \frac{y(z) - Y_0}{1 + \exp[-a(x - \theta(z))]}$$

where $f(x, z)$ is the fitted response (logit-transformed PTLT or correct evidence), x the signal level, a the slope, and z the experimental condition (emotion and feature visibility). This corresponds to a logistic function with lower (0% signal) and upper (100% signal) asymptotes whose values are Y_0 and $y(z)$, respectively. When x is equal to the threshold value $\theta(z)$, $f(x, z)$ is halfway between Y_0 and $y(z)$. Upper asymptote and threshold are assumed to be linearly dependent on the experimental conditions:

$$\begin{aligned} y(z) &= Y_F + \delta_H(z)dY_H \\ \theta(z) &= x_{0FE} + \delta_F(z)\delta_M(z)dx_{0FM} + \delta_H(z)\delta_E(z)dx_{0HE} \\ &\quad + \delta_H(z)\delta_M(z)dx_{0HM} \end{aligned}$$

where Y_F is the upper asymptote in the fearful face condition, dY_H the difference in upper asymptote for the happy face condition, x_{0FE} the perceptual threshold in the fearful eye+ face condition, and dx_{0FM} , dx_{0HE} , and dx_{0HM} the difference in threshold for the fearful eye-, happy eye+, and happy eye- face conditions, respectively. $\delta_H(z)$, $\delta_F(z)$, $\delta_M(z)$ and $\delta_E(z)$ are binary variables equal to 1 in the happy, fearful, eye- and eye+ conditions, respectively, and equal to 0 otherwise. Because eye and mouth

are equally visible at 100% signal, trials with 100% face signal were discarded from the fit and the model did not include a difference in asymptote between the eye+ and eye- conditions. We considered subject-dependent random effects for x_{0FE} , a , and Y_F . Their inclusion was based on Bayesian information criterion. Residuals were considered to be normally distributed.

(iv) Software

Analyses were conducted in Matlab 7.9.0529 and R v. 3.2.0. Mixed-effects model analyses [58] were run in R using nlme v. 3.1.120 [59], car 2.0.25 [60] and lme4 1.1.7 [61]. A control analysis (electronic supplementary material, figure S3) was performed with the Computer Vision System Toolbox in Matlab 8.2.0.701, using its implementation of the Viola-Jones automated face and eye detection algorithm that is pre-trained on a large number of upright frontal faces and is sensitive to facial features and their second-order relations [62]. Data are openly accessible online at <https://doi.org/10.6084/m9.figshare.3439349.v1> [63].

3. Results

(a) Univariate and multivariate measures of face detection

Visual preference for faces over juxtaposed noise has been used in earlier studies [64] as a univariate proxy for face detection because the visual preference for faces over noise in infants should be strong [57]. As expected, infants in all age groups showed a visual preference for the face side that increased with face visibility (overall PTLT to the face side: 66.18 ± 0.68 ; figure 2a).

If an infant's looking behaviour can be used to locate the side of the face (left or right), that is strong evidence that the infant detected the face [48], regardless of whether the infant showed a reliable visual preference during the entire trial as measured by PTLT. We introduced a multivariate measure of face detection evidence by using a classifier to locate the side of the face (i.e. discriminating face from noise) based on PTLT and other characteristics of looking behaviour (see Method). The side of the face was located from infant looking behaviour at the level of single trials with $80.92\% \pm 1.22$ cross-validation accuracy. Accuracy and correct multivariate detection evidence (correct log-odds) increased with face visibility as expected (figure 2b,c). Several aspects of looking behaviour (duration of first look to both sides, median duration of looks to both sides) significantly contributed to accurately locating face side besides PTLT (electronic supplementary material, table S2), confirming that the multivariate approach provides increased sensitivity compared to PTLT alone.

Linear mixed-effects models revealed no effect of infant gender on PTLT to the face side (logit-transformed, $\chi^2[1] = 0.34$, $p = 0.559$) or multivariate discrimination (correct evidence, $\chi^2[1] = 0.16$, $p = 0.687$). Data were pooled across this variable in further analyses.

(b) Face detection thresholds

We fitted nonlinear mixed-effects models to infant responses (psychometric curves) to estimate face detection thresholds. Due to sample-size based limitations in the number of parameters, the analysis was restricted to estimating the face detection threshold for the Fearful eye+ condition and differences in detection threshold between this and each of the other conditions (Fearful eye-, Happy eye+, Happy eye-), across all age groups.

Psychometric curves of the PTLT to the face side revealed a significantly lower threshold for the Fearful eye+ face condition ($44.41 \pm 1.98\%$ face signal; electronic supplementary material, table S3; figure 3a) than for the Happy eye- face condition (difference: $5.20 \pm 2.62\%$ face signal, 95% CI [0.001 0.103]), but not the other conditions (electronic supplementary material, table S3; figure 3a), across all age groups. Subject-dependent random effects were retained for x_{0FE} and Y_F , and rejected for a based on BIC.

A similar result was found when applying psychometric curve modelling to the correct multivariate face versus noise discrimination evidence; the face detection threshold for the Fearful eye+ condition ($44.07 \pm 2.14\%$ face signal; electronic supplementary material, table S4; figure 3c) was significantly lower than the detection threshold for the Happy eye- condition (increase in threshold: $7.90 \pm 2.52\%$ face signal, 95% CI [0.030 0.128]) but not the other conditions (Wald confidence intervals, $\alpha = 5\%$; electronic supplementary material, table S4; figure 3c).

Similar models were used to estimate the difference in threshold between the Fearful eye- condition and other conditions, or between the Happy eye+ condition and other conditions (electronic supplementary material, tables S5-S8). Results are summarized in figure 4. Overall, psychometric curve modelling of infant looking data revealed face detection thresholds at about 44% signal, with an increase of about 5% signal in threshold for Happy eye- condition compared to the Fearful eye+ condition, and intermediate thresholds for Happy eye+ and Fearful eye- conditions depending on whether PTLT alone (figure 4a) or correct multivariate discrimination evidence (figure 4b) was used as a measure of face versus noise detection.

To clarify whether these differences in detection thresholds reflected a main effect of facial expression, a main effect of eye visibility, or an interaction between the two, and to test for an effect of age, we conducted further analyses focused on the linear portion of the psychometric curves corresponding to trials around the fitted detection thresholds (40-50% signal). These trials correspond to levels of signal where most variations in face detection performance are expected to occur.

(c) Levels of face detection around threshold

A linear mixed-effects model analysis of the (logit-transformed) PTLT around the detection thresholds (40-50% face signal; figure 3b,c) revealed a significant main effect of age ($\chi^2[2] = 9.62$, $p = 0.008$) and an interaction of age with facial emotion and eye visibility ($\chi^2[2] = 6.62$, $p = 0.037$) driven by a significant effect of facial emotion ($\chi^2[1] = 6.33$, $p = 0.012$) at 3.5 months, a marginal interaction of facial emotion and eye visibility ($\chi^2[1] = 3.1046$, $p = 0.078$) at 3.5 months, and a marginal effect of eye visibility at 12 months ($\chi^2[1] = 3.05$, $p = 0.081$).

Correct discrimination evidence increased with age generally (main effect of age, $\chi^2[2] = 14.35$, $p < 0.001$; figure 3e). Based on correct multivariate discrimination evidence, fearful faces were detected preferentially relative to happy faces around the threshold (40-50% signal), regardless of age (linear mixed-effects model: main effect of face emotion, $\chi^2[1] = 6.03$, $p = 0.014$; no interaction with age and no other significant effects, all $ps > 0.05$; figure 3f).

Overall, the results point to a fearful face detection advantage around threshold (40-50% signal), compared to happy

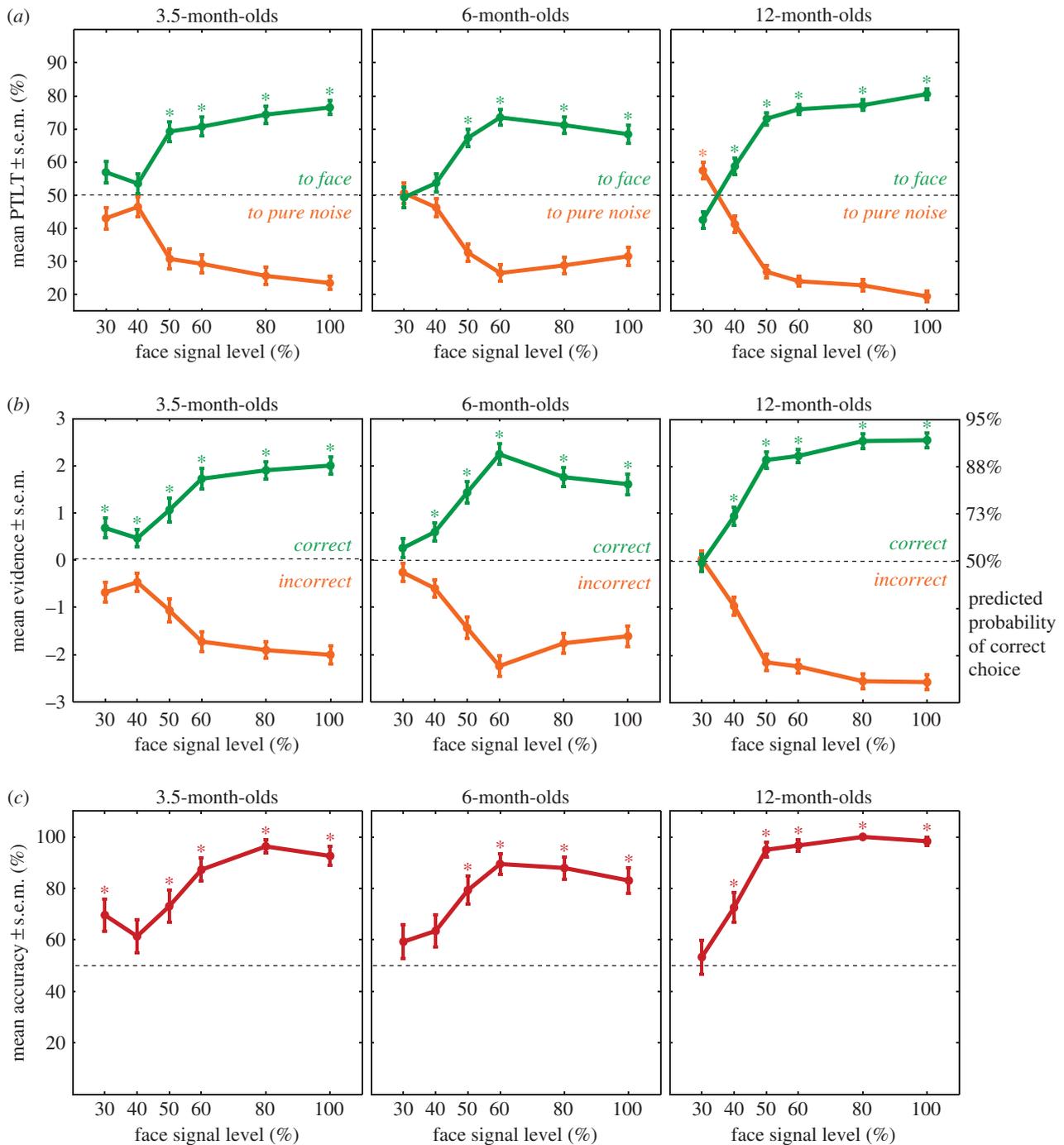


Figure 2. Face detection across signal levels and age groups. (a) Visual preference for the face side versus the noise side. (b,c) Locating the face side from looking behaviour. (b) Discrimination evidence (log-odds). (c) Face side classification accuracy. Student's *t*-tests against chance, $\alpha = 0.05$, Holm–Bonferroni corrected. (Online version in colour.)

faces. Results were mixed when considering PTLTs for the face side alone, as the effect of face emotion was restricted to 3.5-month-olds on this measure. However, correct discrimination evidence, a more comprehensive multivariate measure inclusive of PTLTs and other aspects of looking behaviour (e.g. first look) revealed a detection advantage for fearful faces compared to happy faces across all age groups (i.e. it did not significantly interact with age).

4. Discussion

We conducted a face versus noise detection task with 3.5-, 6- and 12-month-old infants, i.e. before, during and after the previously described developmental emergence of the attentional bias for fearful faces [18], to test the hypothesis that

infants detect fearful faces better than happy faces. We derived a multivariate measure of face detection inclusive of visual preference, modelled the resulting psychometric curves, and examined whether levels of detection around threshold varied according to facial emotion, eye visibility, and age. Results were generally consistent with our main hypothesis. There was evidence of a detection advantage for fearful faces compared to happy faces, across all age groups when considering a multivariate measure, and in 3.5-month-olds only when considering visual preference alone.

(a) Perceptual biases and threat sensitivity in infancy

An attentional bias to fearful faces emerges in infancy between 5–7 months for static faces [18,25] and 3.5–5 months

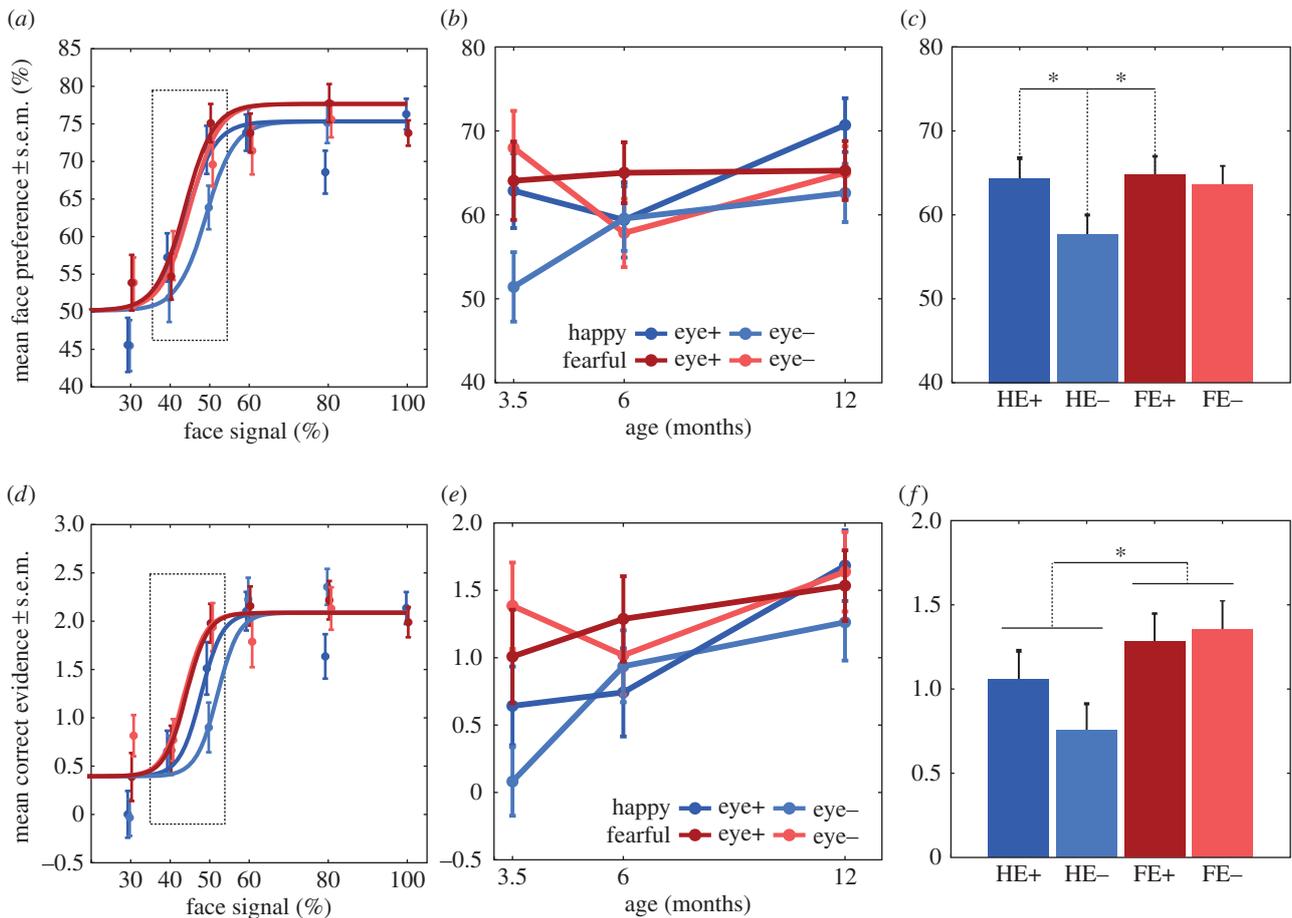


Figure 3. Influence of facial emotion, eye visibility and infant age on face detection. Face detection was measured by (a–c) visual preference for the face side and (d–f) multivariate face versus noise discrimination (correct evidence). (a,d) Psychometric curve modelling and estimated face detection thresholds (grey boxes). (b,c,e,f) Levels of face detection around threshold, (b,e) at each age and (c,f) across ages (c,f: Student's *t*-tests for independent samples or linear mixed model, as appropriate, $\alpha = 0.05$). E+, eye+, more visible eyes; E–, eye–, less visible eyes; F, fearful; H, happy. (Online version in colour.)

for dynamic faces [65] (but see [66]). This effect is robust and has been replicated over a variety of paradigms (e.g. [67]). Its underlying mechanism is unclear: the hypothesis that it was linked to direct experience with fearful faces after the onset of crawling was recently refuted [65]. Sensitivity to fearful faces in younger infants also remains debated [66]; younger infants sometimes exhibit a visual preference for happy over fearful faces [37,68], but some sensitivity to fear has been evidenced in electrophysiological responses at 3.5 months [69]. Deep limbic regions remain inaccessible to functional neuroimaging in awake infants [70], and data linking threat processing in infancy to developmental mechanisms have received multiple interpretations. Two hypotheses have been proposed to explain the development of fear learning: early sensitivity [28,71], and functional maturation at 5–7 months [25]. According to the former hypothesis [71], early sensitivity to threat-relevant stimuli (e.g. snake shapes) facilitates fear learning even with limited direct or vicarious fearful experiences with these stimuli [28]. A readiness to detect fearful faces could presumably scaffold early experiences with these expressions, leading to increased attention-holding by fearful faces later on. The present results align with this notion, and to our knowledge represent the first evidence of facilitated fear detection in infancy, and the first behavioural evidence of fear sensitivity at 3.5 months. The latter hypothesis [22–27] suggests a link between the onset of the attentional fear bias and that of functional connectivity between limbic, visual, and attentional

networks [18]; this hypothesis predicts an absence of fear sensitivity before 5–7 months [25]. The present results diverge from this prediction, but it is also possible that the enhanced detection of fear and attentional fear bias reflect different functional connections from limbic to visual and attentional networks, respectively.

(b) Features driving emotional face detection in infants

Previous studies in adults have uncovered a role for low-level cues, such as global amplitude spectra, in face detection [38,39]. The present results cannot be driven by global contrast or global amplitude spectra, as these were equated across conditions and between face and noise. Applying an established computational model of face detection (Viola–Jones [38,62]) to all stimuli revealed comparable levels of automatic face (or eye) detection by the algorithm for fearful versus happy faces (electronic supplementary material, figure S3). Thus, the fear detection advantage evidenced here cannot be attributed to a greater objective resemblance of noisy fearful faces with a generic face template, at least when it comes to representational aspects captured by the algorithm. Further research is needed to determine which other cues, such as local amplitude or contrast in the eye or mouth region [38], drive fearful face detection in infants. As the eyes are a critical part of the face template from 3.5 months onward [41,72], infant perception may be attuned to low-level characteristics of fearful eyes. The diagnostic

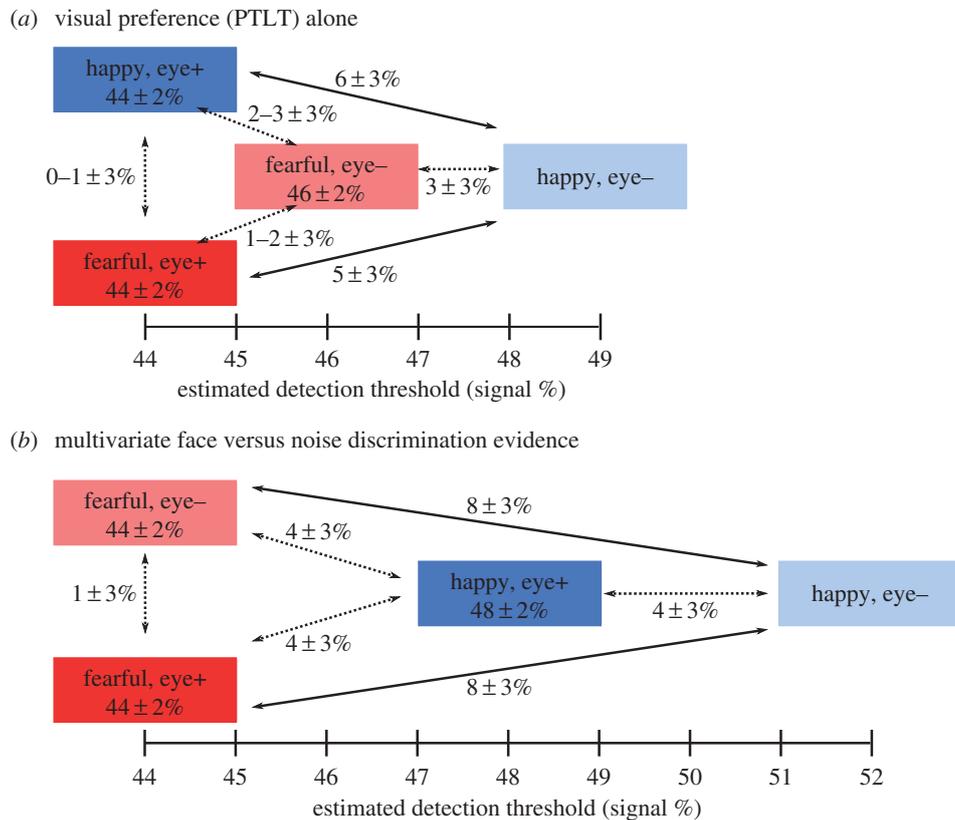


Figure 4. Summary of estimated detection thresholds, across all ages, for each condition. (a) Detection thresholds based on visual preference alone. Trials around threshold (main text) revealed a detection advantage for fearful faces at 3.5 months. (b) Detection thresholds based on multivariate face versus noise discrimination (correct evidence). Trials around threshold (main text) revealed a detection advantage for fearful faces across all ages. (Online version in colour.)

character of the eyes in fearful faces could cause infants to direct their visual attention to fearful eyes, facilitating detection of the face [14,73,74]. However, there was no clear evidence for an effect of eye visibility, either alone or in interaction with facial emotion, although it is possible that any such effects may be revealed by a stronger experimental manipulation of eye visibility or larger sample size. Parts of the data did suggest a possible role of eye visibility in happy face detection by infants. To our knowledge, this has not been reported before, but aligns with other findings [41].

(c) Revisiting 'double psychophysics' with multivariate pattern analysis

Most behavioural studies in infancy do not present a specific hypothesis regarding which variable should distinguish between conditions—the hypothesis is on the difference itself (but see [75]). Teller's 'double psychophysics' method [48] has been proposed as a solution to this problem, and to our knowledge, the current study is the first to implement it with MVPA [42,43]. Specifically, we introduced a measure of face versus noise discrimination based on the statistical relationship between behavioural patterns (e.g. looking preference) and stimulus category (face or noise). This method is not specific to looking times or to face detection and may be applied more broadly to different behavioural tasks. For example, eye-tracking provides richer descriptions of looking behaviour than looking times (e.g. gaze shifts and scanning patterns), making the results from MVPA potentially stronger and more sensitive. Stimulus–response relationships are important to the study of cognitive development, but are

often difficult to study in infants [76]. We propose that multivariate analysis of behavioural data represents a significant step in that direction, as it specifically tests for stimulus–response relationships and obviates the need for *a priori* assumptions about which behavioural variable should be the most informative.

(d) Limitations

Sample sizes in the current study were typical of infant behavioural research. Numbers of near-threshold trials were limited by the lack of prior reports of perceptual thresholds for phasic noise in infancy. Future research should determine whether the readiness to detect fearful faces (compared to happy faces) in infancy generalizes to naturalistic settings beyond the laboratory. Comparing detection of fearful versus angry versus sad faces will also clarify whether the effect applies just to threat-relevant stimuli (anger and fear) or more generally to negative novel expressions (fear, anger, and sadness) [28].

In conclusion, we used multivariate pattern analysis applied to infant looking behaviour to estimate face detection thresholds for fearful and happy faces in 3.5-, 6- and 12-month-olds. Results supported the hypothesis of a superior detection of fearful faces as early as 3.5 months, compared to happy faces. Further research is needed to determine which characteristics of fearful faces facilitated their detection, and whether this advantage represents an early instance in which emotional salience scaffolds social fear learning.

Authors' contributions. L.B., R.C. and O.P. conceived and designed the experiments. R.C. provided code to generate the stimuli. L.B. and

O.P. performed the experiments. L.B. and R.L. analysed the data. L.B., P.C.Q., R.L., R.C., K.L. and O.P. drafted the manuscript. All authors gave final approval for publication.

Competing interests. We have no competing interests.

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References

- Ekman P, Oster H. 1979 Facial expressions of emotion. *Annu. Rev. Psychol.* **30**, 527–554. (doi:10.1146/annurev.ps.30.020179.002523)
- Darwin C. 1872 *The expression of the emotions in man and animals*. London, UK: John Murray.
- Waller BM, Micheletta J. 2013 Facial expression in nonhuman animals. *Emot. Rev.* **5**, 54–59. (doi:10.1177/1754073912451503)
- Burrows AM. 2008 The facial expression musculature in primates and its evolutionary significance. *Bioessays* **30**, 212–225. (doi:10.1002/bies.20719)
- Dezecache G, Mercier H, Scott-Phillips TC. 2013 An evolutionary approach to emotional communication. *J. Pragmat.* **59**, 221–233. (doi:10.1016/j.pragma.2013.06.007)
- Pessoa L, Adolphs R. 2010 Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. *Nat. Rev. Neurosci.* **11**, 773–783. (doi:10.1038/nrn2920)
- Lozier LM, Vanmeter JW, Marsh AA. 2014 Impairments in facial affect recognition associated with autism spectrum disorders: a meta-analysis. *Dev. Psychopathol.* **26**, 933–945. (doi:10.1017/S0954579414000479)
- Pollak SD, Kistler DJ. 2002 Early experience is associated with the development of categorical representations for facial expressions of emotion. *Proc. Natl Acad. Sci. USA* **99**, 9072–9076. (doi:10.1073/pnas.142165999)
- Moulson MC, Westerlund A. 2009 The effects of early experience on face recognition: an event-related potential study of institutionalized children in Romania. *Child Dev.* **80**, 1039–1056. (doi:10.1111/j.1467-8624.2009.01315.x)
- Muñoz LC. 2009 Callous-unemotional traits are related to combined deficits in recognizing afraid faces and body poses. *J. Am. Acad. Child Adolesc. Psychiatry* **48**, 554–562. (doi:10.1097/CHI.0b013e31819c2419)
- Brennan AM, Harris AWF, Williams LM. 2014 Neural processing of facial expressions of emotion in first onset psychosis. *Psychiatry Res.* **219**, 477–485. (doi:10.1016/j.psychres.2014.06.017)
- Calder AJ, Young AW, Keane J, Dean M. 2000 Configural information in facial expression perception. *J. Exp. Psychol. Hum. Percept. Perform.* **26**, 527–551. (doi:10.1037/0096-1523.26.2.527)
- LoBue V. 2009 More than just another face in the crowd: superior detection of threatening facial expressions in children and adults. *Dev. Sci.* **12**, 305–313. (doi:10.1111/j.1467-7687.2008.00767.x)
- Schyns PG, Petro LS, Smith ML. 2007 Dynamics of visual information integration in the brain for categorizing facial expressions. *Curr. Biol.* **17**, 1580–1585. (doi:10.1016/j.cub.2007.08.048)
- Phelps EA, Ling S, Carrasco M. 2006 Emotion facilitates perception and potentiates the perceptual benefits of attention. *Psychol. Sci.* **17**, 292–299. (doi:10.1111/j.1467-9280.2006.01701.x)
- Morris JS, DeBonis M, Dolan RJ. 2002 Human amygdala responses to fearful eyes. *Neuroimage* **17**, 214–222. (doi:10.1006/nimg.2002.1220)
- Johnson MH. 2005 Subcortical face processing. *Nat. Rev. Neurosci.* **6**, 766–774. (doi:10.1038/nrn1766)
- Leppänen JM, Nelson CA. 2009 Tuning the developing brain to social signals of emotions. *Nat. Rev. Neurosci.* **10**, 37–47. (doi:10.1038/nrn2554)
- Nelson CA. 1987 The recognition of facial expressions in the first two years of life: mechanisms of development. *Child Dev.* **58**, 889–909. (doi:10.2307/1130530)
- Quinn PC, Anzures G, Izard CE, Lee K, Pascalis O, Slater AM, Tanaka JW. 2011 Looking across domains to understand infant representation of emotion. *Emot. Rev.* **3**, 197–206. (doi:10.1177/1754073910387941)
- Geangu E, Ichikaw H, Lao J, Kanazawa S, Yamaguchi MR, Caldara R, Turati C. 2016 Culture shapes 7-month-olds' perceptual strategies in discriminating facial expressions of emotion. *Curr. Biol.* **26**, R663–R664. (doi:10.1016/j.cub.2016.05.072)
- Leppänen JM, Peltola MJ, Mantymaa M, Koivuluoma M, Salminen A, Puura K. 2010 Cardiac and behavioral evidence for emotional influences on attention in 7-month-old infants. *Int. J. Behav. Dev.* **34**, 547–553. (doi:10.1177/0165025410365804)
- Peltola MJ, Leppänen JM, Vogel-Farley VK, Hietanen JK, Nelson CA. 2009 Fearful faces but not fearful eyes alone delay attention disengagement in 7-month-old infants. *Emotion* **9**, 560–565. (doi:10.1037/a0015806)
- Peltola MJ, Leppänen JM, Palokangas T, Hietanen JK. 2008 Fearful faces modulate looking duration and attention disengagement in 7-month-old infants. *Dev. Sci.* **11**, 60–68. (doi:10.1111/j.1467-7687.2007.00659.x)
- Leppänen JM, Nelson CA. 2012 Early development of fear processing. *Curr. Dir. Psychol. Sci.* **21**, 200–204. (doi:10.1177/0963721411435841)
- Jessen S, Grossmann T. 2014 Unconscious discrimination of social cues from eye whites in infants. *Proc. Natl Acad. Sci. USA* **111**, 16 208–16 213. (doi: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. (doi:10.1016/j.cortex.2014.11.007)
- LoBue V, Rakison DH. 2013 What we fear most: a developmental advantage for threat-relevant stimuli. *Dev. Rev.* **33**, 285–303. (doi:10.1016/j.dr.2013.07.005)
- Rakison DH, Derringer J. 2008 Do infants possess an evolved spider-detection mechanism? *Cognition* **107**, 381–393. (doi:10.1016/j.cognition.2007.07.022)
- LoBue V, Rakison DH, DeLoache JS. 2010 Threat perception across the life span: evidence for multiple converging pathways. *Curr. Dir. Psychol. Sci.* **19**, 375–379. (doi:10.1177/0963721410388801)
- DeLoache JS, LoBue V. 2009 The narrow fellow in the grass: human infants associate snakes and fear. *Dev. Sci.* **12**, 201–207. (doi:10.1111/j.1467-7687.2008.00753.x)
- LoBue V, DeLoache JS. 2010 Superior detection of threat-relevant stimuli in infancy. *Dev. Sci.* **13**, 221–228. (doi:10.1111/j.1467-7687.2009.00872.x)
- Vuilleumier P. 2005 How brains beware: neural mechanisms of emotional attention. *Trends Cogn. Sci.* **9**, 585–594. (doi:10.1016/j.tics.2005.10.011)
- Dakin SC, Hess RF, Ledgeway T, Achtman RL. 2002 What causes non-monotonic tuning of fMRI response to noisy images? *Curr. Biol.* **12**, 476–477. (doi:10.1016/S0960-9822(02)00960-0)
- Rodger H, Vizioli L, Ouyang X, Caldara R. 2015 Mapping the development of facial expression recognition. *Dev. Sci.* **18**, 926–939. (doi:10.1111/desc.12281)
- Malatesta CZ, Haviland JM. 1982 Learning display rules: the socialization of emotion expression in infancy. *Child Dev.* **53**, 991–1003. (doi:10.2307/1129139)
- La Barbera JD, Izard CE, Vietze P, Parisi SA. 1976 Four- and six-month-old infants' visual responses to joy, anger, and neutral expressions. *Child Dev.* **47**, 535–538. (doi:10.2307/1128816)
- Crouzet SM, Thorpe SJ. 2011 Low-level cues and ultra-fast face detection. *Front. Psychol.* **2**, 342. (doi:10.3389/fpsyg.2011.00342)
- Torralba A, Oliva A. 2003 Statistics of natural image categories. *Netw. Comput. Neural Syst.* **14**, 391–412. (doi:10.1088/0954-898X/14/3/302)
- Vanderwert RE, Westerlund A, Montoya L, McCormick SA, Miguel HO, Nelson CA. 2015 Looking to the eyes influences the processing of emotion on face-sensitive event-related potentials in 7-month-old infants. *Dev. Neurobiol.* **75**, 1154–1163. (doi:10.1002/dneu.22204)
- Gliga T, Csibra G. 2007 Seeing the face through the eyes: a developmental perspective on face expertise. *Prog. Brain Res.* **164**, 323–339. (doi:10.1016/S0079-6123(07)64018-7)

42. Haynes J-D, Rees G. 2006 Decoding mental states from brain activity in humans. *Nat. Rev. Neurosci.* **7**, 523–534. (doi:10.1038/nrn1931)
43. Norman KA, Polyn SM, Detre GJ, Haxby JV. 2006 Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends Cogn. Sci.* **10**, 424–430. (doi:10.1016/j.tics.2006.07.005)
44. Cauchoix M, Barragan-Jason G, Serre T, Barbeau EJ. 2014 The neural dynamics of face detection in the wild revealed by MVPA. *J. Neurosci.* **34**, 846–854. (doi:10.1523/JNEUROSCI.3030-13.2014)
45. Emberson LL, Zinszer BD, Raizada RD. S, Aslin RN. 2017 Decoding the infant mind: multichannel pattern analysis (MVPA) using fNIRS. *PLoS ONE* **12**, e0172500. (doi:10.1371/journal.pone.0172500)
46. Tseng PH, Cameron IGM, Pari G, Reynolds JN, Munoz DP, Itti L. 2013 High-throughput classification of clinical populations from natural viewing eye movements. *J. Neurol.* **260**, 275–284. (doi:10.1007/s00415-012-6631-2)
47. Stahl D, Pickles A, Elsabbagh M, Johnson MH. 2012 Novel machine learning methods for ERP analysis: a validation from research on infants at risk for autism. *Dev. Neuropsychol.* **37**, 274–298. (doi:10.1080/87565641.2011.650808)
48. Teller DY. 1979 The forced-choice preferential looking procedure: a psychophysical technique for use with human infants. *Infant Behav. Dev.* **2**, 135–153. (doi:10.1016/S0163-6383(79)80016-8)
49. Gori M, Del Viva M, Sandini G, Burr DC. 2008 Young children do not integrate visual and haptic form information. *Curr. Biol.* **18**, 694–698. (doi:10.1016/j.cub.2008.04.036)
50. Dobkins KR, Anderson CM, Lia B. 1999 Infant temporal contrast sensitivity functions (tCSFs) mature earlier for luminance than for chromatic stimuli: evidence for precocious magnocellular development? *Vision Res.* **39**, 3223–3239. (doi:10.1016/S0042-6989(99)00020-6)
51. Lundqvist D, Flykt A, Öhman A. 1998 *The Karolinska directed emotional faces*. Stockholm, Sweden: Karolinska Inst.
52. Willenbockel V, Sadr J, Fiset D, Horne GO, Gosselin F, Tanaka JW. 2010 Controlling low-level image properties: the SHINE toolbox. *Behav. Res. Methods* **42**, 671–684. (doi:10.3758/BRM.42.3.671)
53. Tiddeman B. 2005 Towards realism in facial image transformation: results of a wavelet MRF method. *Comput. Graph. Forum* **24**, 449–456. (doi:10.1111/j.1467-8659.2005.00870.x)
54. Wang Z, Bovik AC, Sheikh HR, Simoncelli EP. 2004 Image quality assessment: from error visibility to structural similarity. *IEEE Trans. Image Process.* **13**, 600–612. (doi:10.1109/TIP.2003.819861)
55. Brainard DH. 1997 The psychophysics toolbox. *Spat. Vis.* **10**, 433–436. (doi:10.1163/156856897X00357)
56. Csibra G, Hernik M, Mascaro O, Tatone D, Lengyel M. 2016 Statistical treatment of looking-time data. *Dev. Psychol.* **52**, 521–536. (doi:10.1037/dev0000083)
57. Fantz RL. 1961 The origin of form perception. *Sci. Am.* **204**, 66–72. (doi:10.1038/scientificamerican0561-66)
58. Laird NM, Ware JH. 1982 Random-effect models for longitudinal data. *Biometrics* **38**, 963–974. (doi:10.2307/2529876)
59. Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2012 nlme: Linear and nonlinear mixed effects models. R Package version 3.1.105.
60. Fox F, Weisberg S. 2011 *An R companion to applied regression*, 2nd edn. Thousand Oaks CA: Sage. See <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>.
61. Bates D, Maechler M, Bolker B. 2013 lme4: Linear mixed-effects models using Eigen and syntax. R Packag. version 1.0-4.
62. Viola P, Jones M. 2001 Rapid object detection using a boosted cascade of simple features. In *Conference on Computer Vision and Pattern Recognition (CVPR)*. Vol. 1, pp. 1-511–1-518. Piscataway, NJ: IEEE.
63. Bayet L, Quinn PC, Laboussière R, Caldara R, Lee K, Pascalis O. 2017 Data from: Fearful but not happy expressions boost face detection in human infants. Figshare (doi.org/10.6084/m9.figshare.3439349.v1)
64. Gelskov SV, Kouider S. 2010 Psychophysical thresholds of face visibility during infancy. *Cognition* **114**, 285–292. (doi:10.1016/j.cognition.2009.09.012)
65. Heck A, Hock A, White H, Jubran R, Bhatt RS. 2016 The development of attention to dynamic facial emotions. *J. Exp. Child Psychol.* **147**, 100–110. (doi:10.1016/j.jecp.2016.03.005)
66. Grossmann T, Jessen S. 2017 When in infancy does the ‘fear bias’ develop? *J. Exp. Child Psychol.* **153**, 149–154. (doi:10.1016/j.jecp.2016.06.018)
67. Jessen S, Grossmann T. 2016 The developmental emergence of unconscious fear processing from eyes during infancy. *J. Exp. Child Psychol.* **142**, 334–343. (doi:10.1016/j.jecp.2015.09.009)
68. Farroni T, Menon E, Rigato S, Johnson MH. 2007 The perception of facial expressions in newborns. *Eur. J. Dev. Psychol.* **4**, 2–13. (doi:10.1080/17405620601046832)
69. Hoehl S, Wiese L, Striano T. 2008 Young infants’ neural processing of objects is affected by eye gaze direction and emotional expression. *PLoS ONE* **3**, e2389. (doi:10.1371/journal.pone.0002389)
70. Minagawa-Kawai Y, Mori K, Hebden JC, Dupoux E. 2008 Optical imaging of infants’ neurocognitive development: recent advances and perspectives. *Dev. Neurobiol.* **68**, 712–728. (doi:10.1002/dneu.20618)
71. Ohman A, Mineka S. 2001 Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychol. Rev.* **108**, 483–522. (doi:10.1037/0033-295X.108.3.483)
72. Dupierrix E, de Boisferon AH, Méary D, Lee K, Quinn PC, Di Giorgio E, Simion F, Tomonaga M, Pascalis O. 2014 Preference for human eyes in human infants. *J. Exp. Child Psychol.* **123**, 138–146. (doi:10.1016/j.jecp.2013.12.010)
73. Scheller E, Büchel C, Gamer M. 2012 Diagnostic features of emotional expressions are processed preferentially. *PLoS ONE* **7**, e41792. (doi:10.1371/journal.pone.0041792)
74. Smith ML, Cottrell GW, Gosselin F, Schyns PG. 2005 Transmitting and decoding facial expressions. *Psychol. Sci.* **16**, 184–189. (doi:10.1111/j.0956-7976.2005.00801.x)
75. Cohen LB. 1972 Attention-getting and attention-holding processes of infant visual preferences. *Child Dev.* **43**, 869–879. (doi:10.2307/1127638)
76. Aslin RN, Fiser J. 2005 Methodological challenges for understanding cognitive development in infants. *Trends Cogn. Sci.* **9**, 92–98. (doi:10.1016/j.tics.2005.01.003)