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The development of the relationship between auditory and visual neural sensitivity and autonomic arousal from 6 m to 12 m

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A B S T R A C T

The differential sensitivity hypothesis argues that environmental sensitivity has the bivalent effect of predisposing individuals to both the risk-inducing and development-enhancing influences of early social environments. However, the hypothesis requires that this variation in environmental sensitivity be general across domains. In this study, we focused on neural sensitivity and autonomic arousal to test domain generality. Neural sensitivity can be assessed by correlating measures of perceptual sensitivity, as indexed by event-related potentials (ERP) in electrophysiology. The sensitivity of autonomic arousal can be tested via heart rate changes. Domain generality was tested by comparing associations in perceptual sensitivity across auditory and visual domains, and associations between sensitivity in sensory domains and heart rate. We contrasted ERP components in auditory (P3) and visual (P1, N290 and P4) detection-of-difference tasks for N = 68 infants longitudinally at 6 and 12 months of age. Domain generality should produce correlated individual differences in sensitivity across the two modalities, with higher levels of autonomic arousal associating with increased perceptual sensitivity. Having controlled for multiple comparisons, at 6 months of age, the difference in amplitude of the P3 component evoked in response to standard and deviant tones correlated with the difference in amplitude of the P1 N290 and P4 face-sensitive components evoked in response to fearful and neutral faces. However, this correlation was not found at 12 months of age. Similarly, autonomic arousal correlated with neural sensitivity at 6 months but not at 12 months. The results suggest bottom-up neural perceptual sensitivity is domain-general across auditory and visual domains and is related to autonomic arousal at 6 months but not at 12 months of age. We interpret the development of the association of these markers of ES within a neuroconstructivist framework and with respect to the concept of interactive specialisation. By 12 months of age, more experience of visual processing may have led to top-down endogenous attention mechanisms that process visual information in a way that no longer associates with automatic auditory perceptual sensitivity.

Individuals vary systematically in their sensitivity or "permeability" to experiential and contextual influences on development and health (Boyce, 2015). Environmental Sensitivity (ES) theorists posit that there is a common factor of sensitivity along which individuals differ in their ability to register and process environmental stimuli (Pluess, 2015). Those who are especially sensitive to environmental effects in the immediate term are unusually susceptible not only to the risk-inducing but also to the development-enhancing influences of early social environments (Belsky et al., 2007; Boyce and Ellis, 2005; Ellis et al., 2011).

But what exactly does it mean, mechanistically, for one individual to

be more sensitive than another to both risk-inducing and development-enhancing influences? Within the field of ES, a wide range of traits have been used to index sensitivity that can be categorised into genetic (polygenic risk scores (Nelemans et al., 2021)), physiological (e.g., cortisol reactivity (Obradović et al., 2010), autonomic nervous system activity (Weyn et al., 2022) and behavioural/psychological sensitivity factors (e.g., negative emotionality (Kim and Kochanska, 2012) (For a review see Belsky and Pluess, 2013). Much research is based on reporting cross-over interactions where the effect of a positive (maternal empathy (Pitzer et al., 2011)) or negative (maternal depression (Netsi

et al., 2015; Sacchi et al., 2018)) contextual measure on some behavioural outcome (infant sleep (Netsi et al., 2015), infant motor activity (Sacchi et al., 2018), later externalising problems (Pitzer et al., 2011) is moderated by the value of a sensitivity measure. This provides support for the bivalency of sensitivity propounded by ES theorists. However, studies that look specifically at only one index of sensitivity are not able to address whether an individual's environmental sensitivity varies across different levels of measurement or whether differences in sensitivity in all domains covary (Pluess, 2015; Stamps, 2016). Theoretically all measures of immediate environmental sensitivity should correlate for it to be a domain-general trait. In addition, to our knowledge, no previous research has looked at whether the elements of the environment to which infants are most sensitive changes across brain and perceptual development with the aim of understanding whether the responses which index ES change across development. This study considers two branches, one considering correlations between the sensitivity of different perceptual modalities within the neural domain, the other from perceptual modalities to autonomic arousal and thus between the neural and autonomic domains, all being possible proximal measures of environmental sensitivity.

The hypothesis that environmental sensitivity (ES) has the bivalent effect proposed by differential susceptibility theory requires that sensitivity be general across domains. This paper set out to examine whether individual differences in ES to immediate environmental effects, as previously operationalized in separate studies looking at neural responses to visual and auditory perception, associated within individuals. Furthermore, whether the environmental effects to which infants are most sensitive change over development in terms of how any association between the measures of sensitivity in the different domains developed from 6-months to 12-months.

Theories of brain and perceptual development are relevant to understanding how any associations between the sensitivity of visual and auditory neural domains develop. Interactive Specialization is situated within a broader context of work on "neuroconstructivism" (Elman et al., 1996; Mareschal et al., 2007; Karmiloff-Smith, 2009). It posits that the way environmental stimuli are processed changes repeatedly as a function of development as the infant progressively selects and processes different kinds of input. Furthermore, in early postnatal development, perception of stimuli is thought to be driven exogenously by features of the stimuli, but through development, endogenous top-down processes are thought to increasingly affect which features are perceived (Colombo, 2001; Haith, 1980; Johnson et al., 1991; Ruff and Rothbart, 2001). It has also been suggested that increased expertise in processing input specific to one's own environment is gained at the expense of a heightened ability to perceive all exogenous input. This occurs through processes such as synaptic pruning (Kerszberg et al., 1992), leading to "perceptual narrowing" (Scott et al., 2007) and the increasing specialisation of functional cortical areas with development (Neville et al., 1992; Durston et al., 2006). Theories on the development of face processing in particular have looked at whether the degree of domain specificity in the cortical face-processing system changes with development. One account argues that the cortical tissue activated by faces is initially activated by a broad range of visual stimuli, but over time it develops from a broadly tuned, non-specific, complex figure recognition system into one tuned to upright human faces of the type most encountered in their environment (Nelson, 1993, 2001), which decreases the ability to discriminate complex figures with which there is less experience. Thus, early in development, an initial broad multisensory perceptual tuning is thought to be the result of a relative lack of cross-modal interactions, meaning that young infants do not integrate even co-occurring, low-level features of sensory information into a single percept, as they do later in development (Boothe, 2010), and instead process input from auditory and visual modalities separately and in parallel (Lewkowicz and Ghazanfar, 2009). A domain-general level of sensitivity would suggest that individual differences in sensitivity in the visual domain will associate with individual differences in sensitivity in the auditory domain.

Event-related potentials (ERPs) evoked in response to external stimuli have been used to chart the development of pre-attentive processes of perception (Kushnerenko et al., 2002). In the auditory domain, neural markers of automatic auditory perception can be induced using oddball paradigms where frequently presented 'standard' tones are interspersed with less frequent 'deviant' tones. Recording deviance-elicited brain responses using EEG is a feasible way to assess automatic auditory discrimination and regularity detection abilities in even very young infants (Kushnerenko et al., 2013). The mismatch response (MMR) is a neurophysiological indicator of automatic, pre-attentive change detection between consecutive sounds and heightened sensitivity to deviant stimulus (Näätänen, Alho, 1995; Wetzel and Schröger, 2014). In infants younger than 12 months of age the MMR is often found as a positive deflection between 150 and 300 ms post change onset (Morr et al., 2002; Garcia-Sierra et al., 2011; Kushnerenko et al., 2013). One way to interpret individual differences in ERP amplitude is in terms of differences in involuntary attentional orienting. This is because a (positive) deflection at this latency means the MMR can merge/overlap with the P3a, which is generally understood to be the central electrophysiological marker of involuntary attentional orienting to a novel or unexpected sound (Friedman et al., 2001; Squires et al., 1975). It indexes involuntary (bottom-up, saliency driven) attention mechanisms (Escera et al., 2000; Friedman et al., 2001). This automatic orienting and attentional capture could be interpreted as less automatic inhibition of response (Kushnerenko, 2002) and therefore greater automatic neural sensitivity to environmental effects (Wass et al., 2018). Furthermore, a larger positive component to the deviant stimulus has been found to associate with markers of ES in infants such as negative reactivity to sensory stimuli (Marshall et al., 2009).

In the visual domain, the sensitivity of the sensory system is linked to the processing of emotional information (Grossmann, 2010). A common indicator of involuntary neural sensitivity in infants is increased neural responsiveness to emotional over neutral faces (James et al., 2018). From 6-months, ERP components associated with infant perceptual sensitivity to faces (occipitotemporal P1, N290 and P4 components) are reliably larger for fearful facial expressions than neutral faces as well as other negative or positive facial expressions. In 7-month-old infants the P4 was larger in response to fearful than neutral or happy faces (Leppänen et al., 2007). 7-month-old infants had a larger P4 for fearful than angry faces (Kobiella et al., 2007). 7-month-old infants rated higher in perceptual sensitivity had larger N290 responses to fearful than to happy faces (Jessen and Grossmann, 2015). The largest differences have been found over occipitotemporal regions implicated in face perception but not frontocentral regions implicated in attention (Safar and Moulson, 2020). This has been interpreted as increased early perceptual sensitivity in detecting low-level facial signs of threat such as wide-open eyes and increased size of the white sclera around the dark pupil in fearful faces (Johnson, 2005; Whalen et al., 2004) presaging the attentional bias for fearful faces (James et al., 2018).

In the autonomic domain, one autonomic correlate of sensitivity in infants, is higher heart rate (HR), which has been found to associate with hypervigilance (Mammen et al., 2017). Associations between autonomic activity and sensory perception are largely limited to behavioural markers such that increased autonomic arousal associates with decreased voluntary attention control and increased responsivity to salient targets (Alexander et al., 2007; Arnsten, 2009; Liston et al., 2009). Only recently have researchers looked at how neural sensitivity, measured in terms of involuntary auditory attention using an auditory oddball task, varies with levels of autonomic arousal (Wass et al., 2019). They found that 5–7-year-old children with higher autonomic arousal showed larger P150/P3a amplitudes in response to small acoustic contrasts (500–750 Hz). This supported the notion that higher autonomic arousal associated with less inhibition of response to exogenous stimuli, which meant that even small acoustic contrasts could potentially elicit a P3a-like automatic orienting response.

The current study collected ERP data from infants presented with an auditory-oddball paradigm and a visual emotional faces paradigm. We examined whether individual differences in bottom-up, neural sensitivity, indexed by the difference in the amplitude of components evoked in response to auditory and visual stimuli were correlated over temporal and occipital regions respectively implying domain general sensitivity, or uncorrelated, implying that neural sensitivity is domain specific. We also examined how this domain specificity or generality changed between 6 m and 12 m. In addition, we examined the relationship between neural sensitivity and autonomic arousal. Based on previous findings, we predicted that to support the theory that ES is domain general, increased autonomic arousal should associate with heightened neural sensitivity to differences in auditory stimuli as well as differences in visual stimuli.

1. Method

1.1. Participants

Infant-parent dyads attended the BabyLab at the University of East London on two occasions – first when the infants were 6 m old and a second visit when the infant was 12 m old. The participating parent-infant dyads were recruited from local children's centres, baby sensory classes and new-parent support groups. Parents gave informed consent prior to the commencement of data collection.

1.1.1. Participant exclusions

At phase-one, 82 typically developing infants, (male 42 female 40), with a mean *(SD)* age of 27.5 *(2.4)* weeks on the day of testing, attended.

EEG – 6 m: Data from a number of participants at phase one were unavailable due either to insufficiently good quality recording from one of the measures (designated so after visual inspection of the raw data and referral to video and session notes on the affective state of the infant during the recording) and were dropped before being processed (N = 6), or fewer than 70% of the maximum number of auditory oddball trials in each condition trials on which to base the analysis (Monroy et al., 2021) (N = 8) or fewer than 50% of the maximum number of emotional faces trials (N = 16) (Leppänen et al., 2007). In total EEG data were available for N = 68 and N = 60 participants for the auditory oddball and emotional faces paradigms, respectively.

ECG – 6 m: Insufficiently good ECG data (designated so after visual inspection of the raw data when the analysis software had identified almost the entire recording as noisy based on the default noise detection level of medium) led to a loss of data from N = 8 participants.

ECG data were available for N = 74 participants; both ECG and EEG data were available from N = 60 and N = 55 for the auditory oddball/emotional faces tasks respectively. The average age *(SD)* of participants who contributed both usable ECG and EEG faces data was 27.08 *(2.23)* weeks on the day of testing.

At phase-two, 68 of the initial cohort of 82 babies returned (male 36 female 32) with a mean *(SD)* age of 53.03 *(3.04)* weeks on the day of testing. Insufficiently good quality EEG data led to the loss of data from N = 12 participants (see above). Insufficiently good ECG data (see above) led to a loss of data from N = 5 participants. After pre-processing, participants were excluded due to not reaching the inclusion threshold for minimum numbers of trials (fewer than 70% of the maximum number of trials in each condition for auditory oddball and fewer than 50% of the maximum number of trials in each condition for emotional faces) for the EEG auditory oddball data N = 5 and for the faces data: N = 9. In total, EEG auditory-oddball data were available for N = 51 participants and EEG faces data were available for N = 47 participants; ECG data were available for N = 63 participants; both ECG and EEG data were available from N = 46 for the emotional faces data and N = 49 for the auditory oddball data. The average *(SD)* of participants who contributed both usable ECG and EEG data on the second visit was 53.8 *(2.99)* weeks on the day of testing.

1.2. Equipment

EEG was recorded using a high-density 128-channel HydroCel Geodesic Sensor Net (HGSN) produced by EGI (EGI, Eugene, OR). The EEG signal was referenced to the vertex, recorded at a 500 Hz sampling rate with band-pass filters set from 0.1 to 100 Hz using an Infinite Impulse Response filter. Prior to recording, the impedance of each electrode was manually checked to ensure that they were below 100 kΩm. ECG was recorded using a BioPac (Santa Barbara, CA) system recording at 1000 Hz. ECG was recorded using three disposable Ag–Cl electrodes, placed in a modified lead II position. Stimuli were presented using Matlab. A camera placed just above the stimuli-presentation screen video-recorded the behaviour of the infants for coding of looking behaviour during the visual paradigm.

1.3. Procedure

Infants were seated on parents' laps and presented with four, approx. 60-second blocks each of a visual and an auditory paradigm presented in an interspersed manner. In addition, to attract attention and calm infants, and thereafter to maintain attention, a 60-second excerpt showing nursery rhymes sung by the children's TV entertainer Mr Tumble was shown prior to each block of auditory stimuli - making 12 blocks in total. If participants were engaged with stimuli and calm, testers would proceed straight to the next block without pausing. In total, data-collection, including preparation, recording, breaks and EEG cap removal, lasted approximately 40 min per participant.

1.3.1. Auditory oddball paradigm

This consisted of four blocks of 100 trials (400 trials in total). Each block consisted of: 70 'standard' 500 Hz tones; 15 'deviant' 750 Hz tones; 15 'noise' (broadband white-noise) segments. The intensity of the tone and white-noise sounds was 70 dB sound-pressure level (SPL). The harmonic tones of 500 and 750 Hz fundamental frequency were constructed from the three lowest partials, with the second and third partials having a lower intensity than the first one by 3 and 6 dB, respectively. The harmonic tones were used instead of sinusoids for two reasons. Firstly, because it has been shown previously that complex tones result in larger N250 amplitudes in children then sinusoids (Čeponiené et al., 2001). Secondly, because we aimed to use the same paradigm that was used in a number of longitudinal and cross-sectional studies in infants and children in order to increase our understanding of the previously observed effects (Kushnerenko et al., 2007).

The duration of all sounds was 100 ms, including 5-ms rise and 5-ms fall times. The interstimulus (offset-to-onset) interval was 700 ms. The order in which the trials were presented was pseudo-randomised in order to ensure that two deviant and noise trials were always separated by at least two standard trials.

1.3.2. Emotional face paradigm

This paradigm consisted of the neutral and fearful expressions of 12 young (under 30-years) women's faces taken from the Nim Stim faces database (Tottenham et al., 2009). The faces were pseudo-randomised so that the same face did not appear more than twice consecutively. Both facial expressions –neutral and fearful - appeared 23 times (+/- 2) each per block. There were four blocks, making 92 trials of each facial expression in total. The reason that 12 different faces were chosen for this study was to provide a variety of ethnicities that would reflect the demographic spread of participating families. A fixation appeared on the screen for 1000 ms followed by a face for 500 ms (see Fig. 1. for example fixations and faces). This meant that the ISI between faces was 1000 ms. Evidence suggests that the optimal ISI for infant engagement and sustained attention during stimulus presentation is 600– 1000 ms, which increases the presentation complexity and provides sufficient time for information processing (Xie and Richards, 2016).
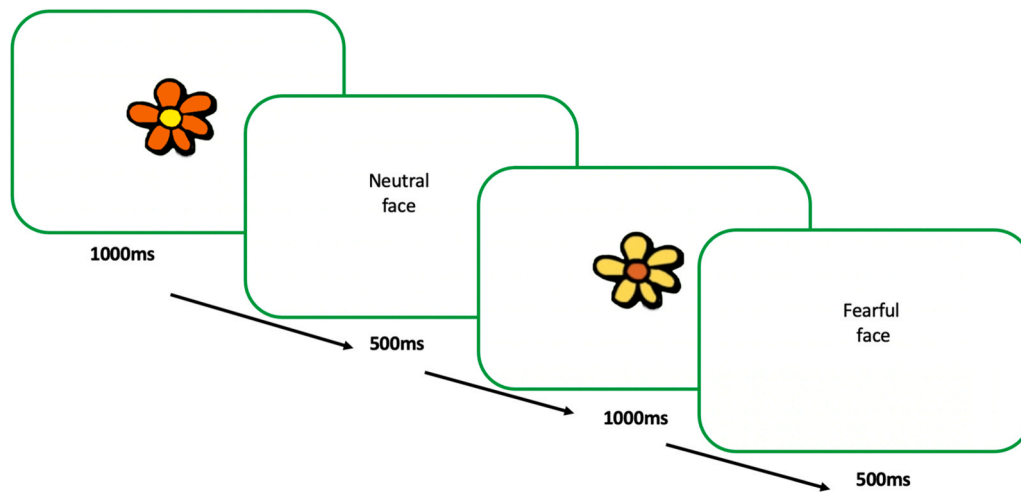
Fig. 1. presentation sequence of stimuli for emotional face processing paradigm.

1.4. Data analysis

EEG data was processed using NetStation software (version 5.4.2). The vertex-referenced EEG was algebraically recomputed to an average reference. The signal was low-pass filtered off-line at 30 Hz using a Finite Impulse Response filter and segmented into epochs starting 100 ms before and ending 800 ms after the stimulus onset. Artifact detection settings identified bad channels as those in which the amplitude exceeded 200 μV using a moving average of 80 ms. With infant nets there are no horizontal or lower eye channels. Blink detection is performed on a moving average of 80 ms from the upper eye-channel minus its inverse. The threshold for exclusion was 140uV. Channels were marked bad for the entire recording if bad for greater than 30% of segments. Trials were marked bad if they contained more than 30 bad channels (see supplementary materials 2. for additional artifact detection specifications). Activity in bad channels was replaced with the average activity of surrounding good channels using spherical spline interpolation; For higher channel counts such as 128 used here, this approximation increases in validity compared to systems using fewer channels. The average number of channels interpolated was 18.97 (15.2%) at 6 m and 11.78 (9.5%) at 12 m.

1.4.1. EEG - Auditory oddball task

Exclusions. At 6 m, the mean (range) [SD] number of trials included was 224 (210−270) [19] for standard; 47 (42−60) [4] for deviant; 48 (42−60) [4] for noise[2]; At 12 m the mean (range) (SD) number of trials included was 254 (196−280) [19] for standard; 55 (42−60) [4] for deviant; 55 (41−60) [4] for noise. This number of accepted trials has proven to be sufficient for this type of paradigm (Kushnerenko et al., 2013a; Guiraud et al., 2011; DehaeneLambertz and Dehaene, 1994; Friederici et al., 2007; Kushnerenko et al., 2013b, 2008).

Extracting average amplitude and latency. The valid ERPs obtained for each stimulus type were first averaged to create a per-participant mean waveform. The average of fronto-central channels was used (24, 20, 13, 19, 12, 11, 6, 5, 4, 124, 118, 112 (see Fig. 2. c)) as the largest MMR/P3 was expected to occur over this area (Gumenyuk et al., 2005, 2004) and because it corresponded to those used to analyse data collected using the same paradigm previously (Kushnerenko et al., 2007,

2002b; Wass et al., 2019). Epochs were baseline-corrected to the average amplitude in the 100 ms pre-stimulus period. The grand average (GA) waveform showed a clear difference between the amplitude of the P3 component in response to standard and deviant tones (see Fig. 2. a and b). Therefore, the mean amplitude of the ERP to standard tones between 200 and 400 ms post stimulus onset was subtracted from the mean amplitude of the ERP to deviant tones in the same window to create a difference score between standard and deviant tones. Analysing the difference wave within this time-window was also in line with longitudinal and cross-sectional research using the same paradigm (Kushnerenko et al., 2007, 2002; Wass et al., 2019). As the ERPs represent the overlapping activity of several components which can commence at the same time or follow each other very quickly in infants both 'positive mismatch' and 'negative mismatch' components can be observed at about the same latencies. Therefore, the positive or negative orientation of the difference wave can reflect different processes in individual infants. Average amplitude was chosen as the most objective way to compare values between the standard and deviant conditions (Luck, 2014). This is because the latency of the peak is variable and sometimes it is not possible to identify the peak at all in young infants.

1.4.2. EEG – Emotional faces task

Exclusions. The video-recording of the infant during the emotional faces blocks was coded in one-second bins whether they were looking (1) or not (0). Using a Matlab script, trials were excluded in which the infant was not looking at the screen. At 6 m, the mean (range) [SD] number of trials included was 67 (46−91) [10] for neutral faces; 68 (48−91) [9] for fearful faces. For the 12 m data, Matlab events recorded when the infant was attending to the screen during the emotional faces paradigm. Trials were excluded in which the infant was not attending to the screen. At 12 m the mean (range) [SD] number of trials included was 47 (39−59) [5] for neutral faces; 46 (40−58) [5] for fearful faces.

Extracting average amplitude and latency. The Grand Average (GA) waveform showed clear P1, N290 and P4 components in response to both face conditions (see Fig. 3. a and b). Therefore, the mean amplitude of the response to neutral faces in windows corresponding to the components P1 and P4 (between 50 and 150 ms and 350 and 450 ms post stimulus onset) was subtracted from the mean amplitude of the response to fearful faces in the same windows. As the N290 is a negative-going component the mean amplitude of the response to fearful faces was subtracted from the mean amplitude response to neutral faces in the window 250–350 ms post stimulus onset to create a difference score reflecting the absolute size of the difference in amplitude response evoked by the two conditions for this negative component. The average of occipital channels was used (64, 58, 51, 52, 59, 65, 69, 53, 60, 66, 70,

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[2] Running the analysis using an equal number of pseudo-randomly selected standard to deviant trials produced a waveform which did not differ from that in which all standard trials were used. All standard trials were used in the analyses here in order to minimise any decrease in the signal-to-noise ratio (SNR) of the difference wave as a result of fewer trials in the standard condition.
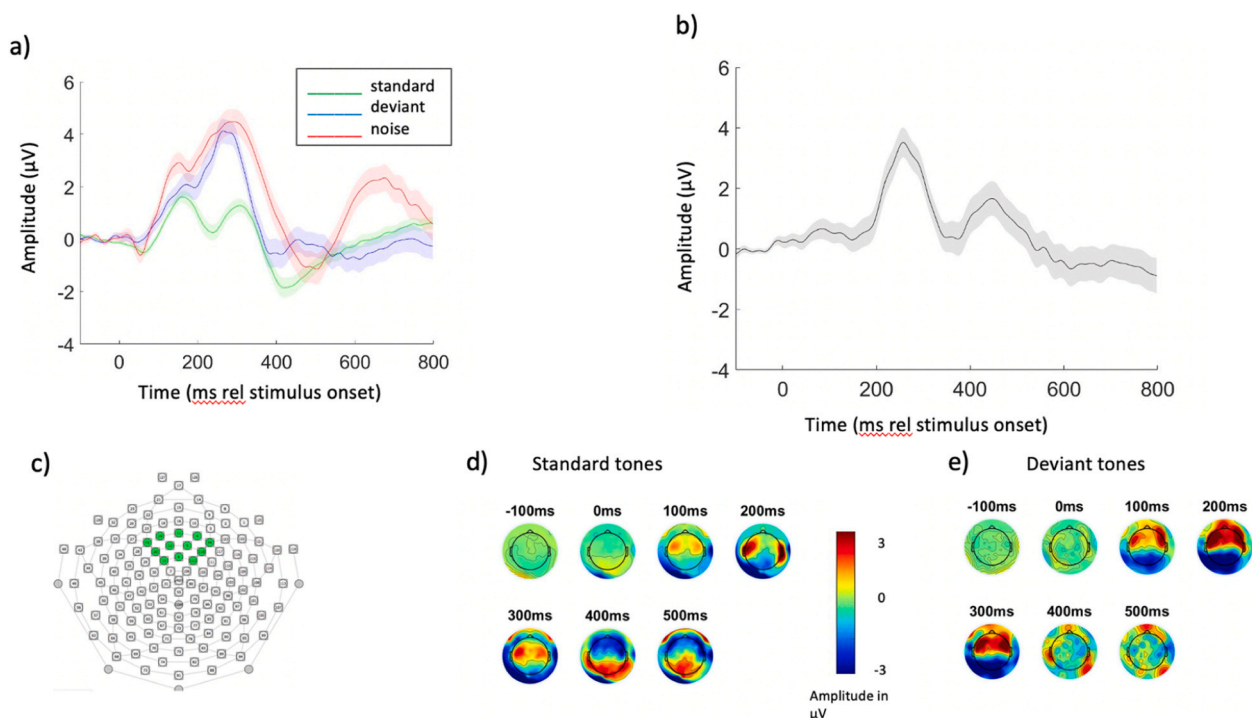
Fig. 2. a) Grand average ERPs at 6 m to auditory oddball task. Shaded areas represent the error bars, calculated as the Standard Error of the Mean b) Deviant-Standard difference wave (grand average). Shaded areas represent the error bars, calculated as the Standard Error of the Mean. c) Electrode locations used to calculate all ERPs. The locations used are marked in green. d) and e) Topoplots showing response to standard d) and deviant e) tones at 100 ms intervals starting at 100 ms pre-stimulus onset and ending 500 ms post stimulus onset. Each topoplot shows an average of activity + /- 50 ms around the given value (i.e. −100 ms shows the average from −150 ms to −50 ms).

Fig. 3. a) Grand average ERPs at 12 m to auditory oddball task b) Deviant - Standard difference wave (grand average). Shaded areas represent the error bars, calculated as the Standard Error of the Mean c) and d) Topoplots showing response to standard c) and deviant d) tones at 100 ms intervals starting at 100 ms pre-stimulus onset and ending 500 ms post stimulus onset. Each topoplot shows an average of activity + /− 50 ms around the given value (i.e. −100 ms shows the average from −150 ms to −50 ms).
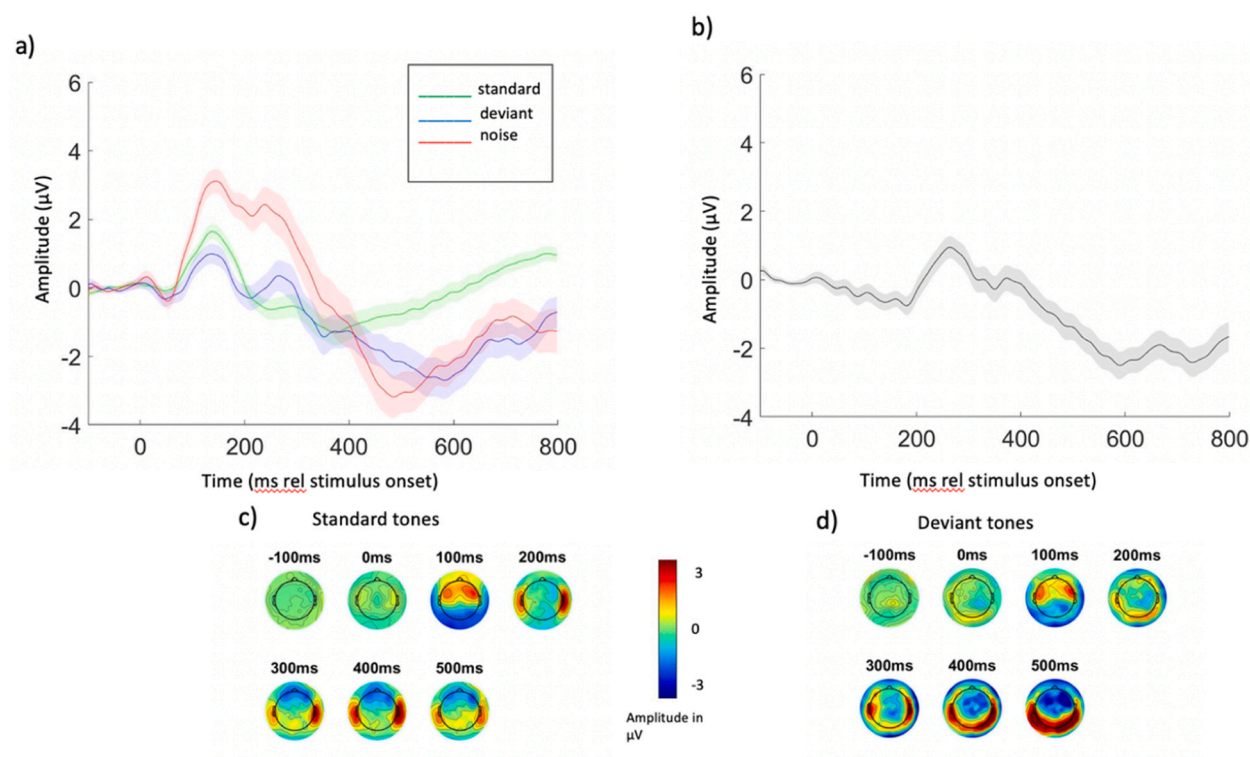
61 67, 71, 62, 72, 75, 76, 77, 78, 83, 84, 85, 86, 89, 90, 91, 92, 95, 96, 97, 98 (see Fig. 4. c)) as the largest infant facial perception components (P1, N290 and P4) were expected to occur over this area for a 128-electrode EEG cap (Haan et al., 2002; Halit et al., 2003; Vogel et al., 2012; Leppänen et al., 2007).

1.4.3. ECG

Raw ECG data were analysed using Kubios software (Tarvainen et al., 2014). The R-wave time instants are automatically detected by applying the built-in QRS detection algorithm based on the Pan–Tompkins algorithm (Pan and Tompkins, 1985). The software automatically identified noise segments (using default setting of medium) based on the raw ECG data and from the interbeat interval data (RR or pulse-to-pulse intervals). Automatic artifact detection and rejection criteria were used to identify artifactual beats from the time series data consisting of differences between successive RR intervals and corrected in Kubios. The method has been validated (Lipponen and Tarvainen, 2019). Information on the algorithms used to process the raw ECG data in Kubios is included in supplementary materials. Heart rate was averaged across the duration of the recording while infants were presented with stimuli in order to replicate analyses using the same paradigm with 5–7-yr-old children (Wass et al., 2019).

1.5. Statistical Analysis

After correcting for multiple comparisons using the Benjamini-Hochberg correction to control the false discovery rate, Bayesian statistics were used throughout. Bayesian statistics allow accepting and rejecting the null hypothesis to be put on an equal footing by providing a direct measure of the strength of evidence not only for but also against the study hypothesis, unlike frequentist statistical approaches, which do not determine whether non-significant results support a null hypothesis over a theory, or whether the data are just insensitive (Andraszewicz et al., 2015). Analyses were carried out using JASP software (Love et al., 2019). Bayesian Factor (BF) 10 values greater than 1 signal more confidence in rejecting the null hypothesis and values less than 1 signal more evidence in favour of the null. (See supplementary materials 3 for standardized interpretation of BF values).

2. Results

In Analysis 1 we examine the relationship between auditory and visual neural sensitivity at 6 m and 12 m. In Analysis 2 we examine the relationship between autonomic states and neural sensitivity at 6 m and 12 m.

2.1. Preliminary analyses – descriptive

2.1.1. Auditory task

Fig. 2. shows the grand average ERPs at 6 months in response to standard and deviant tones and white noise (Fig. 2a); the deviant-standard difference waveform (Fig. 2b); and the electrode locations used to calculate all auditory ERPs (Fig. 2c). ERPs to standard tones consist of the P150 followed by N250, and then the P300. ERPs to deviant tones and white noise represent a typical waveform consisting of a large and prolonged positive peak (merged P150 and early phase of P3a) (Kushnerenko et al., 2002). This resulted in the largest difference in amplitude of response to the frequently-presented standard tones and the less-frequent deviant tones occurring at around 300 ms post stimulus onset. Topoplots show the development of the voltage distribution in seven 100 ms bins from 100 ms before stimulus onset to 500 ms after stimulus onset showing an average of activity 50 ms around the peak (Figs. 2d and 2e).

Fig. 3. shows the same information from the 12 m visit: grand average ERPs following the standard, deviant and noise tones at 12 m (Fig. 3a)); and the deviant-standard difference waveform (Fig. 3b)). ERPs to standard tones consist of the merged P150 and early phase of the P3 (or a P3 with a shorter latency), whereas ERPs to deviant tones represent a less merged double peak for the P150 and P3 in the same time window. This resulted in a deviant – standard difference wave peaking at a lower amplitude than at 6 m at around 300 ms post stimulus onset.
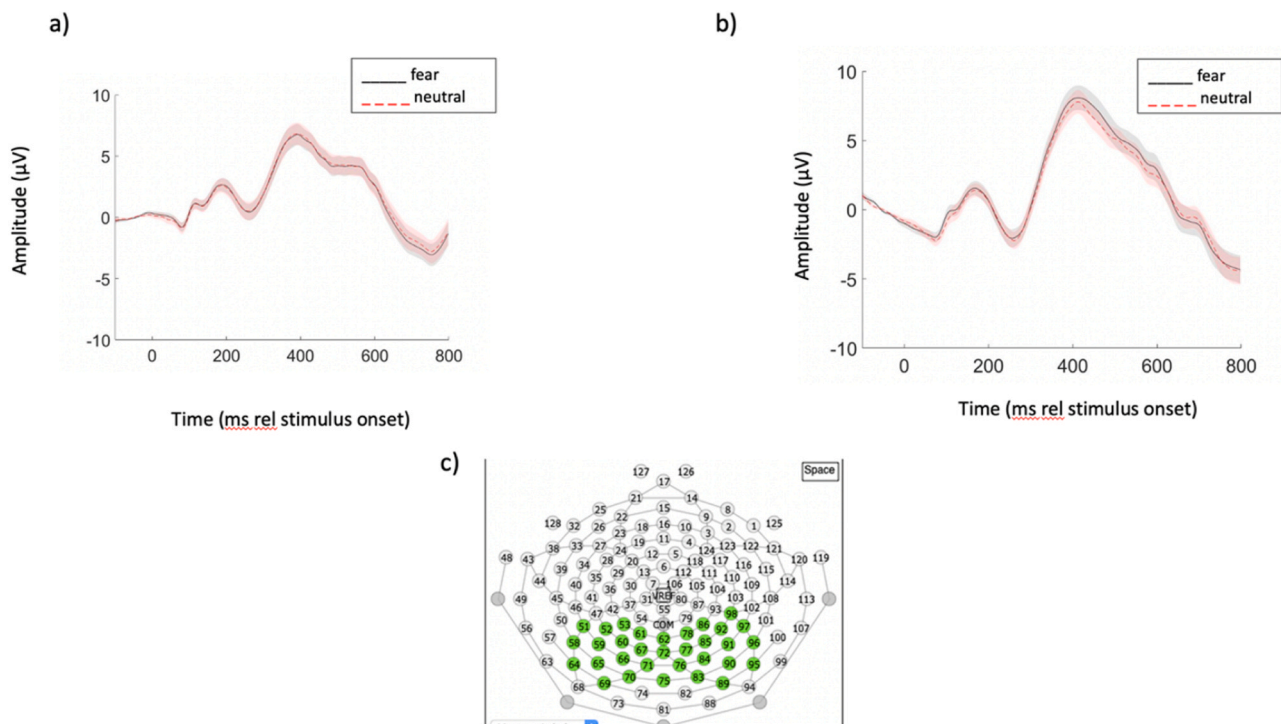

Fig. 4. a) grand average ERPS to emotional faces at 6 m. and b) 12 m. Shaded areas represent the error bars, calculated as the Standard Error of the Mean c) Electrode locations used to calculate all ERPs. The locations used are marked in green.

2.1.2. Visual task

Fig. 4. Shows the grand average ERPs in response to fearful faces and neutral faces at 6 m and 12 m. The grand average waveforms clearly show P1, N290 and P4 components in response to faces at both ages. Topoplots show the development of the voltage distribution in seven 100 ms bins from 100 ms before stimulus onset to 500 ms after stimulus onset showing an average of activity + /- 50 ms around the given value at both 6 m and 12 m.Fig. 5.

2.2. Analysis 1 – the development of associations between automatic neural sensitivity to auditory and visual stimuli

In Analysis 1 we examine how the relationship between neural sensitivity to auditory and visual stimuli develops between 6 m and 12 m of age.

2.2.1. 6-month data

First, we examined the associations between our auditory (the difference in amplitude of the P3 to standard and deviant tones) and visual (the difference in amplitude of the P1, N290 and P4 to neutral and fearful faces) neural sensitivity measures at 6 m. Scatterplots illustrate the strength and direction of the correlation between each set of two variables (Fig. 6. a, c, e; The BFs above 1 indicate correlations for which the evidence from the current study is more likely under the hypothesis that there is a relationship between those variables in the population than not. That there is a positive relationship between the P3 auditory difference component and the P1 visual difference component in the population is nine times more likely from our evidence than not. That there is a negative relationship between the P3 auditory difference and the N290 visual difference component is 12 times more likely than not. That there is a positive relationship between the P3 auditory difference and the P4 visual difference component is five times more likely than not. Plots showing the prior and posterior distributions of the true population correlation show how evidence from the current study has updated the prior distribution (Fig. 6. b, d, f).

Table 1. shows the results of Bayesian Pearson correlations and Bayes Factor (BF) analyses. The Bayes Factor (BF10) for the relationship between the difference in the auditory P3 between standard and deviant tones and the visual P1 between neutral and fearful faces at 6 m is 9. The BF for the negative relationship between the difference in the auditory P3 between standard and deviant tones and the visual N290 between neutral and fearful faces at 6 m is 12. The BF for the relationship between the difference in the auditory P3 between standard and deviant tones and the visual P4 between neutral and fearful faces at 6 m is 5. All results indicate there is moderate-strong evidence for rejecting the null hypothesis at 6 m.

2.2.2. 12-month data

Next, we conducted identical analyses on the 12-month data. Scatterplots illustrate the lack of a correlation between the two variables (Fig. 7. a, c, e); The BF01 above 1 indicates correlations for which the evidence from the current study is more likely under the null hypothesis that there is no relationship between those variables in the population. Plots showing the prior and posterior distributions of the true population correlation show how evidence from the current study has updated the prior distribution (Fig. 7. b, d, f).

Table 2. shows the results of the Bayesian Pearson correlations and Bayes Factor (BF) analyses for the 12-month data. The BF10 (the likelihood of the data under the alternative compared to the null) for the relationship between the difference in the P3 component for standard and deviant tones and the difference in the P1 component for neutral and fearful faces at 12 m is 0.2. The BF10 for the relationship between the difference in the P3 component for standard and deviant tones and the difference in the N290 component for neutral and fearful faces is 0.2. The BF10 for the relationship between the difference in the P3 component for standard and deviant tones and the difference in the P4 component for neutral and fearful faces is 0.2. This can be interpreted as our evidence being "moderately" more likely under the null hypothesis that these measures of neural sensitivity are not correlated in the population at 12 m.

Fig. 5. a and b) Topoplots showing 6 m response to neutral a) and fearful b) faces at 100 ms intervals starting at 100 ms before stimulus onset and ending 500 ms post stimulus onset. c and d) Topoplots s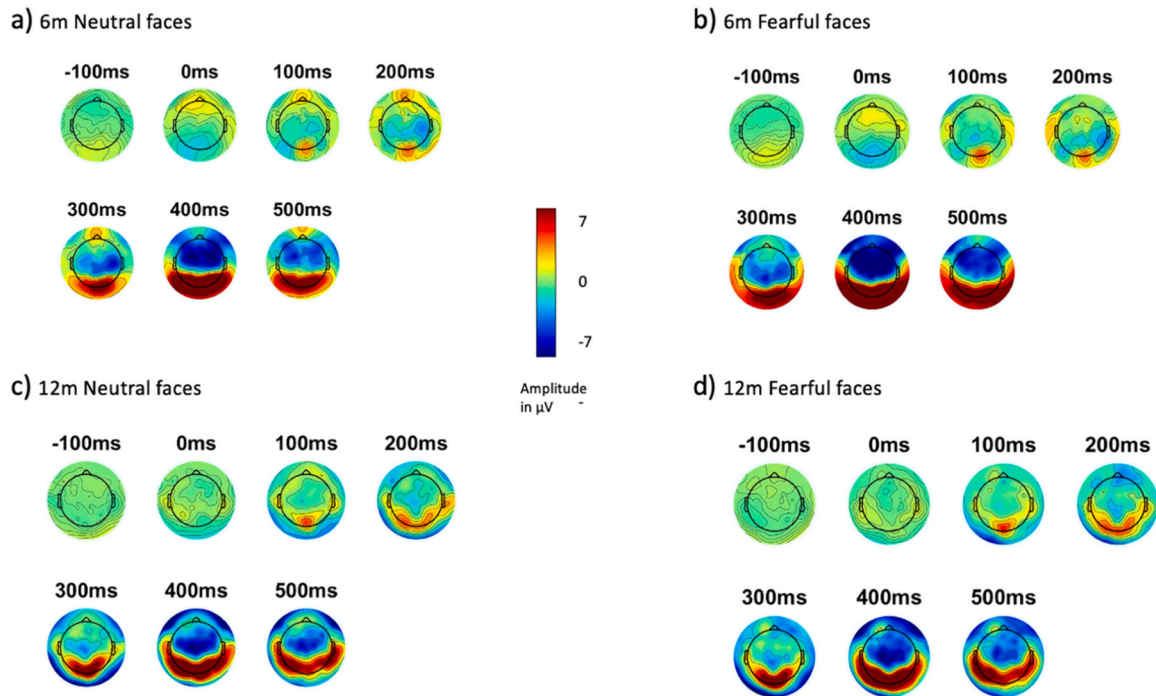howing 12 m response to neutral c) and fearful d) faces at 100 ms intervals starting at 100 ms before stimulus onset and ending 500 ms post stimulus onset. Each topoplot shows an average of activity + /− 50 ms around the given value (i.e. −100 ms shows the average from −150 ms to −50 ms). Topoplots were produced on data that was subject to channel interpolation outside of the main preprocessing.
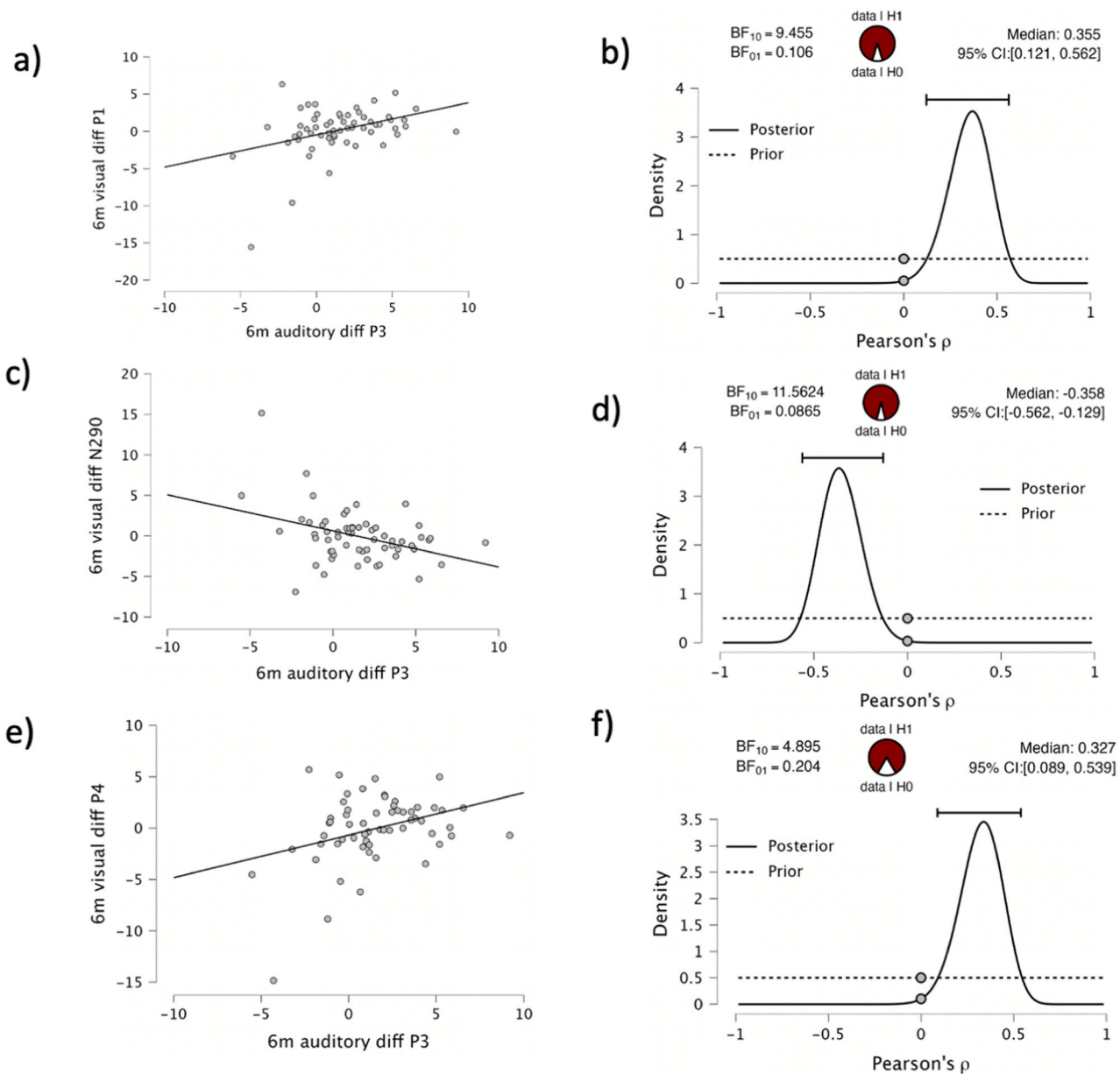
Fig. 6. Correlations between measures of visual and auditory sensitivity at 6 m: Scatterplots showing strength and direction of the Bayesian Pearson correlation between the two variables analysed (Fig. 6. a, c, e); Plots showing the prior and posterior distributions of the true population correlation (Fig. 6. b, d, f). The BF is also presented graphically with the unit circle in the output. The shaded area corresponds to the evidence in favour of the alternative hypothesis (indicated in the graphic in Fig. 6b) by "Data | H1″, and the unshaded area corresponds to evidence in favour of the null "Data \ H0″. The ratio of the shaded area to the unshaded area can be seen to be about 9:1 (6b), 12:1 (6d) 5:1 (6 f), which is the value of BF10.

Overall, the results from Analysis 1 indicate that at 6-months of age, indices of neural sensitivity to auditory information (P3) and visual information (P1 and P4) are correlated positively, whereas the auditory difference P3 is negatively correlated with the visual difference N290. However, by 12-months of age any association between these measures has disappeared.

2.3. Analysis 2 – the association between autonomic arousal and visual and auditory neural sensitivity

For the second analysis, we examine how autonomic arousal related to neural sensitivity at 6 m and 12 m. We operationalised autonomic arousal as heart rate (HR) in beats per minute (BPM) averaged across the recording. Neural sensitivity on the auditory task was operationalised as the amplitude difference in the P3 components in response to standard and deviant tones. Neural sensitivity on the visual task was operationalised as the amplitude difference in the P1, N290 and P4 components in response to fearful and neutral faces. At 6 m, HR correlated negatively with the auditory P3 difference and the visual P4 difference. However, HR correlated positively with the visual N290 difference. No correlation at a statistically significant level was found between HR and the difference between facial expressions in the P1 component. Follow-up analyses showed that autonomic arousal associated with a larger negative-going N290 in response to fearful but not neutral faces.

Scatterplots illustrate the strength and direction of the correlation between each set of two variables (Fig. 8. a, c, e). Our evidence shows that a negative relationship between average HR in BPM over the entire recording and the difference in the P3 component for standard and deviant tones and the P4 component for neutral and fearful faces is twice and four times respectively as likely as no relationship in the population.

Table 1

Bayesian Pearson Correlations for neural auditory and visual sensitivity measures at 6 m. Some of the Bayes Factors are exceptionally high: the BF for the association between visual diff P1 and visual diff P4 is 6.036 * 10^6. This example shows how a Bayesian analysis allows researchers to report a useful estimate of the exceptionally high strength of evidence (6 million to 1in favour of the alternative hypothesis) that would not be possible with a Pvalue.

Bayesian Pearson Correlations									
Variable		1. 6 m auditory diff_P3		2. 6 m visual diff P1		3. 6 m visual diff N290		4. 6 m visual diff P4	
1. 6 m auditory diff P3	n	—							
	Pearson's r	—							
	BF_{10}	—							
2.6 m visual diff P1	n	59		—					
	Pearson's r	0.363		—					
	BF_{10}	9.458		—					
3. 6 m visual diff N290	n	60		60		—			
	Pearson's r	-0.373	*	-0.917	* **	—			
	BF_{10}	11.562		4.017e+ 21		—			
4. 6 m visual diff P4	n	59		60		60		—	
	Pearson's r	0.341		0.680	* **	-0.869	* **	—	
	BF_{10}	4.895		6.036e+ 6		2.254e+ 16		—	

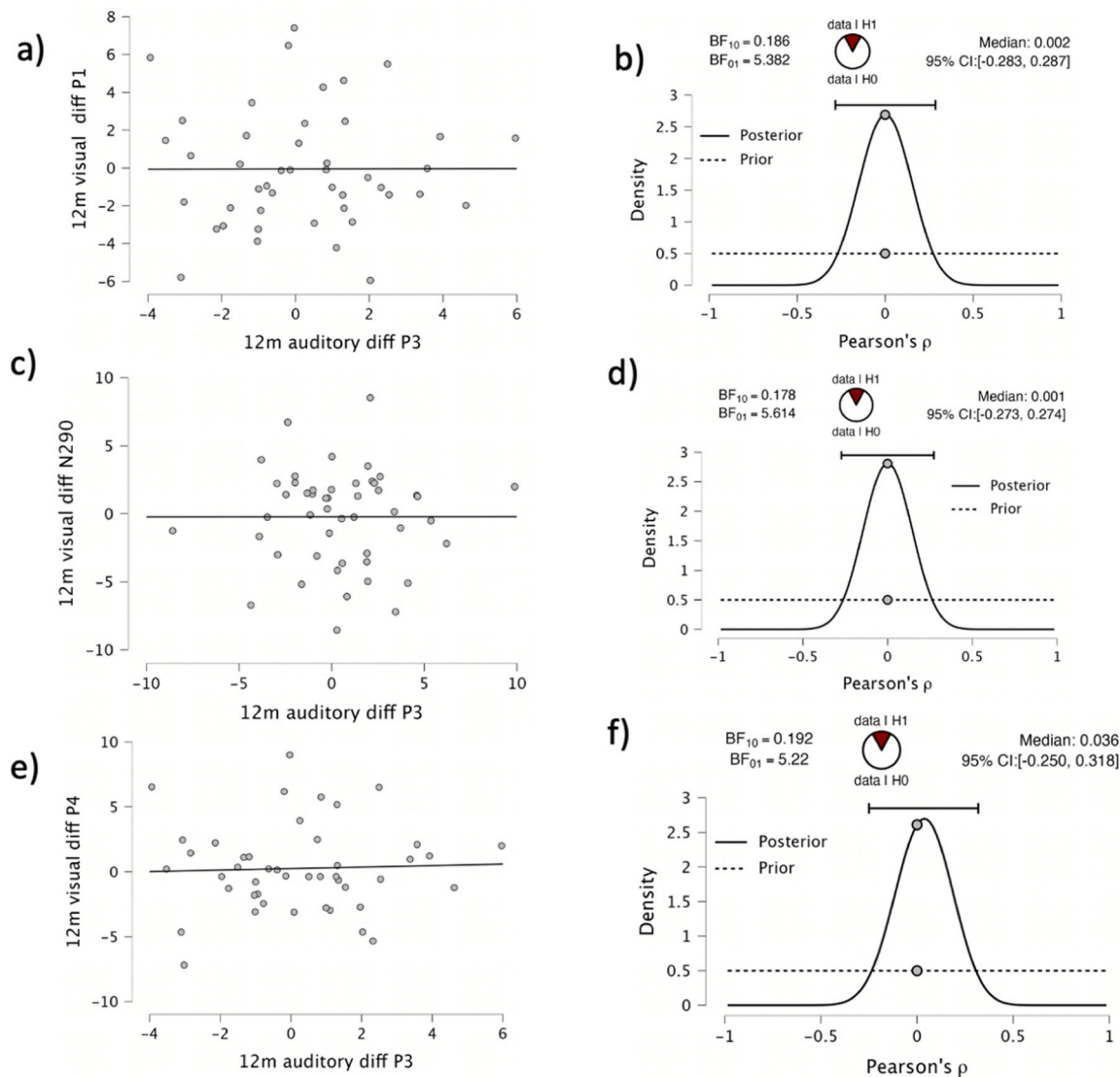* $BF_{10} > 10$, * * $BF_{10} > 30$, * ** $BF_{10} > 100$

Fig. 7. Correlations between measures of visual and auditory sensitivity at 12 m: Bayesian correlation pairwise plots showing strength and direction of the Bayesian Pearson correlation between the two variables analysed (Fig. 7.a, c, e); Plots showing the prior and posterior distributions of the true population correlation (Fig. 7. b, d, f).

Table 2

Bayesian Pearson Correlations for neural auditory and visual sensitivity measures at 12 m.

Bayesian Pearson Correlations							
Variable		1. 12 m auditory diff P3	2. 12 m visual diff P1		3. 12 m visual diff N290		4. 12 m visual diff P4
1. 12 m auditory diff P3	n	—					
	Pearson's r	—					
	BF$_{10}$	—					
2. 12 m visual diff P1	n	46	—				
	Pearson's r	-0.021	—				
	BF$_{10}$	0.186	—				
3. 12 m visual diff N290	n	47	47		—		
	Pearson's r	0.001	-0.943	* **	—		
	BF$_{10}$	0.178	6.738e+ 19		—		
4. 12 m visual diff P4	n	46	47		47		—
	Pearson's r	0.035	0.766	* **	-0.865	* **	—
	BF$_{10}$	0.192	3.431e+ 7		1.498e+ 12		—

* BF$_{10}$ > 10, * * BF$_{10}$ > 30, * ** BF$_{10}$ > 100

The BF10 for the positive relationship between average HR in BPM over the entire recording and the difference in the N290 component to neutral and fearful faces shows that a positive correlation is 12 times more likely in the population than not.

Plots showing the prior and posterior distributions of the true population correlation show how evidence from the current study has updated the prior distribution (Fig. 8. b, d, f).

Table 3 shows the Bayesian Pearson Correlations for the autonomic and neural measures.

Scatterplots in Fig. 9. show the strength and direction of the correlation between autonomic arousal and the N290 to fearful faces at 6 m (Fig. 9a) and 12 m (Fig. 9b). Plots showing how the evidence has updated the prior distributions for the relationship at 6 m to be 3 times more likely than not (Fig. 9. C) and at 12 months, that there is no relationship between the variables being three times more likely than that there is.

Table 4. shows the Bayesian Pearson Correlations for autonomic arousal and N290 in response to fear at 6 m and 12 m.

These results indicate that at 6 m there is a negative relationship between physiological arousal and neural sensitivity as operationalised in this study at the auditory P3 component and visual P4 component. However, individuals with higher autonomic arousal during the EEG recording session, responded with a larger difference in amplitude between fearful and neutral faces at the N290 component.Table 5.

Next, we repeated an identical analysis based on the 12 m data. Scatterplots illustrate the strength and direction of the correlation between each of the sets of two variables (Fig. 9. a, c, e); Our evidence shows that no relationship between average HR in BPM over the entire recording and the difference in the P3 component for standard and deviant tones and the, N290 and P4 components for neutral and fearful faces is five, six and four times more likely, respectively, than there being a relationship in the population. Plots showing the prior and posterior distributions of the true population correlation show how evidence from the current study has updated the prior distribution (Fig. 9. b, d,f). Fig. 10.

Overall, the results from Analysis 2 indicate that at 6 m, higher physiological arousal associated with decreased neural sensitivity in the auditory domain (specifically, a smaller difference between the amplitude of responses to standard of deviant tones at the P3 component) and the visual domain (a smaller difference between the amplitude of responses to fearful and neutral faces at the P4 component). However, higher physiological arousal also associated with increased neural sensitivity as measured by the difference between the amplitude of responses to fearful and neutral faces at the N290 component. Autonomic arousal did not correlate with any measures of neural sensitivity at 12 m.

3. Discussion

We used ERP paradigms to measure auditory and visual neural sensitivity in infants at 6 and 12-months while concurrently measuring inter-individual differences in autonomic arousal. Our results had two main features of interest. The first was that at 6 months, neural sensitivity (indexed as difference-detection between conditions) correlated across auditory and visual modalities. Specifically, while there were no differences between responses to fearful and neutral faces at a group level, for those infants with a larger difference in response amplitudes of the P3 component between the standard and deviant conditions in the auditory paradigm, there was also a larger difference in response amplitudes of the P1 and P4 between the neutral and fearful conditions in the visual paradigm. We also found a negative association between the difference in response amplitude of the N290 to neutral and fearful conditions and the difference in response amplitudes of the P3 to the standard and deviant conditions in the auditory paradigm. The same associations were not present at 12-months. Second, at 6 m, infants' autonomic arousal negatively correlated with the auditory difference P3 and the visual difference P4 but positively correlated with the visual difference N290. Any association between autonomic arousal and neural sensitivity disappeared at 12 months despite the 6 m and 12 m EEG measures having comparable levels of noise and variability. We shall discuss these two main findings in turn.

Topoplots of our results show that different cortical regions are being activated in response to the visual and auditory stimuli. While this implies specialisation of cortical areas for visual (occipital) and auditory (temporal) perception, our measures of neural sensitivity nevertheless correlate at 6 m. This correlation of sensitivity measures between neural domains supports the hypothesis that ES is domain general, which is a pre-requisite for differential susceptibility to *both* positive *and* negative environmental effects. A domain-general level of sensitivity, in terms of the early stages of visual and auditory processing has been considered evolutionarily adaptive – to facilitate making novel and serendipitous associations with environmental cues in an uncertain environment (Chiappe and MacDonald, 2005) and as such an index of heightened susceptibility to the effects of the developmental environment for better or for worse.

It is important to note that the auditory and visual stimuli used in this study were not presented concurrently and would not ordinarily co-occur. However, neural responses to both have been used previously to index sensitivity of response in the visual and auditory neural domains. The results of this study suggest this sensitivity was general across neural domains at 6 m but not 12 m. Different accounts of neural and perceptual development will be explored for their contributions to understanding the development of the mechanisms of differential susceptibility and to highlight relationships between theories that are not often linked.
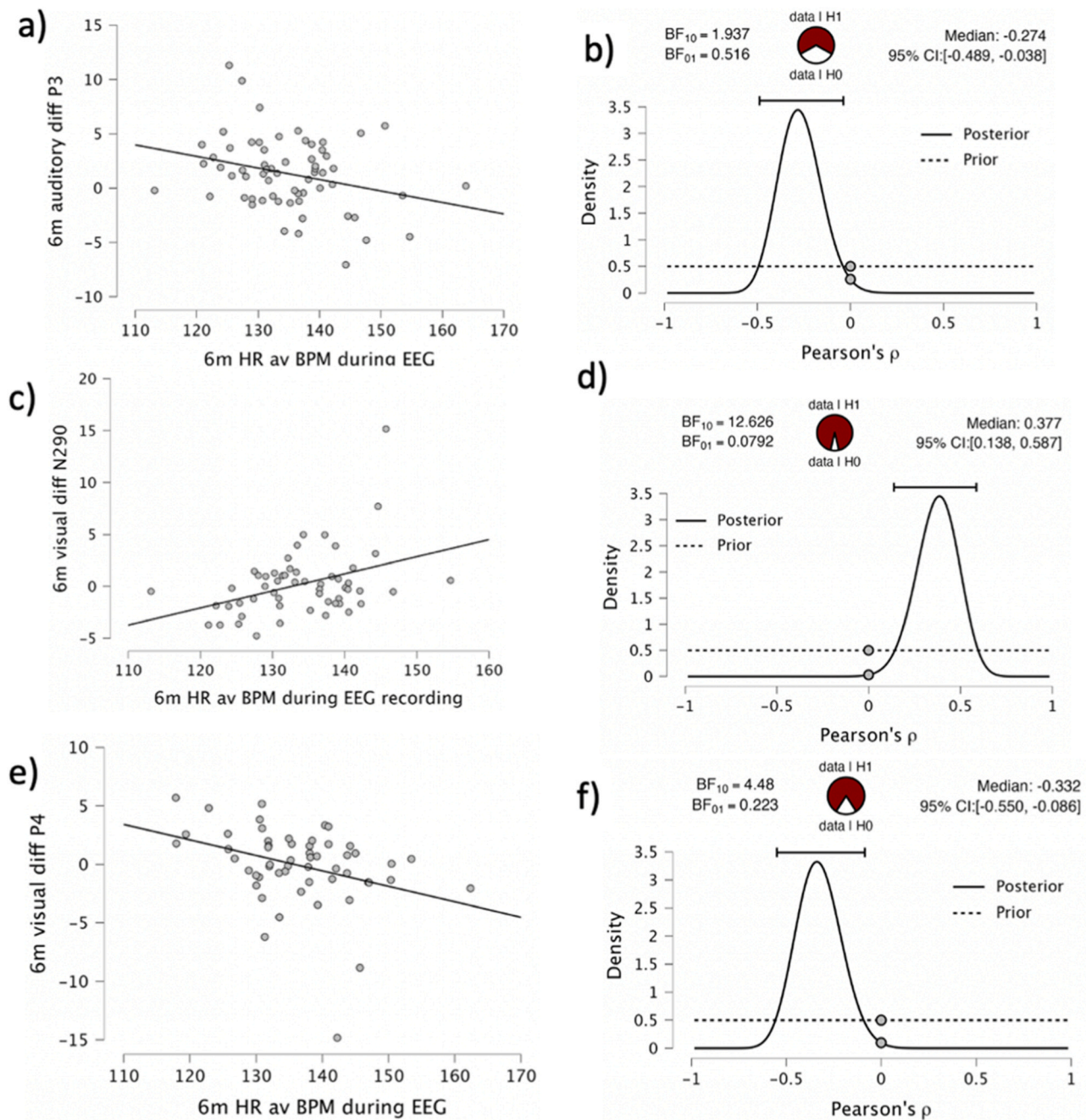
Fig. 8. Correlations between measures of HR and visual and auditory sensitivity at 6 m: Bayesian correlation pairwise plots showing strength and direction of the Bayesian Pearson correlation between the two variables analysed (Fig. 8. a, c, e); Plots showing the prior and posterior distributions of the true population correlation (Fig. 8. b, d, f).

The development of sensitivity, from being domain-general to domain specific, that we found, is in line with accounts that hold that initially separate sensory systems become integrated through repeated experience of concurrent information provided by the different sensory modalities (Birch and Lefford, 1963, 1967). While this may seem counterintuitive, evidence for this account comes from studies of the development of audiovisual speech integration. Prior to 4.5-months, infants perceive even concurrently presented auditory and visual information via separate sensory systems (Bristow et al., 2009; Desjardins and Werker, 2004; Nardini et al., 2010). This early parity of sensitivity to both modalities (even when presented concurrently) is indicated by an absence of the McGurk/fusion effect, which sees perception in one modality (auditory) attenuated by perception in another (visual)

(McGurk and MacDonald, 1976). Intersensory integration of different modalities comes at the expense of a level of sensitivity that is domain general. Our findings corroborate accounts of a level of sensitivity that is initially domain general at 6 m -whether perceiving multi-modal or unimodal stimuli - and thereafter develops differentially in the different domains at 12 m.

The fact that sensitivity measures correlated between domains in this study at 6-months but not 12-months, may be due to a shift away from predominantly stimulus-driven, bottom-up perception. Some accounts of the ontogeny of face-processing argue that postnatally, sub-cortical orienting involving the amygdala modulates activity in face-sensitive cortical regions before the arrival of visual information through the cortical route (Johnson, 2005). This pathway is thought to be maximally

Table 3

Bayesian Pearson Correlations for autonomic and neural measures at 6 m.

Bayesian Pearson Correlations					
Variable		1. BPM 6 m	2. 6 m auditory diff P3	3. 6 m visual diff N290	4. 6 m visual diff P4
1. BPM 6 m	n	—			
	Pearson's r	—			
	BF_{10}	—			
2. 6 m auditory diff P3	n	60	—		
	Pearson's r	-0.287	—		
	BF_{10}	1.937	—		
3. 6 m visual diff N290	n	55	60	—	
	Pearson's r	0.394 *	-0.371 *	—	
	BF_{10}	12.626	10.900	—	
4. 6 m visual diff P4	n	53	59	60	—
	Pearson's r	-0.341	0.254	-0.869 * **	—
	BF_{10}	4.480	1.025	2.254e+ 16	—

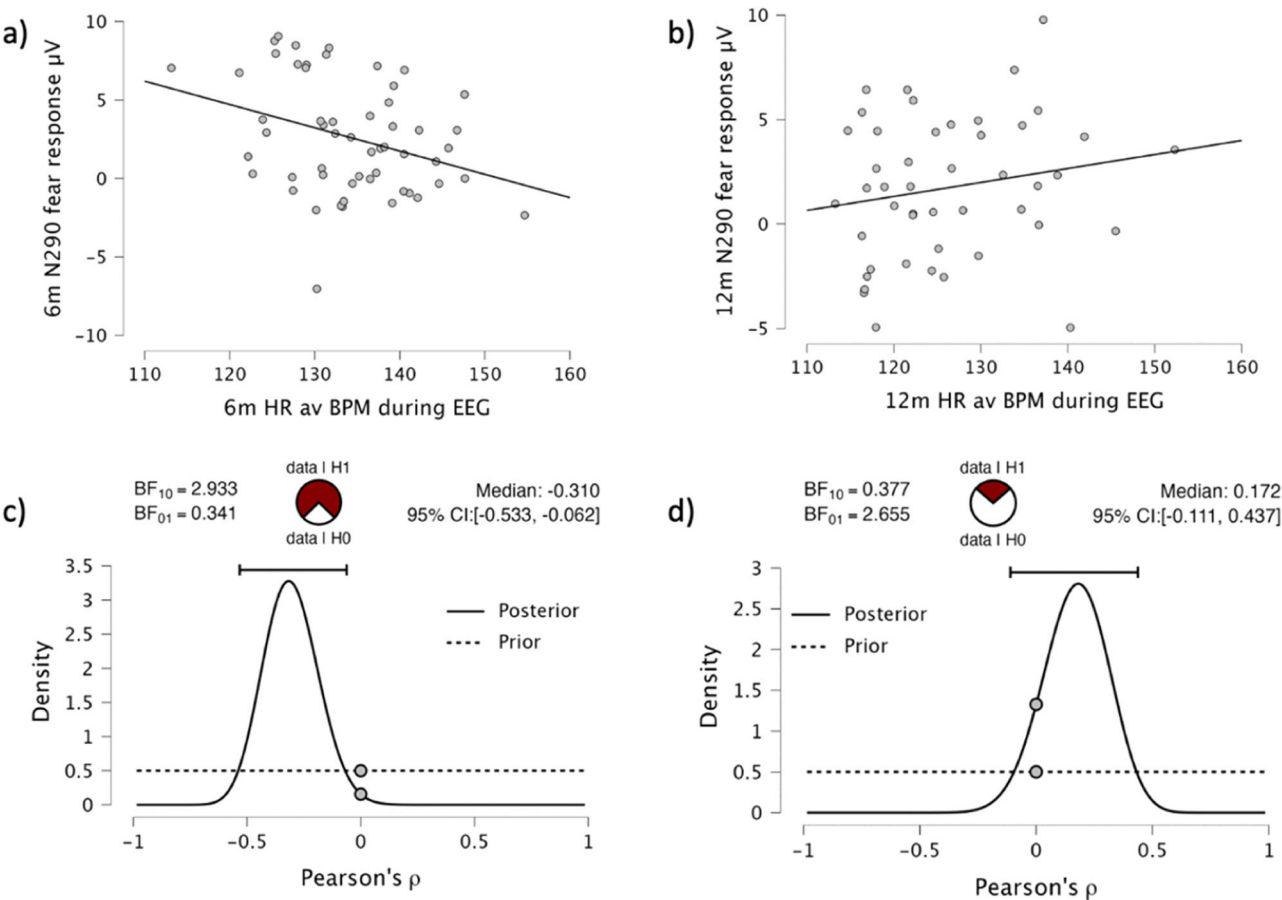* $BF_{10} > 10$, * * $BF_{10} > 30$, * ** $BF_{10} > 100$

Fig. 9. Correlations between measures of HR and visual N290 response to fearful faces at 6 m and 12 m: Bayesian correlation pairwise plots showing strength and direction of the Bayesian Pearson correlation between the amplitude of the 6 m N290 to fear and HR at 6 m (Fig. 9. a) and the amplitude of the 12 m N290 to fear and HR at 12 m (Fig. 9. b); Plots showing the prior and posterior distributions of the true population correlation (Fig. 9. c, d).

sensitive to low-spatial-frequency (LSF) aspects of faces, which selectively differentiates expressions such as fear with wider eyes and open mouths. This early sensitivity to LSF aspects of faces may also be reflected in the functional specificity of components and the direction in which they correlated in this study.

We found a positive association between the P3 auditory component, reflecting pre-attentive, bottom-up difference-detection mechanisms and the P1 and P4 visual components. In adults, the longer-latency visual ERP components, greater than 400 ms after stimulus onset, are thought to reflect top-down mechanisms such as recognition of facial

identity (Barrett et al., 1988; Barrett and Rugg, 1989; Eimer, 2000; Itier and Taylor, 2004) and/or retrieval of semantic information related to faces (Paller et al., 2000). However, the earlier adult N170 component is thought to be related to stages of structural encoding of the physical information in faces, with some studies suggesting that it may only reflect eye detection (Bentin et al., 1996) as opposed to encoding of the entire configuration of facial features (Eimer, 2000). In addition, the adult N170 component can be unaffected by any emotional expression, supporting the hypothesis that structural encoding and expression analysis are independent processes (Eimer, Holmes, 2002). In infants,

Table 4

Bayesian Pearson Correlations for measures of autonomic arousal and N290 response to fearful faces at 6 m and 12 m.

Bayesian Pearson Correlations					
Variable		1. BPM 6 m	2. BPM 12 m	3. 6 m fear N290	4. 12 m fear N290
1. BPM 6 m	n	—			
	Pearson's r	—			
	BF_{10}	—			
2. BPM 12 m	n	59	—		
	Pearson's r	0.446 **	—		
	BF_{10}	72.957	—		
3. 6 m fear N290	n	55	52	—	
	Pearson's r	-0.325	-0.023	—	
	BF_{10}	2.933	0.175	—	
4. 12 m fear N290	n	43	46	41	—
	Pearson's r	-0.049	0.183	0.085	—
	BF_{10}	0.199	0.377	0.223	—

* $BF_{10} > 10$, * * $BF_{10} > 30$, * ** $BF_{10} > 100$

Table 5

Bayesian Pearson Correlations for autonomic and neural measures at 12 m.

Bayesian Pearson Correlations						
Variable		1. BPM 12 m	2. 12 m auditory diff P3	3. 12 m visual diff P1	4. 12 m visual diff N290	5. 12 m visual diff P4
1. BPM 12 m	n	—				
	Pearson's r	—				
	BF_{10}	—				
2. 12 m auditory diff P3	n	49	—			
	Pearson's r	0.045	—			
	BF_{10}	0.198	—			
3. 12 m visual diff P1	n	46	47	—		
	Pearson's r	-0.086	-0.021	—		
	BF_{10}	0.215	0.186	—		
4. 12 m visual diff N290	n	46	47	47	—	
	Pearson's r	-0.009	0.001	-0.943 ***	—	
	BF_{10}	0.178	0.178	6.738e+ 19	—	
5. 12 m visual diff P4	n	46	46	47	47	—
	Pearson's r	-0.089	0.035	0.766 ***	-0.865 ***	—
	BF_{10}	0.217	0.189	3.431e+ 7	1.498e+ 12	—

* $BF_{10} > 10$, * * $BF_{10} > 30$, * ** $BF_{10} > 100$

there is evidence that the adult N170 is preceded by the N290 and P4 components. However, before 12 months of age, the P4 (unlike the N290) component does not seem to be face-specific (Halit et al., 2003). Furthermore, Halit et al. (2004) found the amplitude of the P4 was not sensitive to the difference between face and visual-noise stimuli in 3-month-olds, while the amplitude of the N290 displayed a huge difference (Halit et al., 2004). Research has also shown that the P1 is an obligatory visual component indexing low-level sensory processing and is not face-specific but associated with differences in low-level visual features that exist between face and non-face stimuli (Conte et al., 2020). However, after 7-months, a developmental shift is thought to occur from featural to configural processing of faces. Cohen and Cashon (2001) report that before the age of 7 months, infants process specific features of complex objects but after the age of 7 months they are able to integrate those features into a whole object (Cohen and Cashon, 2001; Conte et al., 2020).

In line with the above evidence from the literature, it is proposed that the difference between the amplitude of the early P1 and P4 components to the fearful and neutral faces at 6 m in this study may be explained by the encoding of the lower-level, perceptual information in the isolated features of the faces such as larger eyes and open or down-turned mouths in the fearful category (Halit et al., 2003). Adult studies have seen larger amplitude N170 components evoked to open as opposed to closed mouths (Puce et al., 2007; Wheaton et al., 2001). Therefore, the components which precede the N170 in infants -the P1 and P4 - are more likely to be affected by the spatial differences of fearful as opposed to neutral faces detected by exogenous attention. The difference in amplitude of the N290 evoked by the two visual conditions may be

partially explained by the recruitment of greater top-down, pre-frontally mediated processing, which would not associate positively with indexes of exogenous perception – the auditory P3 and the visual P1 and P4.

In terms of auditory perception, this differentiation between exogenous perception of low-level sensory features and the more experience-mediated endogenous processing of stimuli corresponds with the proposition that two different mechanisms underlie the auditory tracking of the speech envelope: one derived from the intrinsic oscillatory properties of auditory regions; the other induced by top-down signals coming from other non-auditory regions of the brain (Rimmele et al., 2018). Under non-speech listening conditions, the intrinsic auditory mechanism dominates (Assaneo et al., 2019), which corresponds with the automatic change detection in the processing of non-sematic, lower-level features of non-speech sounds in this study. The disappearance of the association between the amplitude of visual and auditory components by 12 m in this study may capture a transition from bottom-up, stimulus-driven processing of faces to more top-down processing - based on experience - which no longer correlates with the auditory mismatch response which is thought to be automatic and independent of voluntary attention (Cheour et al., 2010; Háden et al., 2016; Wanrooij et al., 2014).

The dissociation of visual and auditory sensitivity by 12 m could also be due to the differential development in the two modalities. There is ample evidence that, very early in development, audio and visual development rates differ. Differential onset of the functioning of sensory systems results in relative independence among emerging systems, thereby reducing competition which helps regulate subsequent neurogenesis and functioning (Turkewitz and Kenny, 1982). Synaptogenesis and synapse elimination occurs at different rates in different cortical
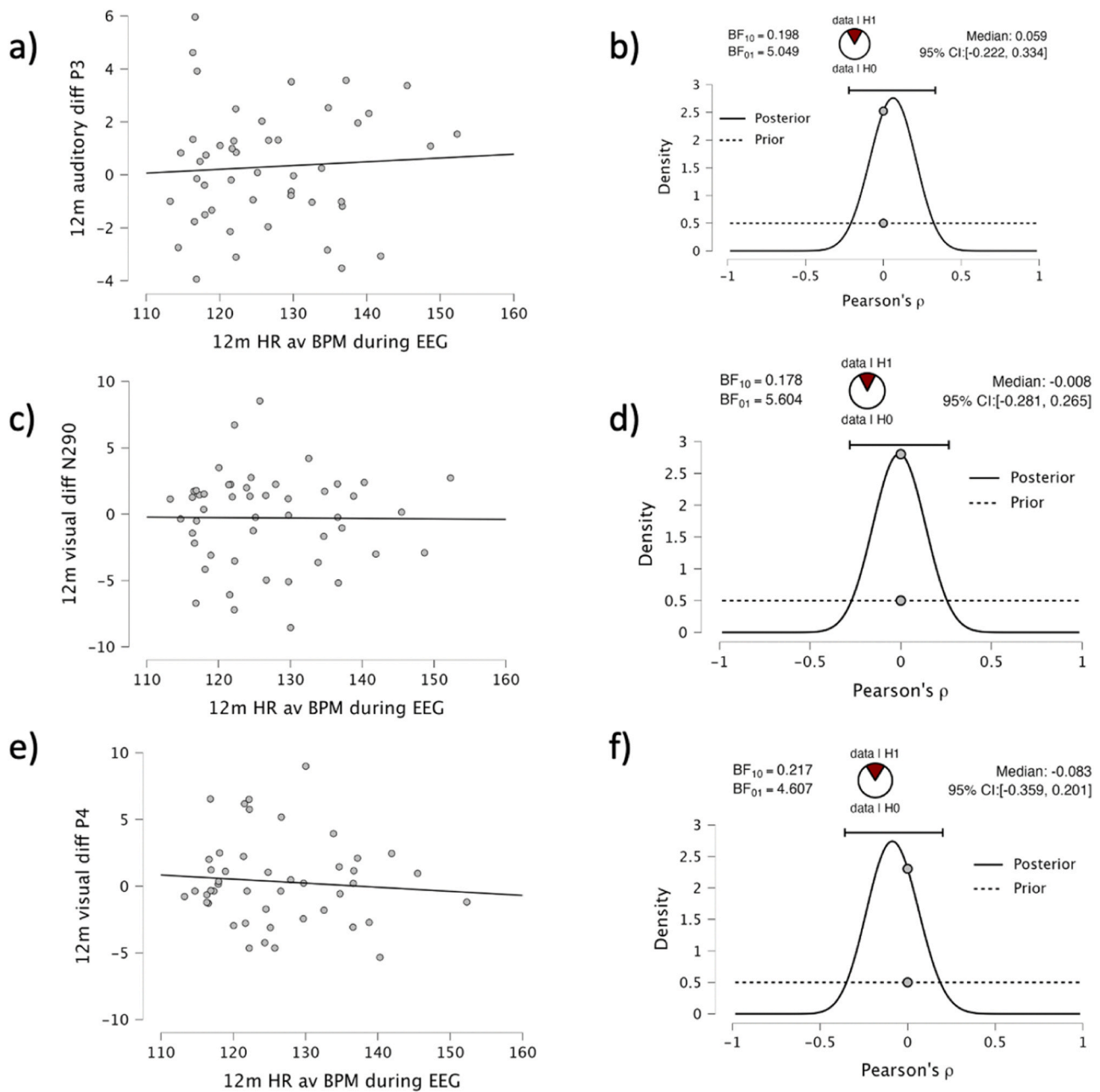
Fig. 10. Correlations between measures of HR and visual and auditory sensitivity at 12 m: Bayesian correlation pairwise plots showing strength and direction of the Bayesian Pearson correlation between the two variables analysed (Fig. 10.a, c, e); Plots showing the prior and posterior distributions of the true population correlation (Fig. 10. b, d, f).

regions in humans. Synaptic density in the auditory cortex is maximal at 3-months of age and synaptic elimination ends at around 12-years, whereas synaptic density in the visual cortex is maximal between 9 and 15-months and synaptic elimination ends at around late adolescence (Huttenlocher and Dabholkar, 1997). Myelination begins earlier in the occipital lobe than in the temporal lobe after birth (Yakovlev, 1967). Complexity measures, such as multiscale entropy (MSE) (Costa et al., 2002) can index maturational changes in brain function. Lippé et al. (2009) found that, while EEG signal complexity increased from one month to 5 years of age in response to auditory and visual stimulation, infants' signal complexity for the visual condition was greater than auditory signal complexity, whereas adults showed the same level of complexity to both types of stimuli. The differential rates of complexity change may reflect a combination of innate and experiential factors on the structure and function of the two separate sensory systems.

The second branch of our findings on the domain generality of ES was that higher heart rate (HR) (measured in BPM averaged across the entire EEG recording) was associated with a larger difference in response amplitude of the visual N290 component to fearful and neutral faces and a smaller difference in the response amplitudes of the visual P4 component and the auditory P3 component in the 6-month-old infants. While HR correlated between 6 m and 12 m, any associations between autonomic arousal and automatic neural sensitivity had disappeared by 12-months despite equal amounts of noise and variability at the two time-points (see error bars in Fig. 2. 3. and 4.) In the same auditory change-detection paradigm as used in this study, while responses to large acoustic contrasts (bursts of white noise) evoked large P3 responses (indexing exogenous, stimulus-driven orienting or distractibility) in all 5–7 year-old children regardless of HR, children with high autonomic arousal also showed a larger P3 component in response to

small acoustic contrasts (500–750 Hz) (Wass et al., 2019). It was proposed that in trials with high HR, the overall brain excitability was higher and therefore more prone to involuntary attention. Thus, even small acoustic contrasts (frequency deviant) could potentially elicit a P3-like response. Therefore, for this study we hypothesized that higher HR would associate with greater neural sensitivity indexed by a larger difference in the amplitude of response to the two conditions in the visual and auditory paradigms. However, we only found a larger difference in the amplitude of response to fearful and neutral faces at one component – the N290. This finding may be explained by the follow-up analyses, which showed that high HR correlated with larger N290 (but not P1 or P4) responses to fearful faces. The differential response at the different components will be addressed below.

Heightened autonomic arousal is an index of sympathetic nervous system (SNS) activity which is involved in quick response mobilising ('fight or flight') (Cacioppo et al., 2000) and as such is considered a defence response (Pavlov, 1927) associated with hypervigilance and sensory reactivity to environmental stimuli (Cheung and Porges, 2013). Relatedly, prior research has found associations between sensory-reactivity and emotional-face processing in children. Projections from the amygdala (part of the neural system responsive to threat (Tovote et al., 2015)) to the occipital cortex may serve to enhance the processing of visually salient stimuli, including facial expressions of emotion (Eimer et al., 2003) and especially fearful expressions (Morris et al., 2002).

The difference in the direction of the correlations between components indexing neural sensitivity and measures of physiological arousal may again be explained by the functional specificity of the components. As mentioned above, previous studies have found evidence of a difference in response amplitude of the N290 between face and non-face visual stimuli suggesting the N290 is face-specific (Halit et al., 2003). However, the P1 is thought to be an obligatory visual component indexing low-level sensory processing and is not face-specific (Conte et al., 2020) and the P4 is thought to reflect structural processing of faces in infants, (Porter et al., 2021) but also does not seem to be face-specific (Halit et al., 2003). The fact that detection of difference at these visual components correlates positively with detection of difference in the P3 auditory component may be because all three index stimulus-driven low-level perception of the sensory properties of the stimuli in the two modalities. For the same reason, the direction of the correlation between HR and the amplitude of the difference between these components is the same - slower heart rate, which is thought to reflect an orienting response (Sokolov, 1963) was associated with greater neural sensitivity in terms of perception of difference between conditions in stimuli for the auditory P3 and the visual P4 component.

This study set out to test the hypothesis that measures of ES would correlate, supporting the notion that sensitivity should be domain general in order to confer susceptibility to all elements of the developmental environment. Evidence presented here suggests that neural sensitivity, in terms of automatic exogenous perception of salient stimuli, covaries in different modalities at 6 m and that autonomic arousal associates with neural sensitivity in both the visual and auditory neural domains; but thereafter, sensitivity in the different domains follows different developmental trajectories. An initial, domain general level of neural sensitivity in different sensory modalities is the result of an early heightened sensitivity of stimulus-driven perception. Relevant to the differential susceptibility hypothesis this may confer advantages in that an organism is initially better equipped than those who are less sensitive to respond to any environmental stimuli and is therefore better able to develop an expertise for the stimuli to which it is predominantly exposed and therefore conditionally adapt to the developmental environment. In terms of whether sensitivity is domain general, these results suggest pre-attentive sensitivity is initially domain general, and associated with autonomic arousal, but that increasing domain specificity of neural modules through processes such as neuroconstructivism and decreasing parity of sensitivity between domains due to intersensory integration,

mean differential developmental trajectories. The same measures of sensitivity no longer correlate either between neural domains or between the neural and autonomic domains. In terms of the domain general sensitivity that is required to confer differential sensitivity to both positive and negative environments, cross sectionally at 6 m, individual differences in sensitivity did correlate between domains. However, the longitudinal findings corroborate accounts of increasing domain specificity, which does not support the differential sensitivity hypothesis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data that has been used is confidential. *The data underlying this article cannot be shared publicly due to* needing to protect the privacy of individuals that participated in the study and because it is part of a dataset contributing to an ongoing PhD project. *The data will be shared on reasonable request to the corresponding author.*

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dcn.2023.101289.

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