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Research report

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

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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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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]].

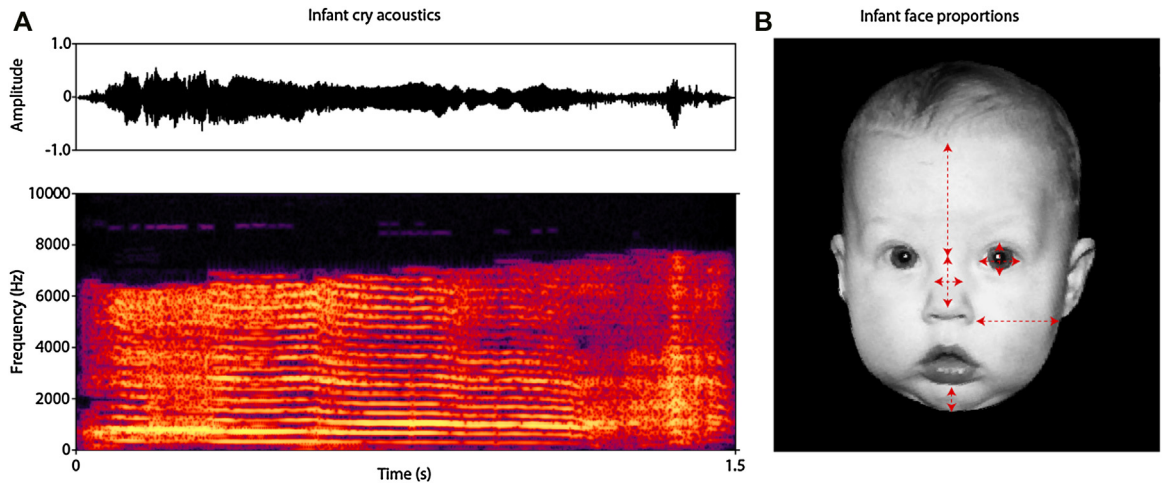

Fig. 1. Examples of infant communicative cues. (A) Waveform (upper) and spectrogram (lower) of a typical infant cry burst, characterized by high and variable pitch. (B) Demonstration of the physical features of a typical infant face, reflecting the 'infant schema': large rounded forehead and cheeks,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

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