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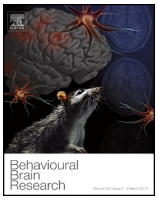

Research report

The neural basis of responsive caregiving behaviour: Investigating temporal dynamics within the parental brain

Katherine S. Young[a,b], Christine E. Parsons[b,c], Alan Stein[b,d], Peter Vuust[c], Michelle G. Craske[a], Morten L. Kringelbach[b,c,*]

[a] Anxiety and Depression Research Center, Department of Psychology, UCLA, Los Angeles, CA, USA
[b] Department of Psychiatry, University of Oxford, Oxford OX3 7JX, UK
[c] Center for Music in the Brain (MIB), Department of Clinical Medicine, Aarhus University, DK & The Royal Academy of Music, Aarhus/Aalborg, Denmark
[d] MRC/Wits Rural Public Health and Health Transitions Research Unit (Agincourt), School of Public Health, Faculty of Health Sciences, University of the Witwatersrand, Johannesburg, South Africa

HIGHLIGHTS

- Synthesis of findings from EEG, MEG and LFPs across studies investigating early sensitivity to infant cues.
- Proposed model of rapid neural reactivity to infant cues within the 'parental brain'.
- Summary of emerging literature on experience-dependent plasticity and disruptions to neural activity in the parental brain.

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ABSTRACT

Whether it is the sound of a distressed cry or the image of a cute face, infants capture our attention. Parents and other adults alike are drawn into interactions to engage in play, nurturance and provide care. Responsive caregiving behaviour is a key feature of the parent-infant relationship, forming the foundation upon which attachment is built. Infant cues are considered to be 'innate releasers' or 'motivational entities' eliciting responses in nearby adults (Lorenz 1943; Murray, 1979) [42,43]. Through the advent of modern neuroimaging, we are beginning to understand the initiation of this motivational state at the neurobiological level. In this review, we first describe a current model of the 'parental brain', based on functional MRI studies assessing neural responses to infant cues. Next, we discuss recent findings from temporally sensitive techniques (magneto- and electroencephalography) that illuminate the temporal dynamics of this neural network. We focus on converging evidence highlighting a specific role for the orbitofrontal cortex in supporting rapid orienting responses to infant cues. In addition, we consider to what extent these neural processes are tied to parenthood, or whether they might be present universally in all adults. We highlight important avenues for future research, including utilizing multiple levels of analysis for a comprehensive understanding of adaptive caregiving behaviour. Finally, we discuss how this research can help us understand disrupted parent-infant relationships, such as in situations where parents' contingent responding to infant cues is disrupted; for example, in parental depression or anxiety where cognitive attentional processes are disrupted.

1. Characteristics of infant cues and adults' responses to them

From the cuteness of their happy smiling faces to the frustration of hearing their cries, infants' emotional expressions engage our attention. This is a vital evolutionary process. By attending to the pre-verbal cues of our offspring, we can provide sensitive care, promoting infant well-being and ultimately ensuring the survival of the species [1,2]. Reacting promptly and sensitively to infant

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[*] Corresponding author at: Department of Psychiatry, Warneford Hospital, University of Oxford OX3 7JX, United Kingdom.
E-mail addresses: gesposito79@gmail.com, morten.kringelbach@queens.ox.ac.uk (M.L. Kringelbach).

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communicative cues is a key parenting capacity [3]. There is broad scientific consensus that child development is profoundly impacted by the quality of early caregiving [for reviews, see [4,5–7]]. More specifically, it has been shown that the sensitivity of parental responses to infant cues can affect children's cognitive and socio-emotional development [8,9].

Infant cues play two primary roles in establishing the relationship between infant and caregiver. First, these cues provide the adult caregiver with a wealth of information about the infants' physiological and affective state [10–12]. In combination with other contextual factors, these signals help to guide the selection of appropriate caregiving behaviour. Secondly, from within days after birth, parents and their infants mirror each other's emotional expressions [13,14]. Parents also modify their behaviour to match the infants' developmental stage, such as by using high and exaggerated pitch in their speech ('infant-directed speech' or 'motherese'), a feature of parental behaviour implicated in sustaining infant attention [15,16]. These pre-verbal interactions form the foundation of a socio-emotional understanding upon which complex attachment relationships can be built [17,18].

Infant cries typically have high and dynamic pitch [ranging between 250 and 700 Hz; [19]] a 'falling' or 'rising-falling' melody, with single bursts lasting between one to three seconds [see Fig. 1; [20]]. In the first few months after birth, infant cries are thought to be largely reflexive [21], occurring when infants are hungry, tired, in pain or separated from their caregiver. Beyond two to three months after birth, greater motor control of the vocal tract permits more variation in cry acoustics and the production of a wider range of vocalisations including laughter and pre-verbal 'babbling' [10,16,22–24]. Investigation of the acoustic characteristics of infant cries supports the notion of the cry as a 'graded signal' in which changes in acoustic features indicate varying levels of distress [25]. A number of studies have demonstrated that higher pitched cries are perceived as sounding 'more distressed' and as having 'greater arousal' by adult listeners, with and without parenting experience [26–29].

Infant faces are characterized by large rounded foreheads and small chins, large low-set eyes, short and narrow noses and bulging cheeks [see Fig. 1; [30–32]]. This configuration, is typically perceived as pleasant and rewarding and has come to be known as the 'Kindchenschema', or more commonly 'cuteness' [33–35]. Soon after birth, infants are capable of producing a range of facial expressions, including smiling and frowning [36]. Improvements in the control of facial muscles support the development of a broader array of facial expressions, including displays of surprise and anger around four months of age [37]. Adult observers are highly sensitive to variations in both infant facial configuration [cuteness; [32,38–40]] and infant facial expression [41].

Early theoretical accounts of parental responsiveness to infants provided different descriptions dependent on the modality of the infant cue. For infant facial cues, Lorenz [42] initially proposed the concept of 'Kindchenschema', whereby the specific configuration of the infant face acted as an 'innate releaser' of caregiving behaviour in adults. For infant vocalisations, early accounts suggested a range of motivations for promoting caregiving behaviour including: (i) terminating an aversive stimulus; (ii) empathic responding to reduce another's distress; or (iii) evolutionarily-driven responding ensuring the wellbeing of offspring [for overview, see [43]]. Later, Murray [43] proposed the 'motivational entity' model for responding to infant vocalisations, more analogous to the 'Kindchenschema' concept. The motivational entity model states that the specific acoustic structure of an infant cry rapidly and universally alerts the listener, while other factors such as the context of care and cognitive appraisal impact the selection of specific caregiving behaviours [44].

These early theories are broadly supported by the modern neuroscientifically-informed model of emotional experience comprising rapid emotional reactions ('core-affect'), which can be modulated by contextual factors, attentional states and cognitive appraisal [45]. The model of 'dual-stream' emotional processing describes the neural architecture supporting such responses, with quick imprecise processing recruiting primarily subcortical regions and slower, more detailed analyses occurring in sensory and higher-order cortical regions [46–48]. Within the dual streams model of emotional processing, the orbitofrontal cortex (OFC) is considered the central hub, providing an interface between the fast and slow processing routes [48]. In the following sections, we describe the neural circuitry implicated in responding to infant cues. It should be noted that this review is not a comprehensive description of studies in this rapidly expanding field, instead aiming to broadly summarize key findings and emerging trends, focusing on temporally-sensitive neuroimaging techniques [for additional recent reviews, focusing of different imaging modalities, see [49,50]].

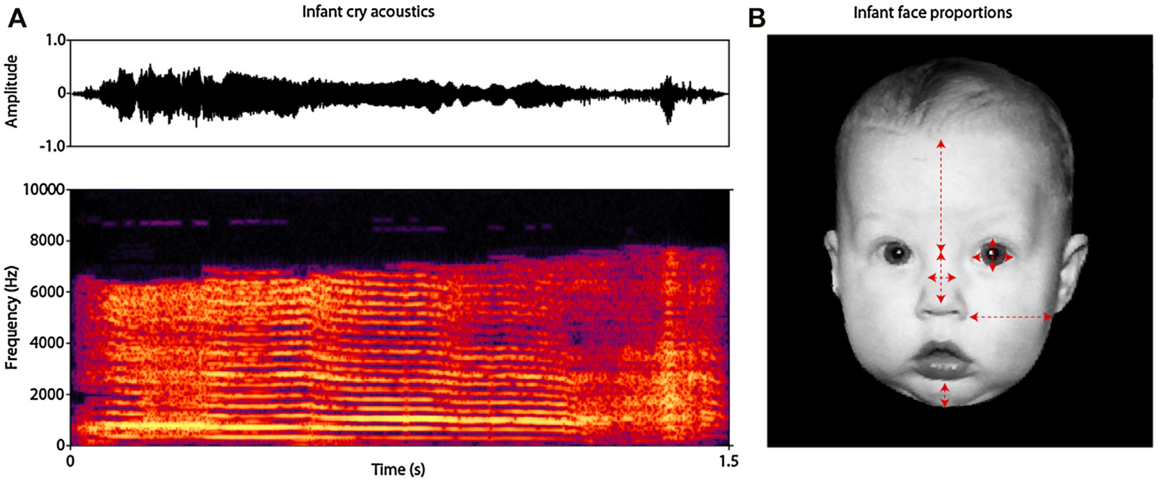

Fig. 1. Examples of infant communicative cues. (A) Waveform (upper) and spectrogram (lower) of a typical infant cry burst, characterized by high and variable pitch. (B) Demonstration of the physical features of a typical infant face, reflecting the 'infant schema': large rounded forehead and cheeks, large low-set eyes, small nose and chin [30–32].

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Table 1
Summary of findings from fMRI studies of the 'parental brain', highlighting neural regions reactive to infant vocal and facial expressions. (MTG: middle temporal gyrus; STS/G: superior temporal sulcus/gyrus; FFG: fusiform gyrus; OFC: orbitofrontal cortex; PFC: prefrontal cortex; PAG: periaqueductal gray; VTA: ventral tegmental area; SMA: supplementary motor area).

	Infant vocal expressions	Infant facial expressions
Temporal lobe		
MTG	Kim et al. [60] Lorberbaum et al. [61] Riem et al. [62] Montoya et al. [63]	Montoya et al. [63] Ranote et al. [64] Barrett et al. [65] Strathearn et al. [66]
STS/G	Kim et al. [60] Lorberbaum et al. [61] Mascaro et al. [67] Bos et al. [68] Riem et al. [62] Montoya et al. [63]	Montoya et al. [63] Ranote et al. [64] Noriuchi et al. [69] Barrett et al. [65] Bartels and Zeki [70] Strathearn et al. [66]
FFG	–	Caria et al. [71] Bartels and Zeki [70] Nitschke et al. [72] Strathearn et al. [66]
Frontal lobe		
OFC	Laurent et al. [73] Mascaro et al. [67]	Baeken et al. [74] Glocker et al. [29] Leibenluft et al. [75] Montoya et al. [63] Nitschke et al. [72] Ranote et al. [64] Strathearn et al. [66] Bartels and Zeki [70] Noriuchi et al. [69]
Anterior cingulate	Lorberbaum et al. [61] Laurent et al. [73]	Caria et al. [71] Noriuchi et al. [69] Barrett et al. [65] Bartels and Zeki [70] Strathearn et al. [66]
PFC	Kim et al. [60] Lorberbaum et al. [61] Laurent et al. [73] Mascaro et al. [67]	Noriuchi et al. [69] Barrett et al. [65] Bartels and Zeki [70] Ranote et al. [64] Strathearn et al. [66]
Insula	Kim et al. [60] Laurent et al. [73] Mascaro et al. [67]	Caria et al. [71] Noriuchi et al. [69] Barrett et al. [65] Bartels and Zeki [70]
Subcortical		
Basal ganglia	Lorberbaum et al. [61] Laurent et al. [73] Mascaro et al. [67] Montoya et al. [63]	Montoya et al. [63] Noriuchi et al. [69] Barrett et al. [65] Bartels and Zeki [70] Strathearn et al. [66]
PAG/VTA	Laurent et al. [73]	Noriuchi et al. [69] Bartels and Zeki [70] Strathearn et al. [66]
Amygdala	Riem et al. [62]	Barrett et al. [65] Leibenluft et al. [75] Ranote et al. [64] Seifritz et al. [76] Strathearn and Kim [77] Bartels and Zeki [70] Strathearn et al. [66]
Thalamus/hypothalamus	Lorberbaum et al. [61]	Caria et al. [71] Noriuchi et al. [69] Barrett et al. [65] Strathearn et al. [66]
Motor		
Motor cortex	Kim et al. [60]	Strathearn et al. [66]
Premotor/SMA	Montoya et al. [63]	Caria et al. [71]

2. Neural responses to infant cues: characterizing networks of the 'parental brain'

Functional MRI studies of adults' responses to infant vocalisations and facial expressions have highlighted a network of regions that may support caregiving behaviour. We refer to this group of regions as the 'parental brain', to encompass both responses in non-parents (the so-called caregiving or parental 'instinct', [51]) and responses among parents that may be experience-dependent (see Table 1; Fig. 2). Studies of responses to both infant facial and vocal cues have demonstrated reactivity in temporal lobe regions (middle temporal gyrus, superior temporal gyrus/sulcus and inferior temporal gyrus/sulcus), frontal lobe regions (anterior cingulate, prefrontal, orbitofrontal and insular cortices), subcortical regions (basal ganglia, amygdala, periaqueductal grey) and motor regions (motor cortex, premotor cortex, supplementary motor area). Cortical areas of the 'parental brain' overlap with those of the 'social brain', a network of neural areas sensitive to social cues [for reviews, see [52,53–55]]. Subcortical (amygdala) and cortical (superior temporal gyrus/sulcus, middle temporal gyrus) regions of the temporal lobe are recruited in the initial processing of affect in the voice [56–59], while occipital and temporal regions (including the fusiform gyrus) are principally recruited for the sensory processing of facial expressions [60]. Activity in these regions is then hypothesised to project to frontal regions, such as the OFC and inferior frontal gyrus for evaluation and higher-order processing [61–63].

The proposed 'social brain' and the 'parental brain' differ in the extent to which they recruit 'survival circuitry', encompassing subcortical and brainstem areas that support reflexive-like responses. Compelling evidence regarding the functioning of subcortical brain regions in parenting behaviour has been obtained from rodent studies. These studies often involve surgical or chemical lesions to specific brain regions to disrupt functioning and observation of behavioural changes. This allows inferences to be made regarding how necessary and/or sufficient specific regions are for the initiation of appropriate caregiving behaviours, conclusions that are difficult to determine in human correlational imaging studies. These studies have demonstrated roles for the amygdala, periaqueductal grey (PAG) and ventral tegmental area in responding to infant distress cues [64]. Each of these regions has also been detected in human neuroimaging studies (see Table 1). Detection of reactivity to infant cues across species within the same brain regions suggests some degree of functional conservation across evolution. Within the parental brain, the amygdala is thought to play a 'vigilance' role, supporting preferential attending to the infant [6]. Rodent studies suggest that the PAG and ventral tegmental area are implicated more in the selection and initiation of caregiving behaviour [64,65].

3. Temporal dynamics of the 'parental brain'

Electroencephalography (EEG), magnetoencephalography (MEG) and local field potential (LFP) recordings have begun to inform our understanding of the time-windows during which specific cortical and subcortical regions are differentially sensitive to infant cues. The majority of studies investigating temporal dynamics within the parental brain have used EEG to assess differences in amplitude or latency of event-related potentials (ERPs; see Box 1) between different types of stimuli or across different groups of participants. Through this work we can begin to build a picture of functional processing in different time frames (see summary in Fig. 3).

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Box 1: Overview of ERPs discussed, including observed latency ranges, putative sources and suggested processing functions. Note that the peak latencies of individual components vary across studies and experimental designs. The putative neural sources and their proposed functions are still actively under investigation [158–162].

ERP Name	Typical latency range (ms)	Putative neuronal source	Proposed function
N100	80–120	Primary and association cortices	‘unexpected stimulus’ detection, modified by attention
N170	140–200	Fusiform and inferior temporal gyri	Neural processing of faces
N200/N2/N245	160–220	Recorded at frontocentral sites, frontal lobe regions	Task relevant physical properties, stimulus classification, visual attention, response conflict
P300	300–500	Recorded at occipital and parietal sites	Detection of stimulus salience
LPP	400–800	Central/Midline, occipital/posterior parietal	Emotion regulation

3.1. *Early detection of infant vocalisations in the brainstem*

Recording from deep brain stimulation electrodes implanted in the PAG of the midbrain, we observed differences in LFPs in response to infant vocalisations compared to constructed control sounds as early as 49 ms after stimulus onset [66]. Compared to natural control sounds (adult cries and animal distress sounds), significant differences were observed at 86 ms. The PAG has been implicated in maternal responsiveness to infant cues in rodent studies [67–69]. Whereas the spatial resolution of LFPs is not sufficient to differentiate PAG activity from that of neighbouring regions, such as the inferior colliculus, these findings suggest that subcortical human brain regions such as the PAG, are involved in fast discrimination of infant vocalisations.

The PAG has an extensive network of anatomical connections including the nearby inferior colliculus [70], amygdala and frontal lobe regions, such as the OFC [71], plausibly allowing rapid propagation of differential responding to infant cues throughout the parental brain network. In addition, this early detection in brainstem regions might support initiation of a state of heightened physiological arousal upon detection of infant cues. Peripheral psychophysiological studies have demonstrated that hearing infant cries can impact the listener’s heart rate, respiration and hand grip strength [although the direction of these effects varies across studies; [72,73–77]]. It is hypothesised that heightened physiological arousal aids the initiation of rapid, effortful caregiving behaviour. Early detection of salient infant cues in the brainstem might there-

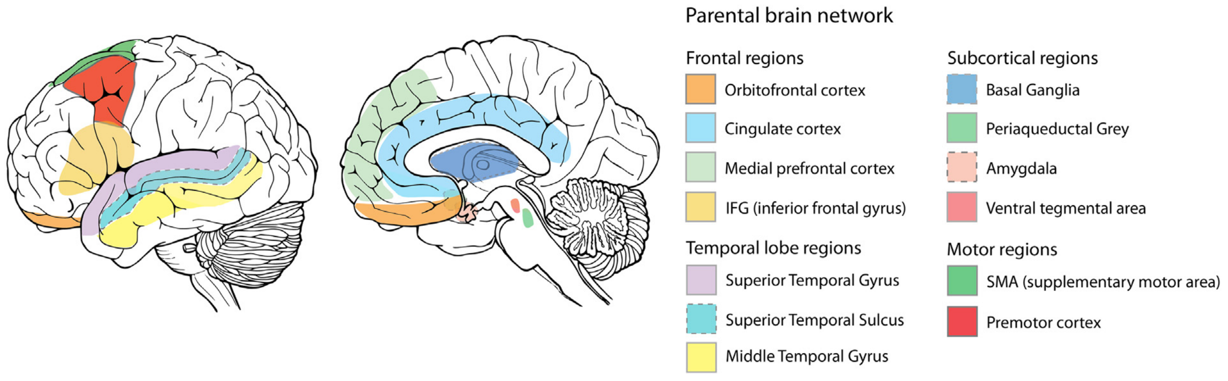

Fig. 2. (A) Schematic diagram of ‘parental brain’—networks of regions recruited in responding to infant cues.

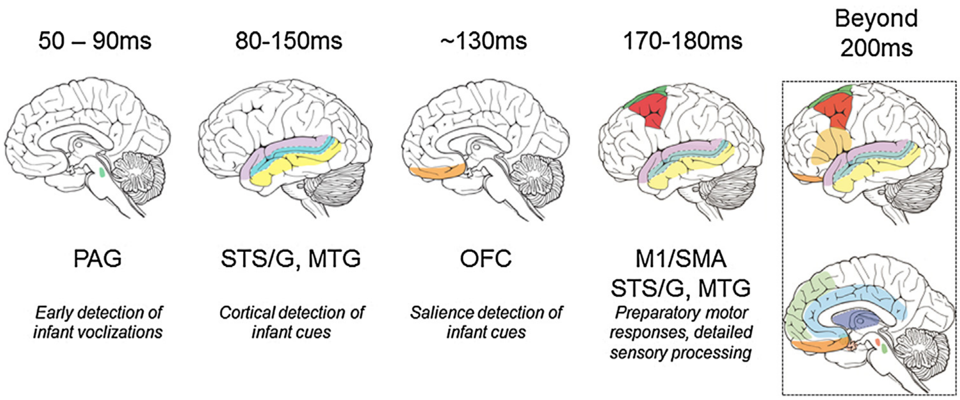

Fig. 3. Proposed timeline of neural activity in response to infant cues across subcortical and cortical regions of the parental brain. Evidence of early detection (<100 ms) of infant cues has been observed in the PAG of the brainstem. Classical sensory processing ERPs (N100/P100) have been shown to be modulated by some features of infant facial expressions. At 130 ms, there is evidence of salience detection, localised to the OFC. Subsequently, further detailed processing of infant cues occurs in a comparable time frame to the initiation of preparatory motor responses. Beyond 200 ms, other regions of the parental brain may support responsive caregiving behaviour. It should be noted that early contributions of subcortical regions, such as the amygdala and ventral tegmental area are less well established due to the greater sensitivity of EEG and MEG to cortical sources of activity, relative to subcortical sources. However, direct recording from subcortical regions, as in the case of LFP recordings of the PAG, indicate that subcortical regions also contribute to early differential processing.

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fore constitute the first step in the pathway to supporting sensitive caregiving behaviour.

3.2. Rapid cortical sensitivity: modulation of the N100

There is conflicting evidence regarding the earliest stage of cortical processing that is sensitive to the affective content of infant cues. One study has demonstrated a main effect of valence of infant facial expressions (happy, neutral, distressed) on the amplitude of N100 responses in both mothers and nulliparous women [78]. Other studies have reported no significant effect of valence on such early responses [79,80]. One proposed explanation for these conflicting findings relates to differences in tasks employed across studies, and specifically in their attentional demands. Directing attention towards infant stimuli (e.g. by requiring participants to identify emotion in stimuli) appears to be linked to differences in earlier stages of stimulus processing [81].

3.3. An early role for the OFC in salience detection of infant cues

The OFC is uniquely positioned at an interface between subcortical and cortical pathways and has established roles in both reward processing and social cognition [4,82–85]. As a central hub linking the dual streams of emotional processing, the OFC is thought to play a crucial role in the coordination of both fast and slow responses to emotional stimuli [47,48,86,87]. The ‘affective prediction hypothesis’ suggests that early in time, the OFC is implicated in ‘tagging’ emotionally salient stimuli [88–90]. This rapid salience detection is thought to influence ongoing sensory processing and prime rapid motor responses [88–90]. Beyond this brief early ‘tagging’ process, activity in the OFC has been shown to represent the reward value of stimuli, likely based on more detailed processing [91]. Representation of stimulus reward is thought to be an important feature of higher-order processing and decision making [92].

There is mounting evidence that the OFC is implicated in the early salience detection of infant cues. In two separate MEG studies of responses to infant facial stimuli, we observed rapid differential activity in the OFC in response to images of infant and adult faces [93,94]. Occurring at around 130 ms post-stimulus presentation, this differential processing is in line with the affective prediction hypothesis and is most likely pre-conscious in nature [95]. In the second of these studies, we additionally demonstrated that early OFC responses to infant faces were disrupted by the presence of a minor facial abnormality [cleft lip; [94]]. This suggests that the specific configuration of infant facial features is critical for eliciting such early neural responses. Extending this work to the auditory domain, we compared neural responses to infant and adult cry vocalisations [96]. Again, we observed a peak of early differential activity localized to the OFC (125–135 ms), as well as a second peak of differential activity slightly later in time (190–200 ms). In combination, these findings support the notion of modality-independent salience detection of infant cues in the OFC (see Fig. 4), a response which could plausibly support rapid orienting towards infant cues.

3.4. Detailed sensory processing (N170 and beyond)

Studies investigating the effect of valence in infant facial expressions on the N170 response, the classical marker of ‘pre-attentive face recognition’, have demonstrated mixed results. Some studies reported no effect of valence on N170 responses [80,81]. However, another study demonstrated larger N170 amplitudes to negative compared to positive infant facial expressions during focused attention in both mothers and non-mothers, as well as a main effect of valence on latency of N170 responses [78]. For later EEG components, findings show greater concordance. Two studies demonstrated effects of valence on responses between 200 and 300 ms (early posterior negativity at 240–300 ms, [78]; N245 at 210–280 ms, [79]). Both intensity and valence of emotional expression were shown to affect the amplitude of P300 responses in one study (375–600 ms, [79]), although another study found no such difference in a comparable time window (300–450 ms, [78]). Two studies have demonstrated modulation of the late positive potential (LPP; 500–800 ms) by valence in infant cues [81,97]. Finally, larger N2 (250–300 ms) responses were demonstrated in response to infant faces compared to pre-pubertal child faces, which in turn had greater responses than that to adult faces [98], an effect which was subsequently localized to fusiform gyrus, anterior cingulate cortex and OFC. These latter differences may be part of the more detailed sensory processing and appraisal proposed in the dual streams models of emotional processing.

3.5. Evidence for preparatory motor responses?

Some preliminary findings suggest that early responses to infant cues might also occur in motor regions of the brain, as proposed in the affective prediction hypothesis. Broadly, fMRI studies have demonstrated motor and supplementary motor cortex reactivity to infant facial and vocal cues (see Table 1). This has led some authors to suggest that this reactivity indicates a preparatory motor response [99], initiated by biologically salient stimuli [100]. In line with this proposal, using MEG, we also observed early differential responding, occurring at around 180 ms to infant vocalisations, localized to motor cortex [96]. In addition, another recent study using transcranial magnetic stimulation demonstrated enhanced motor evoked potentials 100–200 ms after hearing infant cries [an effect which may be specific to female listeners; [101]]. At the behavioural level, both listening to infant cries and looking at infant faces promotes a self-reported desire to enact caregiving responses in adult listeners [32,73,102]. Hearing infant cries has also been shown to significantly increase the speed of motor responses on an effortful motor task [103,104]. Similarly, viewing infant faces promotes effortful responding in adults, as demonstrated through key-pressing tasks [105].

3.6. Summary of temporal dynamics within the parental brain

We outline a proposed timeline of neural activity to infant cues in subcortical and cortical regions of the ‘parental brain’. In brief, specialised processing of infant cues originates in the brainstem, rapidly propagating to sensory cortical regions and the OFC (within 100–150 ms), a process thought to support salience detection. OFC responses then impact both detailed sensory processing in temporal lobe regions and preparatory motor responses in cortical motor regions. Within this ‘parental brain’ network, we therefore propose critical roles for the PAG and OFC. As a key ‘survival structure’ in the brainstem, the PAG may act as a rapid route for engaging broader cortical circuitry, while simultaneously triggering a cascade of adaptive physiological responses. The OFC may then perform more refined ‘salience detection’, influencing ongoing sensory processing and priming cortical motor reactivity, supporting orienting responses towards infants. Through these processes, we suggest that infant cues provide privileged access to neural mechanisms that ignite motivational states across the whole brain, a phenomenon thought to be self-supporting and ‘metastable’ in nature (as described by Kringelbach and colleagues [35]).

4. Experience-dependent plasticity in the parental brain

Infants’ needs are constantly evolving through development and so too must parenting skills. As the infant’s perceptual and communicative skills change, parents automatically, unconsciously adapt their own interactive style, often referred to as ‘intuitive parenting’

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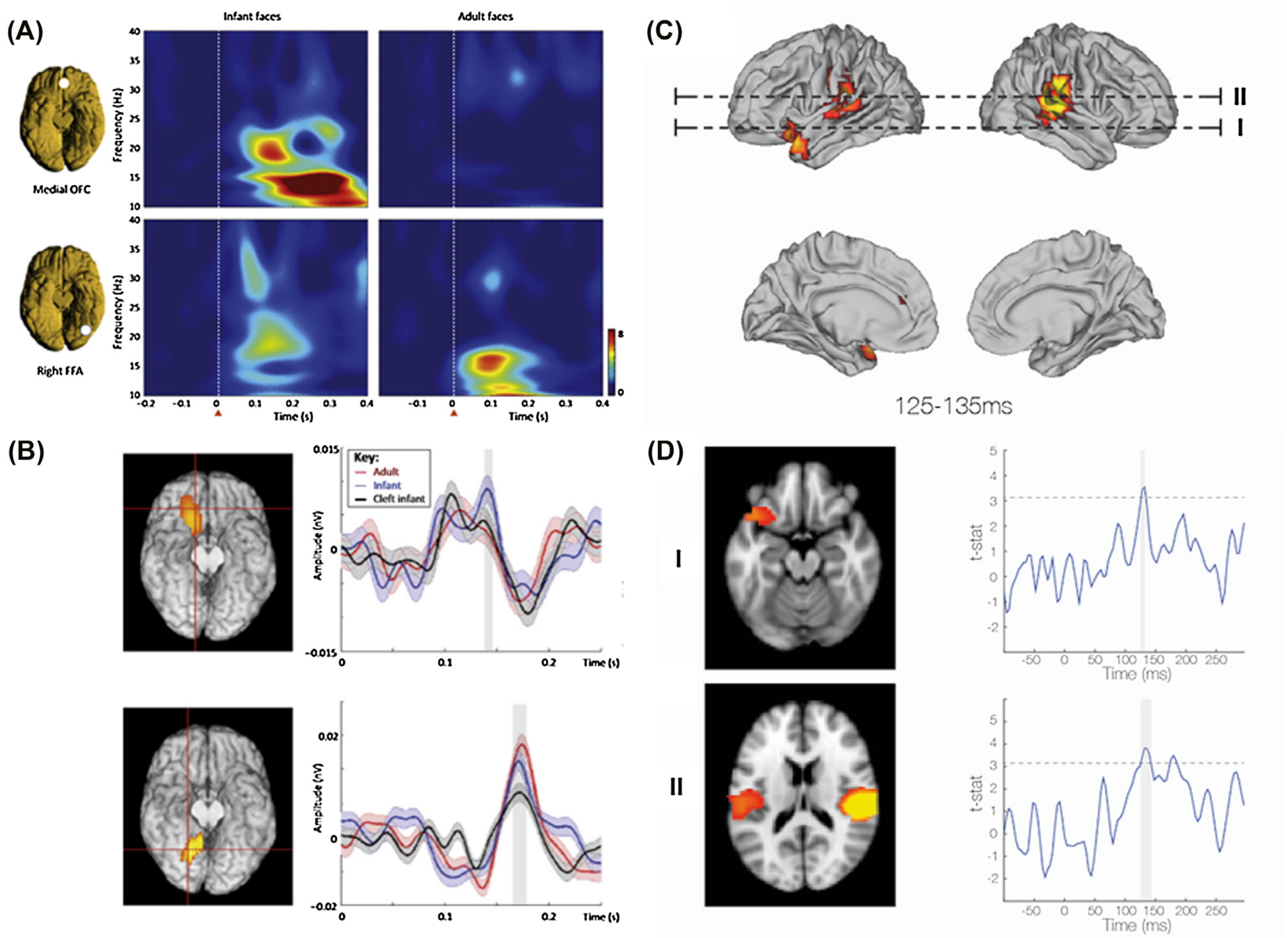

Fig. 4. Rapid salience detection of infant cues occurring around 130 ms in the OFC. (A) Rapid differentiation of infant and adult facial stimuli [93]. (B) Replication of this effect in an independent sample, demonstrating disruption to this response in the presence of an infant facial abnormality [cleft lip; [94]]. C–D) Differential cortical reactivity to infant and adult cry vocalisations was also observed in the OFC and temporal lobe regions, peaking around 130 ms [96].

[106,107]. As with any skill, the development of parenting abilities likely modifies functioning of the underlying neural circuitry (experience-dependent plasticity). Individual differences in the parental brain have been investigated in three primary domains: (1) presumed gender differences in sensitivity to infant cues, (2) the general impact of parental experience through comparison of parents and nulliparous individuals, and (3) the specific impact of experience with one's own infant through comparison of parental responses to own and unknown infant cues.

4.1. Gender differences in sensitivity to infant cues

Behavioural studies of gender differences in responding to infant cues have yielded complex results [for review, see [108]]. Where differences have been demonstrated, these tend to be small in nature, consistent with meta-analytic evidence on gender differences in non-verbal emotion processing [109]. Relatively few studies have investigated these effects at the neural level, although there is evidence to suggest that early (P1) responses to infant faces were greater in women than in men [79,98]. Functional MRI studies have also demonstrated differential responding to infant cries in the in the cingulate cortex between men and women [110,111]. While often assumed that women are both more emotionally reactive and more 'biologically primed' to care for infants, there is limited evidence to support this notion with respect to early differences in neural responding.

4.2. The effect of parenthood on early cortical responses

Parenting experience appears to afford neural processing advantages for infant stimuli. For example, mothers were found to demonstrate shorter N1 latencies in response to infant facial expressions [78] and greater amplitude of N1 peaks in response to cry vocalisations [112] and facial expressions [79] compared to non-mothers. However, other studies have demonstrated no effect of parental status on P1 responses [80]. Across both genders, greater N170 and P3a responses were observed in response to infant faces in parents (both mothers and fathers) compared to non-parents [men and women; [113]], and different patterns of hemispheric asymmetry were observed in N170 responses between mothers and non-mothers [responses were asymmetric in non-mothers, but symmetric in mothers; [80]].

While preliminary, studies including male participants (fathers and non-fathers) have shown potential interaction effects between parental status and gender. Gender differences specific to parents were observed early in time (N160, N245), with mothers showing greater responses than fathers, but no differences between genders in the nonparent group [79]. An interaction between parenthood and gender was also observed in the occipital P300 response, where mothers demonstrated greater responses to infant faces than fathers, who showed greater responses than nonparents [both men and women; [79]].

The extent to which these neural processing differences are driven by experience of caregiving or pregnancy and related neu-

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roendocrinal effects has been assessed in studies comparing neural responses to infant cues in biological and adoptive mothers. Findings to date are mixed, with one study demonstrating no significant differences in ERP responses to infant faces [114], while another showed differences in theta power recorded at frontal electrode sites in responses to smiling, crying and neutral facial expressions between biological and adoptive mothers [115]. There is evidence to suggest that amount of time spent in contact with an infant, and direct caregiving experience are important in modulating parental brain responses, at least in men. One recent fMRI study demonstrated that the amount of time fathers spent in childcare was associated with changes in functional connectivity between early sensory processing regions [116]. This supports the notion of experience-dependent plasticity in the parental brain, an effect that might usefully be investigated in longitudinal studies of the same individuals at different stages of parenthood.

4.3. *Learned sensitivity to own infant cues*

Shortly after birth, mothers and fathers can accurately recognise their own infant, even on the basis of single non-visual cues, such as smell, cry or touch [for review, see [117]]. These remarkable recognition capacities have been the subject of numerous studies comparing parental responsivity to one's own infant compared to an unfamiliar infant or adult. Overall, this work suggests that recognition or responding to own infant cues modulates activity later in time (beyond 200 ms), although again findings are mixed. One study demonstrated no impact of own vs. unknown infant on n170 or P300 responses [113], while two other studies found differential responding to own infant images from 240 to 500 ms [114] and at 600 ms [with no effect at N100/N170; [118]].

Regarding mixed findings across EEG studies discussed above, three general methodological issues can be noted. First, the sample sizes of these studies vary considerably [individual group sizes vary from N = 10 [79] to N = 47, [81]], and lack of power may be an issue particularly for effects such as gender which are typically small in nature. Second, the time windows used for analyses of ERPs vary across studies. Future investigations might benefit from greater standardization or reporting of time windows of interest [119]. In addition, the majority of EEG papers discussed here have examined ERP responses, comparing the amplitude and/or latency of waveforms of interest. Relatively fewer papers have analysed the spectral content of EEG and MEG signals. One recent paper using this approach demonstrated evidence for rapid differential responding to images of own versus unfamiliar infant faces in gamma band activity [120]. This finding is notable given that ERP analysis of the same data failed to demonstrate such an early difference [118]. Analyses of induced activity, in addition to event-related potentials, will provide us with a more comprehensive understanding of the neural mechanisms of caregiving.

5. How do neural responses relate to caregiving behaviour?

Several innovative studies have begun to address the relationship between neural responses to infant cues and behavioural measures of parenting. To date, these studies have compared neural responses either with aspects of caregiving behaviour in healthy adults or in groups of parents affected by conditions known to impact the quality of the parent-infant relationship (such as postnatal depression). An emerging body of work has begun to assess the effect of neuroendocrinal responses (particularly oxytocin) on neural responses to infant cues and caregiving behaviour [e.g., [116,121,122]].

5.1. *Altered reactivity to infant cues*

A number of studies have underlined the importance of sensory brain regions in supporting behavioural sensitivity to infant cues. For instance, fMRI studies have reported that greater activity in auditory cortex to infant cries was associated with better reported maternal care in mothers [123] and more positive parenting thoughts in fathers [124]. Studies of clinical populations have similarly implicated sensory brain regions. Reduced sensory sensitivity to infant cues was demonstrated in pregnant women with depression and in mothers found to neglect their infants. In the study of pregnant women, depressive symptomology was associated with decreased P300 responses to distressed infant faces, but with no effect for responses to happy or neutral faces or infant cry vocalisations [125]. Compared to healthy mothers, mothers who neglected their infants demonstrated reduced modulation of N170 responses to infant facial expressions and reduced LPP responses to crying compared to neutral expressions [97]. In contrast, neural markers indicative of heightened sensitivity to infant cues were observed in mothers with depressive and anxious symptoms. In one study, depressive symptomatology was positively correlated with the amplitude of N170 responses to infant faces [80]. This effect was specifically linked to cognitive and affective, and not to somatic, symptoms. Higher state anxiety in mothers has also been associated with greater LPP amplitude to infant neural expressions [81].

The apparent contradiction across these EEG studies is paralleled in fMRI studies investigating individual differences in emotional reactivity to infant cues, focusing on the amygdala. For example, reduced amygdala reactivity to infant cries was observed in mothers with higher quality relationships with their infants [126]. Increased amygdala activity has been found in mothers with postnatal depression in response to positively-valenced infant face stimuli [both own and other infant faces; [127]], and to negatively or positively-valenced own infant faces [128] compared to healthy mothers. However, not all findings relating to the amygdala have been in the same direction. Barrett and colleagues [129] reported that greater amygdala activity to own positive infant faces was related to lower maternal anxiety, lower parental distress, fewer symptoms of depressed mood, and more positive attachment feelings. Another study found a negative correlation between amygdala response to faces, albeit adult only, and postpartum depression severity, and a negative correlation between amygdala response to faces and infant-related hostility [130].

These contradictory findings require further investigation, both in understanding the network dynamics of activity across regions involved in face processing, as well as possible differences in coping strategies with depressive symptomatology in pregnancy compared to postpartum. Rutherford and colleagues [125] suggest that their findings in pregnant women with depression are associated with heightened avoidance of infant negative affect, perhaps linked to dampening of salience or emotional reactivity to infant distress cues. Noll et al. [80], who demonstrated heightened neural activity to infant cues, instead suggest that this may reflect a maladaptive sensitization to these cues, which might still behaviourally manifest in avoidance behaviour.

A further explanation for these findings may be that 'sensitive' responding to infant cues lies on a U-shaped curve, whereby too little neural reactivity to infant cues is problematic (hypo-reactivity), as is too much reactivity (hyper-reactivity). Participants experiencing depressive symptomology may fall at either end of this proposed curve and demonstrate behavioural interaction difficulties. This would account for differences in the direction of neural effects, with amygdala dysregulation nevertheless being an important mechanism disrupting parental sensitivity. Future work may also consider the impact of comorbid symptoms of anxiety,

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given that differential sensitivity to infant facial emotion has been observed across mothers with depression compared to generalized anxiety disorder [41]. Additionally, it is plausible that sub-regions within the amygdala (or regions located nearby such as the bed nucleus of the stria terminalis) are implicated in different aspects of processing, a possibility that might usefully be investigated with higher-resolution neuroimaging techniques [131,132].

5.2. *Prefrontal emotional regulation*

For frontal regions, studies overall suggest that greater reactivity to infant cries is correlated with more sensitive parenting behaviour. Greater OFC and right ventro-lateral prefrontal cortex activity was associated with higher quality of attachment between mothers and their infants [126]. A similar pattern was observed for the inferior frontal gyrus, with greater activity associated with more sensitive maternal behaviour [133] and less 'restrictive paternal attitudes' [an index of fathers' controlling/negative approach to caregiving, [134]]. In addition, more middle frontal gyrus activity was associated with better perceived maternal care in childhood [123].

Again, clinical studies have provided good evidence for the importance of specific frontal regions in responding to infant cues. In one study comparing responses to negative infant facial emotion, mothers with depression showed reduced responses to their own infant in the dorsal anterior cingulate cortex compared to healthy mothers [135]. Furthermore, greater depressive symptomology was correlated with decreased activity to an 'own infant face' in the OFC and insula, which was interpreted as deficits in self-regulatory and motivational responding. Another study by the same authors, but focused on crying, reported that mothers with depression showed less activity to infant cries in frontal (OFC, prefrontal and anterior cingulate cortices) and reward regions [nucleus accumbens; 135]. Using a different paradigm involving observation and empathizing, another fMRI study again implicated the medial prefrontal cortex and OFC, reporting that maternal depression was associated with greater deactivation of these regions relative to 'rest' [128].

Overall, these studies point to an association between more adaptive caregiving responses and both reduced subcortical and increased prefrontal reactivity to infant cues. This pattern of increased prefrontal activity, paired with decreased subcortical activity has been implicated in 'top-down' emotion regulation capacities, or the ability to control affective responses to experiences [136]. Prefrontal regions are proposed to help regulate the activity of subcortical limbic regions (particularly the amygdala), supporting shifts in emotional reactions. Dysregulation of this system is thought to underlie anxiety disorders, whereby hyper-reactivity of the amygdala to potentially threatening cues, paired with failure to regulate using prefrontal regions, is thought to disrupt regulation of emotional experiences [137]. From this perspective, greater frontal reactivity to infant cries might be considered as a measure of engagement of top-down regulation capacities. It has been suggested that the regulation of emotional responses to infant cues in the context of caregiving behaviour relies on maintaining a balance between amygdala and prefrontal cortical activity [138]. Those individuals with more adaptive parenting behaviours might engage frontal regions more effectively, possibly regulating emotional responses to infant cues.

5.3. *The role of oxytocin in sensitizing neural networks of the parental brain*

Both the oxytocinergic and dopaminergic neuroendocrine systems are thought to play key roles in the parent-infant relationship [139]. While oxytocin may be particularly involved in social processes, the dopaminergic system is more broadly involved in reward processing, reinforcement learning and decision-making [140,141]. These two systems interact across subcortical and cortical brain regions, with oxytocinergic neurons in the hypothalamus projecting to key dopaminergic reward regions of the parental brain, including the ventral tegmental area and ventral striatum [for more detailed overviews, see [6,139,142]].

Early studies of the effects of oxytocin on neural responses to infant cues considered groups of individuals thought to differ in experiences of hormonal fluctuations related to childbirth and breastfeeding. Oxytocin, among other hormones, is central in both processes and so by comparing mothers who had vaginal compared to caesarean section deliveries, and who breast fed compared to bottle fed, observed alterations in neural reactivity might be linked to hormonal differences. Both vaginal delivery and breastfeeding were found to be associated with stronger neural reactivity to the sound of infant cry vocalisations across the superior frontal gyrus and amygdala [143,144], while vaginal delivery was additionally linked to greater reactivity of the hypothalamus [143] and breastfeeding with heightened reactivity in the insula and striatum [144]. These findings from cross-sectional studies have provided an important basis for recent investigations taking peripheral measures of key neuropeptides across individuals to directly assess these relationships.

Studies have demonstrated that close contact with an infant can lead to an increase in oxytocin levels in both mothers and fathers [145], as well as in foster parents [146], demonstrating the ongoing impact of childrearing on hormonal fluctuations. One fMRI study demonstrated that mothers with secure attachment relationships (as compared to mothers with insecure/avoidant attachment) demonstrated both greater oxytocin production upon interaction with their infant and greater activation in the ventral striatum when viewing images of their own infant [147]. Similarly, an EEG study of foster mothers demonstrated that the level of oxytocin release following close contact with their infants was associated with greater P3 ERP responses (a component involved in processing stimulus salience, see Box 1) to images of infant faces [146]. In addition, intranasal oxytocin administration in women without children was associated with greater reactivity in the insula and inferior frontal gyrus and reduced reactivity in the amygdala upon hearing infant cries [148]. Together, these studies suggest that oxytocin may play a key role in sensitising reactivity of reward regions in the 'parental brain', potentially mediating the effect of parent-infant interactions on neural reactivity. This remains an active area of research, with much potential to further our understanding of how our brains adapt to accommodate the demands of parenting.

6. Future directions

While decades of studies have provided a detailed understanding of caregiving in nonhumans, investigations of the human parental brain are coming to the fore [35]. Studies of adults' brain responses to infants have primarily focused on visual cues, encompassing responses to both negatively and positively-valenced facial expressions. The other focus, albeit to a lesser extent, has been on adult responses to negative vocal affect, 'crying'. Infant crying is clearly a powerful, salient stimulus, but parental interactive behaviour is also motivated by positive infant cues (e.g. infant laughter). While not yet thoroughly investigated, responding to infant cues, both positively and negatively valenced, is likely to recruit neural reward circuitry (such as the nucleus accumbens, ventral tegmental area and OFC). Building on previous work, investigation of a range of infant cues varying in valence may help refine the proposed model of the parental brain. More widespread use of temporally-sensitive neuroimaging techniques in the investigation

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of parental experience and disrupted parental behaviour would also be useful in this regard.

The majority of studies described here are passive viewing/listening paradigms in socially isolated contexts. Such studies can of course be criticized for a lack of ecological validity, attempting to measure aspects of social behaviour in the absence of interaction with another individual [149]. One opportunity to overcome this limitation is the use of 'hyperscanning', simultaneous measurement of neural activity from two or more individuals [150]. This would be of particular interest for a broader investigation of parent-infant interactions. Combining measures of behavioural, neural, endocrinal and peripheral psychophysiological responses would also be of much interest, as it has been established that parents and infant synchronise not only in social behaviours (mirroring facial expressions and vocalisations), but also in heart rhythms and oxytocin levels; a constellation of effects known as 'biobehavioural synchrony' [6].

One major future avenue will be to conduct longitudinal studies of adults before, during and after pregnancy, combining behavioural and neuroimaging measures. Such studies are clearly challenging, but hold much promise in providing insight into the neural plasticity underpinning parenting. Similarly, investigation of the evolving relationship at key developmental stages could inform our understanding experience-dependent plasticity within the parental brain. One such stage important for social development is that of shared attention: the capacity to recognise the focus of another's attention and shift one's own attention to the same target (e.g. following another's eye-gaze [151]). This capacity is thought to develop in infants at around 18 months of age [152,153] and is considered a developmental milestone that supports learning and the understanding of others' intentions and behaviours [153]. The process of following another's eye-gaze is thought to be specific to human interactions [154], which may be of particular relevance in understanding the biological basis of human parent-infant relationships. At this stage (18 months), studies of interactions with other familiar adults, such as close family members and day care workers, might be helpful in understanding the broader impact of the 'small world network' of the infant's social experience [155].

In this review, we discuss a number of inconsistent findings. This is a key issue to address, particularly given the current concerns around replication within psychological science [156]. Methodological aspects to address in future work include: (i) using larger sample sizes, particularly for the investigation of subtle individual differences such as the effect of gender, (ii) careful matching of key demographic factors between samples that include 'control' groups and (iii) systematic manipulation of stimuli and task demands, perhaps employing parametric designs to investigate graded responses to stimulus type (as has been demonstrated in other areas of sensory processing research [157]).

7. Conclusion

In this review we summarize current models of the human parental brain, with a particular focus on studies describing the temporal dynamics underlying caregiving responses. Regions identified within fMRI studies, referred to as the 'parental brain', in general overlap with the 'social brain', with the addition of a number of survival-related subcortical regions. Rapid identification and orienting responses to infant cues might be facilitated by discriminative activity in this system, providing privileged access to brain-wide motivational states. We discuss emerging evidence for critical roles of the PAG and OFC in supporting the initiation of responsive caregiving behaviour. In addition, parenthood appears to be associated with extensive experience-dependent plasticity, affecting early stages of processing, while disruptions to parenting behaviour appear related to dysregulation in the balance of activity across prefrontal and subcortical regions. An important future aim would be to attain a level of understanding of parental behaviour that might inform clinical interventions. Longitudinal work examining different stages of parenthood, in addition to conditions challenging parenting, would be particularly helpful in this regard.

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References

[1] C. Darwin, The Expression of the Emotions in Man and Animals, John Murray, London, 1872.
[2] M. Konner, The Evolution of Childhood: Relationships, Emotion, Mind Harvard University Press, 2010.
[3] M.D. Ainsworth, S.M. Bell, D.J. Stayton, Infant-mother attachment and social development: socialization as a product of reciprocal responsiveness to signals, in: M.P.M. Richards (Ed.), The Integration of a Child into a Social World, Cambridge University Press, London, 1974, pp. 99–135.
[4] C.E. Parsons, E.A. Stark, K.S. Young, A. Stein, M.L. Kringelbach, Understanding the human parental brain: a critical role of the orbitofrontal cortex, Soc. Neurosci. 8 (6) (2013) 525–543.
[5] C.E. Parsons, K.S. Young, L. Murray, A. Stein, M.L. Kringelbach, The functional neuroanatomy of the evolving parent-infant relationship, Prog. Neurobiol. 91 (2010) 220–241.
[6] R. Feldman, The adaptive human parental brain: implications for children's social development, Trends Neurosci. (2015).
[7] M.H. Bornstein, C.-S. Hahn, O.M. Haynes, Maternal personality, parenting cognitions, and parenting practices, Dev. Psychol. 47 (3) (2011) 658.
[8] A. Stein, L.E. Malmberg, P. Leach, J. Barnes, K. Sylva, F. Team, The influence of different forms of early childcare on children's emotional and behavioural development at school entry, Child Care Health Dev. 39 (5) (2013) 676–687.
[9] A. Stein, R.M. Pearson, S.H. Goodman, E. Rapa, A. Rahman, M. McCallum, L.M. Howard, C.M. Pariante, Effects of perinatal mental disorders on the fetus and child, Lancet 384 (9956) (2014) 1800–1819.
[10] J. Soltis, The signal functions of early infant crying, Behav. Brain Sci. 27 (4) (2004) 443–458.
[11] D. Rosenstein, H. Oster, Differential facial responses to four basic tastes in newborns, Child Dev. (1988) 1555–1568.
[12] M. Lewis, S.M. Alessandri, M.W. Sullivan, Violation of expectancy, loss of control, and anger expressions in young infants, Dev. Psychol. 26 (5) (1990) 745.
[13] A.N. Meltzoff, M.K. Moore, Imitation of facial and manual gestures by human neonates, Science 198 (4312) (1977) 75–78.
[14] C. Trevarthen, Descriptive analyses of infant communicative behavior, in: H.R. Schaffer (Ed.), Studies in Mother-Infant Interaction, Academic Press, London, 1977, pp. 227–270.
[15] T. Nakata, S.E. Trehub, Infants' responsiveness to maternal speech and singing, Infant Behav. Dev. 27 (4) (2004) 455–464.
[16] P.K. Kuhl, Early language acquisition: cracking the speech code, Nat. Rev. Neurosci. 5 (11) (2004) 831–843.
[17] C. Trevarthen, K.J. Aitken, Infant intersubjectivity: research, theory, and clinical applications, J. Child Psychol. Psychiatry 42 (1) (2001) 3–48.
[18] J. Bowlby, Attachment and loss: retrospect and prospect, Am. J. Orthopsychiatry 52 (4) (1982) 664.
[19] H.L. Golub, M.J. Corwin, A physioacoustic model of the infant cry, in: B.M. Lester, C.F. Boukydis (Eds.), Infant Crying: Theoretical and Research Perspectives, Plenum Press, New York, 1985, pp. 59–82.
[20] O. Wasz-Höckert, K. Michelsson, J. Lind, Twenty-five years of Scandinavian cry research, in: B.M. Lester, C.F. Boukydis (Eds.), Infant Crying: Theoretical and Research Perspectives, Plenum Press, New York, 1985, pp. 83–104.
[21] S.M. Bell, M.D. Ainsworth, Infant crying and maternal responsiveness, Child Dev. 43 (4) (1972) 1171–1190.
[22] P.F. Ostwald, T. Murray, The communicative and diagnostic significance of infant sounds, in: B.M. Lester, C.F. Boukydis (Eds.), Infant Crying: Theoretical and Research Perspectives, Plenum Press, New York, 1985, pp. 139–158.
[23] D.K. Oller, R.E. Eilers, The role of audition in infant babbling, Child Dev. 59 (2) (1988) 441–449.
[24] E.E. Nwokah, H.C. Hsu, O. Dobrowolska, A. Fogel, The development of laughter in mother-infant communication: timing parameters and temporal sequences, Infant Behav. Dev. 17 (1) (1994) 23–35.
[25] C.E. Izard, The Face of Emotion, Appleton-Century-Crofts, New York, 1971.
[26] P.S. Zeskind, T.R. Marshall, The relation between variations in pitch and maternal perceptions of infant crying, Child Dev. 59 (1) (1988) 193–196.

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[27] F.L. Porter, R.H. Miller, R.E. Marshall, Neonatal pain cries: effect of circumcision on acoustic features and perceived urgency, Child Dev. 57 (3) (1986) 790–802.
[28] K.S. Young, C.E. Parsons, A. Stein, M.L. Kringelbach, Interpreting infant vocal distress: the ameliorative effect of musical training in depression, Emotion 12 (6) (2012) 1200.
[29] C.E. Parsons, K.S. Young, E.-M.E. Jegindø, P. Vuust, A. Stein, M.L. Kringelbach, Music training and empathy positively impact adults' sensitivity to infant distress, Front. Psychol. 5 (2014).
[30] T.R. Alley, Head shape and the perception of cuteness, Dev. Psychol. 17 (5) (1981) 650.
[31] B. Hückstedt, Experimental studies of the infant body image, Z. Exp. Angew. Psychol. 12 (3) (1964) 421–450.
[32] M.L. Glocker, D.D. Langleben, K. Ruparel, J.W. Loughead, R.C. Gur, N. Sachser, Baby schema in infant faces induces cuteness perception and motivation for caretaking in adults, Ethology 115 (3) (2009) 257–263.
[33] S.H. Sternglanz, J.L. Gray, M. Murakami, Adult preferences for infantile facial features: an ethological approach, Anim. Behav. 25 (1977) 108–115.
[34] K.A. Hildebrandt, H.E. Fitzgerald, Adults' responses to infants varying in perceived cuteness, Behav. Process. 3 (2) (1978) 159–172.
[35] M.L. Kringelbach, E.A. Stark, C. Alexander, M.H. Bornstein, A. Stein, On cuteness unlocking the parental brain and beyond, Trends Cogn. Sci. (2016).
[36] D.S. Messinger, Positive and negative. Infant facial expressions and emotions, Curr. Dir. Psychol. Sci. 11 (1) (2002) 1–6.
[37] M.W. Sullivan, M. Lewis, Contextual determinants of anger and other negative expressions in young infants, Dev. Psychol. 39 (4) (2003) 693.
[38] J.S. Lobmaier, R. Sprengelmeyer, B. Wiffen, D.I. Perrett, Female and male responses to cuteness, age and emotion in infant faces, Evol. Hum. Behav. 31 (1) (2010) 16–21.
[39] C.E. Parsons, K.S. Young, N. Kumari, A. Stein, M.L. Kringelbach, The motivational salience of infant faces is similar for men and women, PLoS One 6 (5) (2011) e20632.
[40] R. Sprengelmeyer, D. Perrett, E. Fagan, R. Cornwell, J. Lobmaier, A. Sprengelmeyer, H. Aasheim, I. Black, L. Cameron, S. Crow, The cutest little baby face a hormonal link to sensitivity to cuteness in infant faces, Psychol. Sci. 20 (2) (2009) 149–154.
[41] A. Arteche, J. Joormann, A. Harvey, M. Craske, I.H. Gotlib, A. Lehtonen, N. Counsell, A. Stein, The effects of postnatal maternal depression and anxiety on the processing of infant faces, J. Affect. Disord. 133 (1–2) (2011) 197–203.
[42] K. Lorenz, Die angeborenen formen Möglicher erfahrung. [Innate forms of potential experience], Z. Tierpsychol. 5 (1943) 235–519.
[43] A.D. Murray, Infant crying as an elicitor of parental behavior: an examination of two models, Psychol. Bull. 86 (1) (1979) 191.
[44] A.D. Murray, Aversiveness is in the mind of the beholder: perception of infant crying by adults, in: B.M. Lester, C.F. Boukydis (Eds.), Infant Crying: Theoretical and Research Perspectives, Plenum Press, New York, 1985, pp. 217–239.
[45] L.F. Barrett, B. Mesquita, K.N. Ochsner, J.J. Gross, The experience of emotion, Annu. Rev. Psychol. 58 (2007) 373.
[46] E.T. Rolls, Précis of The brain and emotion, Behav. Brain Sci. 23 (02) (2000) 177–191.
[47] J.E. LeDoux, Emotion circuits in the brain, Annu. Rev. Neurosci. 23 (1) (2000) 155–184.
[48] L.F. Barrett, M. Bar, See it with feeling: affective predictions during object perception, Philos. Trans. R. Soc. B: Biol. Sci. 364 (1521) (2009) 1325–1334.
[49] M. Pereira, A. Ferreira, Neuroanatomical and neurochemical basis of parenting: dynamic coordination of motivational, affective and cognitive processes, Horm. Behav. 77 (2016) 72–85.
[50] P. Kim, L. Strathearn, J.E. Swain, The maternal brain and its plasticity in humans, Horm. Behav. 77 (2016) 113–123.
[51] C.E. Parsons, K.S. Young, A. Stein, M.L. Kringelbach, Intuitive parenting: understanding the neural mechanisms of parents' adaptive responses to infants, Curr. Opin. Psychol. (2017), in press.
[52] D.M. Amodio, C.D. Frith, Meeting of minds: the medial frontal cortex and social cognition, Nat. Rev. Neurosci. 7 (4) (2006) 268–277.
[53] R. Adolphs, Cognitive neuroscience of human social behaviour, Nat. Rev. Neurosci. 4 (3) (2003) 165–178.
[54] C.D. Frith, The social brain? Philos. Trans. R. Soc. B: Biol. Sci. 362 (1480) (2007) 671–678.
[55] U. Frith, C. Frith, The social brain: allowing humans to boldly go where no other species has been, Philos. Trans. R. Soc. B: Biol. Sci. 365 (1537) (2010) 165–175.
[56] G. Yovel, P. Belin, A unified coding strategy for processing faces and voices, Trends Cogn. Sci. 17 (6) (2013) 263–271.
[57] T. Ethofer, S. Anders, S. Wiethoff, M. Erb, C. Herbert, R. Saur, W. Grodd, D. Wildgruber, Effects of prosodic emotional intensity on activation of associative auditory cortex, Neuroreport 17 (3) (2006) 249–253.
[58] S. Frühholz, W. Trost, D. Grandjean, The role of the medial temporal limbic system in processing emotions in voice and music, Prog. Neurobiol. 123 (0) (2014) 1–17.
[59] P. Belin, S. Fecteau, C. Bedard, Thinking the voice: neural correlates of voice perception, Trends Cogn. Sci. 8 (3) (2004) 129–135.
[60] P. Fusar-Poli, A. Placentino, F. Carletti, P. Landi, M. Abbamonte, Functional atlas of emotional faces processing: a voxel-based meta-analysis of 105 functional magnetic resonance imaging studies, J. Psychiatry Neurosci. 34 (6) (2009) 418.
[61] S. Frühholz, D. Grandjean, Processing of emotional vocalizations in bilateral inferior frontal cortex, Neurosci. Biobehav. Rev. 37 (10 Pt. 2) (2013) 2847–2855.
[62] A. Schirmer, S.A. Kotz, Beyond the right hemisphere: brain mechanisms mediating vocal emotional processing, Trends Cogn. Sci. 10 (1) (2006) 24–30.
[63] S. Frühholz, M. Gschwind, D. Grandjean, Bilateral dorsal and ventral fiber pathways for the processing of affective prosody identified by probabilistic fiber tracking, Neuroimage (2015).
[64] J.K. Rilling, L.J. Young, The biology of mammalian parenting and its effect on offspring social development, Science 345 (6198) (2014) 771–776.
[65] J.S. Lonstein, F. Lévy, A.S. Fleming, Common and divergent psychobiological mechanisms underlying maternal behaviors in non-human and human mammals, Horm. Behav. 73 (2015) 156–185.
[66] C.E. Parsons, K.S. Young, M. Joensson, E. Brattico, J.A. Hyam, A. Stein, A.L. Green, T.Z. Aziz, M.L. Kringelbach, Ready for action: a role for the human midbrain in responding to infant vocalizations, Soc. Cogn. Affect. Neurosci. 9 (7) (2014) 977–984.
[67] J.S. Lonstein, J.M. Stern, Role of the midbrain periaqueductal gray in maternal nurturance and aggression: C-fos and electrolytic lesion studies in lactating rats, J. Neurosci. 17 (9) (1997) 3364–3378.
[68] C.M. Miranda-Paiva, N.S. Canteras, M.H. Sukikara, A.G. Nasello, I.I. Mackowiak, L.F. Felicio, Periaqueductal gray cholecystokinin infusions block morphine-induced disruption of maternal behavior, Peptides 28 (3) (2007) 657–662.
[69] M.H. Sukikara, S.R. Mota-Ortiz, M.V. Baldo, L.F. Felicio, N.S. Canteras, The periaqueductal gray and its potential role in maternal behavior inhibition in response to predatory threats, Behav. Brain Res. 209 (2) (2010) 226–233.
[70] E. Dujardin, U. Jürgens, Afferents of vocalization-controlling periaqueductal regions in the squirrel monkey, Brain Res. 1034 (1–2) (2005) 114–131.
[71] C. Cavada, T. Compañy, J. Tejedor, R.J. Cruz-Rizzolo, F. Reinoso-Suárez, The anatomical connections of the macaque monkey orbitofrontal cortex. A review, Cereb. Cortex 10 (3) (2000) 220–242.
[72] B. Bleichfeld, B.E. Moely, Psychophysiological responses to an infant cry: comparison of groups of women in different phases of the maternal cycle, Dev. Psychol. 20 (6) (1984) 1082–1091.
[73] T. Del Vecchio, A. Walter, S.G. O'Leary, Affective and physiological factors predicting maternal response to infant crying, Infant Behav. Dev. 32 (1) (2009) 117–122.
[74] A.R. Wiesenfeld, C.Z. Malatesta, L.L. DeLoach, Differential parental response to familial and unfamiliar infant distress signals, Infant Behav. Dev. 4 (3) (1981) 281–295.
[75] J.J. Furedy, A.S. Fleming, D. Ruble, H. Scher, J. Daly, D. Day, R. Loewen, Sex differences in small-magnitude heart-rate responses to sexual and infant-related stimuli: a psychophysiological approach, Physiol. Behav. 46 (5) (1989) 903–905.
[76] K.J. Joosen, J. Mesman, M.J. Bakermans-Kranenburg, S. Pieper, P.S. Zeskind, M.H. Van Ijzendoorn, Physiological reactivity to infant crying and observed maternal sensitivity, Infancy 18 (2012).
[77] M.J. Bakermans-Kranenburg, M.H. van Ijzendoorn, M.M.E. Riem, M. Tops, L.R.A. Alink, Oxytocin decreases handgrip force in reaction to infant crying in females without harsh parenting experiences, Soc. Cogn. Affect. Neurosci. 7 (8) (2012) 951–957.
[78] M.J. Peltola, S. Yrttiaho, K. Puura, A.M. Proverbio, N. Mononen, T. Lehtimäki, J.M. Leppänen, Motherhood and oxytocin receptor genetic variation are associated with selective changes in electrocortical responses to infant facial expressions, Emotion 14 (3) (2014) 469.
[79] A.M. Proverbio, V. Brignone, S. Matarazzo, M. Del Zotto, A. Zani, Gender and parental status affect the visual cortical response to infant facial expression, Neuropsychologia 44 (14) (2006) 2987–2999.
[80] L.K. Noll, L.C. Mayes, H.J. Rutherford, Investigating the impact of parental status and depression symptoms on the early perceptual coding of infant faces: an event-related potential study, Soc. Neurosci. 7 (5) (2012) 525–536.
[81] S.M. Malak, M.J. Crowley, L.C. Mayes, H.J. Rutherford, Maternal anxiety and neural responses to infant faces, J. Affect. Disord. 172 (2015) 324–330.
[82] M.L. Kringelbach, The human orbitofrontal cortex: linking reward to hedonic experience, Nat. Rev. Neurosci. 6 (9) (2005) 691–702.
[83] P.H. Rudebeck, E.A. Murray, The orbitofrontal oracle: cortical mechanisms for the prediction and evaluation of specific behavioral outcomes, Neuron 84 (6) (2014) 1143–1156.
[84] K.C. Berridge, M.L. Kringelbach, Pleasure systems in the brain, Neuron 86 (3) (2015) 646–664.
[85] D.H. Zald, J.V. Pardo, The neural correlates of aversive auditory stimulation, Neuroimage 16 (3 Pt. 1) (2002) 746–753.
[86] M. Bar, The proactive brain: using analogies and associations to generate predictions, Trends Cogn. Sci. 11 (7) (2007) 280–289.
[87] R. Adolphs, Neural systems for recognizing emotion, Curr. Opin. Neurobiol. 12 (2) (2002) 169–177.
[88] M. Chaumon, K. Kveraga, L. Barrett, M. Bar, Visual predictions in the orbitofrontal cortex rely on associative content, Cereb. Cortex (2013).
[89] M. Bar, K.S. Kassam, A.S. Ghuman, J. Boshyan, A.M. Schmid, A.M. Dale, M.S. Hämäläinen, K. Marinkovic, D.L. Schacter, B.R. Rosen, Top-down facilitation of visual recognition, Proc. Natl. Acad. Sci. U. S. A. 103 (2) (2006) 449–454.
[90] F. D'Hondt, M. Lassonde, O. Collignon, F. Lepore, J. Honoré, H. Sequeira, Emotions guide us: behavioral and MEG correlates, Cortex 49 (9) (2013) 2473–2483.

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[91] M.L. Kringelbach, E.T. Rolls, Neural correlates of rapid reversal learning in a simple model of human social interaction, Neuroimage 20 (2) (2003) 1371–1383.
[92] K.C. Berridge, M.L. Kringelbach, Affective neuroscience of pleasure: reward in humans and animals, Psychopharmacology 199 (3) (2008) 457–480.
[93] M.L. Kringelbach, A. Lehtonen, S. Squire, A.G. Harvey, M.G. Craske, I.E. Holliday, A.L. Green, T.Z. Aziz, P.C. Hansen, P.L. Cornelissen, A specific and rapid neural signature for parental instinct, PLoS One 3 (2) (2008) e1664.
[94] C.E. Parsons, K.S. Young, H. Mohseni, M.W. Woolrich, K.R. Thomsen, M. Joensson, L. Murray, T. Goodacre, A. Stein, M.L. Kringelbach, Minor structural abnormalities in the infant face disrupt neural processing: a unique window into early caregiving responses, Soc. Neurosci. 8 (4) (2013) 268–274.
[95] B. Libet, Reflections on the interaction of the mind and brain, Prog. Neurobiol. 78 (3) (2006) 322–326.
[96] K.S. Young, C.E. Parsons, E.-M.J. Elmholdt, M.W. Woolrich, T.J. van Hartevelt, A.B. Stevner, A. Stein, M.L. Kringelbach, Evidence for a caregiving instinct: rapid differentiation of infant from adult vocalizations using magnetoencephalography, Cereb. Cortex (2015) bhv306.
[97] M.J. Rodrigo, I. León, I. Quiñones, A. Lage, S. Byrne, M.A. Bobes, Brain and personality bases of insensitivity to infant cues in neglectful mothers: an event-related potential study, Dev. Psychopathol. 23 (01) (2011) 163–176.
[98] A.M. Proverbio, F. Riva, A. Zani, E. Martin, Is it a baby? Perceived age affects brain processing of faces differently in women and men, J. Cogn. Neurosci. 23 (11) (2011) 3197–3208.
[99] A. Caria, S. de Falco, P. Venuti, S. Lee, G. Esposito, P. Rigo, N. Birbaumer, M.H. Bornstein, Species-specific response to human infant faces in the premotor cortex, Neuroimage 60 (2) (2012) 884–893.
[100] K.R. Scherer, Appraisal considered as a process of multilevel sequential checking., in: K.R. Scherer, A. Schorr, T. Johnstone (Eds.), Appraisal Processes in Emotion: Theory, Methods, Research, Oxford University Press, New York, 2001, pp. 92–120.
[101] I. Messina, L. Cattaneo, P. Venuti, N. de Pisapia, M. Serra, G. Esposito, P. Rigo, A. Farneti, M.H. Bornstein, Sex-specific automatic responses to infant cries: TMS reveals greater excitability in females than males in motor evoked potentials, Front. Psychol. 6 (2015).
[102] P. Schuetze, P.S. Zeskind, Relations between women's depressive symptoms and perceptions of infant distress signals varying in pitch, Infancy 2 (4) (2001) 483–499.
[103] K.S. Young, C.E. Parsons, A. Stein, M.L. Kringelbach, Motion and emotion: depression reduces psychomotor performance and alters affective movements in caregiving interactions, Front. Behav. Neurosci. 9 (February) (2015).
[104] C.E. Parsons, K.S. Young, E. Parsons, A. Stein, M.L. Kringelbach, Listening to infant distress vocalizations enhances effortful motor performance, Acta Paediatrica: Int. J. Paediatr. 101 (4) (2012) e189–e191.
[105] C.E. Parsons, K.S. Young, N. Kumari, A. Stein, M.L. Kringelbach, The motivational salience of infant faces is similar for men and women, PLoS One 6 (5) (2011).
[106] M. Papousek, Communication in early infancy: an arena of intersubjective learning, Infant Behav. Dev. 30 (2) (2007) 258–266.
[107] C. Trevarthen, L. Murray, P. Hubley, Psychology of infants, Sci. Found. Clin. Paediatr. 2 (1981) 211–274.
[108] C.E. Parsons, K.S. Young, E.M. Jegindoe Elmholdt, A. Stein, M.L. Kringelbach, Interpreting infant emotional expressions: parenthood has differential effects on men and women, Q. J. Exp. Psychol. (2016) 1–11.
[109] A.E. Thompson, D. Voyer, Sex differences in the ability to recognise non-verbal displays of emotion: a meta-analysis, Cogn. Emotion 28 (7) (2014) 1164–1195.
[110] E. Seifritz, F. Esposito, J.G. Neuhoff, A. Lüthi, H. Mustovic, G. Dammann, U. Von Bardeleben, E.W. Radue, S. Cirillo, G. Tedeschi, Differential sex-independent amygdala response to infant crying and laughing in parents versus nonparents, Biol. Psychiatry 54 (12) (2003) 1367–1375.
[111] N. De Pisapia, M.H. Bornstein, P. Rigo, G. Esposito, S. De Falco, P. Venuti, Gender differences in directional brain responses to infant hunger cries, Neuroreport 24 (3) (2013) 142.
[112] M. Purhonen, R. Kilpeläinen-Lees, A. Pääkkönen, H. Yppärilä, J. Lehtonen, J. Karhu, Effects of maternity on auditory event-related potentials to human sound, Neuroreport 12 (13) (2001) 2975–2979.
[113] O. Weisman, R. Feldman, A. Goldstein, Parental and romantic attachment shape brain processing of infant cues, Biol. Psychol. 89 (3) (2012) 533–538.
[114] D.J. Grasso, J.S. Moser, M. Dozier, R. Simons, ERP correlates of attention allocation in mothers processing faces of their children, Biol. Psychol. 81 (2) (2009) 95–102.
[115] M. Hernández-González, R. Hidalgo-Aguirre, M. Guevara, M. Pérez-Hernández, C. Amezcua-Gutiérrez, Observing videos of a baby crying or smiling induces similar but not identical, electroencephalographic responses in biological and adoptive mothers, Infant Behav. Dev. 42 (2016) 1–10.
[116] E. Abraham, T. Hendler, I. Shapira-Lichter, Y. Kanat-Maymon, O. Zagoory-Sharon, R. Feldman, Father's brain is sensitive to childcare experiences, Proc. Natl. Acad. Sci. U. S. A. 111 (27) (2014) 9792–9797.
[117] C.E. Parsons, K.S. Young, L. Murray, A. Stein, M.L. Kringelbach, The functional neuroanatomy of the evolving parent-infant relationship, Prog. Neurobiol. 91 (3) (2010) 220–241.
[118] M.H. Bornstein, M.E. Arterberry, C. Mash, Differentiated brain activity in response to faces of own versus unfamiliar babies in primipara mothers: an electrophysiological study, Dev. Neuropsychol. 38 (6) (2013) 365–385.
[119] J. Gross, S. Baillet, G.R. Barnes, R.N. Henson, A. Hillebrand, O. Jensen, K. Jerbi, V. Litvak, B. Maess, R. Oostenveld, Good practice for conducting and reporting MEG research, Neuroimage 65 (2013) 349–363.
[120] G. Esposito, S. Valenzi, T. Islam, C. Mash, M. Bornstein, Immediate and selective maternal brain responses to own infant faces, Behav. Brain Res. 278 (2015) 40–43.
[121] P.A. Bos, E.J. Hermans, E.R. Montoya, N.F. Ramsey, J. van Honk, Testosterone administration modulates neural responses to crying infants in young females, Psychoneuroendocrinology 35 (1) (2010) 114–121.
[122] P.A. Bos, E.R. Montoya, D. Terburg, J. van Honk, Cortisol administration increases hippocampal activation to infant crying in males depending on childhood neglect, Hum. Brain Mapp. 35 (10) (2014) 5116–5126.
[123] P. Kim, J.F. Leckman, L.C. Mayes, M.A. Newman, R. Feldman, J.E. Swain, Perceived quality of maternal care in childhood and structure and function of mothers' brain, Dev. Sci. 13 (4) (2010) 662–673.
[124] P. Kim, P. Rigo, J.F. Leckman, L.C. Mayes, P.M. Cole, R. Feldman, J.E. Swain, A prospective longitudinal study of perceived infant outcomes at 18–24 months: neural and psychological correlates of parental thoughts and actions assessed during the first month postpartum, Front. Psychol. 6 (2015).
[125] H.J. Rutherford, K.M. Graber, L.C. Mayes, Depression symptomatology and the neural correlates of infant face and cry perception during pregnancy, Soc. Neurosci. 11 (4) (2016) 467–474.
[126] H.K. Laurent, J.C. Ablow, The missing link: mothers' neural response to infant cry related to infant attachment behaviors, Infant Behav. Dev. 35 (4) (2012) 761–772.
[127] K.E. Wonch, C.B. de Medeiros, J.A. Barrett, A. Dudin, W.A. Cunningham, G.B. Hall, M. Steiner, A.S. Fleming, Postpartum depression and brain response to infants: differential amygdala response and connectivity, Soc. Neurosci. (2016) 1–18.
[128] D. Lenzi, C. Trentini, E. Macaluso, S. Graziano, A.M. Speranza, P. Pantano, M. Ammaniti, Mothers with depressive symptoms display differential brain activations when empathizing with infant faces, Psychiatry Res.: Neuroimaging 249 (2016) 1–11.
[129] J. Barrett, K.E. Wonch, A. Gonzalez, N. Ali, M. Steiner, G.B. Hall, A.S. Fleming, Maternal affect and quality of parenting experiences are related to amygdala response to infant faces, Soc. Neurosci. 7 (3) (2012) 252–268.
[130] E.L. Moses-Kolko, S.B. Perlman, K.L. Wisner, J. James, A.T. Saul, M.L. Phillips, Abnormally reduced dorsomedial prefrontal cortical activity and effective connectivity with amygdala in response to negative emotional faces in postpartum depression, Am. J. Psychiatry (2010).
[131] S. Koelsch, Towards a neural basis of music-evoked emotions, Trends Cogn. Sci. 14 (3) (2010) 131–137.
[132] M. Lebow, A. Chen, Overshadowed by the amygdala: the bed nucleus of the stria terminalis emerges as key to psychiatric disorders, Mol. Psychiatry 21 (4) (2016) 450–463.
[133] E.D. Musser, H. Kaiser-Laurent, J.C. Ablow, The neural correlates of maternal sensitivity: an fMRI study, Develop. Cogn. Neurosci. 2 (4) (2012) 428–436.
[134] J.S. Mascaro, P.D. Hackett, H. Gouzoules, A. Lori, J.K. Rilling, Behavioral and genetic correlates of the neural response to infant crying among human fathers, Soc. Cogn. Affect. Neurosci. 9 (11) (2014) 1704–1712.
[135] H.K. Laurent, J.C. Ablow, A cry in the dark: depressed mothers show reduced neural activation to their own infant's cry, Soc. Cogn. Affect. Neurosci. 7 (2) (2012) 125–134.
[136] K.N. Ochsner, J.A. Silvers, J.T. Buhle, Functional imaging studies of emotion regulation: a synthetic review and evolving model of the cognitive control of emotion, Ann. N. Y. Acad. Sci. 1251 (1) (2012) E1–E24.
[137] H. Jazaieri, A.S. Morrison, P.R. Goldin, J.J. Gross, The role of emotion and emotion regulation in social anxiety disorder, Curr. Psychiatry Rep. 17 (1) (2015) 1–9.
[138] P. Pechtel, L.M. Murray, L.E. Brumariu, K. Lyons-Ruth, Reactivity, regulation, and reward responses to infant cues among mothers with and without psychopathology: an fMRI review, Trans. Develop. Psychiatry 1 (2013).
[139] L. Strathearn, Maternal neglect: oxytocin, dopamine and the neurobiology of attachment, J. Neuroendocrinol. 23 (11) (2011) 1054–1065.
[140] M.H. Van IJzendoorn, M.J. Bakermans-Kranenburg, A sniff of trust: meta-analysis of the effects of intranasal oxytocin administration on face recognition, trust to in-group, and trust to out-group, Psychoneuroendocrinology 37 (3) (2012) 438–443.
[141] R. Wigton, J. Radua, P. Allen, B. Averbeck, A. Meyer-Lindenberg, P. McGuire, S.S. Shergill, P. Fusar-Poli, Neurophysiological effects of acute oxytocin administration: systematic review and meta-analysis of placebo-controlled imaging studies, J. Psychiatry Neurosci. 40 (1) (2015) E1–22.
[142] M. Galbally, A.J. Lewis, M.V. IJzendoorn, M. Permezel, The role of oxytocin in mother-infant relations: a systematic review of human studies, Harv. Rev. Psychiatry 19 (1) (2011) 1–14.
[143] J.E. Swain, E. Tasgin, L.C. Mayes, R. Feldman, R. Todd Constable, J.F. Leckman, Maternal brain response to own baby-cry is affected by cesarean section delivery, J. Child Psychol. Psychiatry 49 (10) (2008) 1042–1052.
[144] P. Kim, R. Feldman, L.C. Mayes, V. Eicher, N. Thompson, J.F. Leckman, J.E. Swain, Breastfeeding, brain activation to own infant cry, and maternal sensitivity, J. Child Psychol. Psychiatry 52 (8) (2011) 907–915.
[145] R. Feldman, I. Gordon, I. Schneiderman, O. Weisman, O. Zagoory-Sharon, Natural variations in maternal and paternal care are associated with

Please cite this article in press as: K.S. Young, et al., The neural basis of responsive caregiving behaviour: Investigating temporal dynamics within the parental brain, Behav Brain Res (2016), http://dx.doi.org/10.1016/j.bbr.2016.09.012

systematic changes in oxytocin following parent?infant contact, Psychoneuroendocrinology 35 (8) (2010) 1133–1141.
[146] J. Bick, M. Dozier, K. Bernard, D. Grasso, R. Simons, Foster mother-infant bonding: associations between foster mothers' oxytocin production, electrophysiological brain activity, feelings of commitment, and caregiving quality, Child Dev. 84 (3) (2013) 826–840.
[147] L. Strathearn, P. Fonagy, J. Amico, P.R. Montague, Adult attachment predicts maternal brain and oxytocin response to infant cues, Neuropsychopharmacology 34 (13) (2009) 2655–2666.
[148] M.M.E. Riem, M.J. Bakermans-Kranenburg, S. Pieper, M. Tops, M.A. Boksem, R.R. Vermeiren, M.H. van IJzendoorn, S.A. Rombouts, Oxytocin modulates amygdala, insula, and inferior frontal gyrus responses to infant crying: a randomized controlled trial, Biol. Psychiatry 70 (3) (2011) 291–297.
[149] L. Schilbach, A second-person approach to other minds, Nat. Rev. Neurosci. 11 (6) (2010) 449.
[150] I. Konvalinka, A. Roepstorff, The two-brain approach: how can mutually interacting brains teach us something about social interaction? Front. Hum. Neurosci. 6 (2012).
[151] M. Tomasello, Joint attention as social cognition, in: C. Moore, P. Dunham (Eds.), Joint Attention: Its Origins and Role in Development, Lawrence Erlbaum Associates, Hillsdale, NJ, 1995, pp. 103–130.
[152] U. Frith, C.D. Frith, Development and neurophysiology of mentalizing, Philos. Trans. R. Soc. Lond. B: Biol. Sci. 358 (1431) (2003) 459–473.
[153] M. Tomasello, M. Carpenter, J. Call, T. Behne, H. Moll, Understanding and sharing intentions: the origins of cultural cognition, Behav. Brain Sci. 28 (05) (2005) 675–691.
[154] M. Tomasello, B. Hare, H. Lehmann, J. Call, Reliance on head versus eyes in the gaze following of great apes and human infants: the cooperative eye hypothesis, J. Hum. Evol. 52 (3) (2007) 314–320.
[155] H. Lagercrantz, Connecting the brain of the child from synapses to screen-based activity, Acta Paediatr. (2016).
[156] S.E. Maxwell, M.Y. Lau, G.S. Howard, Is psychology suffering from a replication crisis? What does failure to replicate really mean? Am. Psychol. 70 (6) (2015) 487.
[157] S.G. Horovitz, B. Rossion, P. Skudlarski, J.C. Gore, Parametric design and correlational analyses help integrating fMRI and electrophysiological data during face processing, Neuroimage 22 (4) (2004) 1587–1595.
[158] S.J. Luck, An Introduction to the Event-related Potential Technique, MIT press, 2014.
[159] D. Tomé, F. Barbosa, K. Nowak, J. Marques-Teixeira, The development of the N1 and N2 components in auditory oddball paradigms: a systematic review with narrative analysis and suggested normative values, J. Neural Transm. 122 (3) (2015) 375–391.
[160] R.J. Itier, M.J. Taylor, N170 or N1? Spatiotemporal differences between object and face processing using ERPs, Cereb. Cortex 14 (2) (2004) 132–142.
[161] S. Sur, V. Sinha, Event-related potential: an overview, Ind. Psychiatry J. 18 (1) (2009) 70.
[162] G. Hajcak, A. MacNamara, D.M. Olvet, Event-related potentials, emotion, and emotion regulation: an integrative review, Dev. Neuropsychol. 35 (2) (2010) 129–155.