



The functional neuroanatomy of the evolving parent–infant relationship

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ABSTRACT

Infant survival and the development of secure and cooperative relationships are central to the future of the species. In humans, this relies heavily on the evolving early parent–infant social and affective relationship. While much is known about the behavioural and psychological components of this relationship, relatively little is known about the underlying functional neuroanatomy. Affective and social neuroscience has helped to describe the main adult brain networks involved, but has so far engaged very little with developmental findings. In this review, we seek to highlight future avenues for research by providing a coherent framework for describing the parent–infant relationship over the first 18 months. We provide an outline of the evolving nature of the relationship, starting with basic orienting and recognition processes, and culminating in the infant's attainment of higher socio-emotional and cognitive capacities. Key social and affective interactions, such as communication, cooperative play and the establishment of specific attachments propel the development of the parent–infant relationship. We summarise our current knowledge of the developing infant brain in terms of structure and function, and how these relate to the emergent abilities necessary for the formation of a secure and cooperative relationship with parents or other caregivers. Important roles have been found for brain regions including the orbitofrontal, cingulate, and insular cortices in parent–infant interactions, but it has become clear that much more information is needed about the developmental time course and connectivity of these regions.

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Abbreviations: PFC, prefrontal cortex; OFC, orbitofrontal cortex; ERP, event-related potential; Nc, negative central; NIRS, near-infrared spectroscopy; PET, positron emission tomography; fMRI, functional magnetic resonance imaging; IFG, inferior frontal gyrus; EEG, electroencephalography; STG, superior temporal gyrus; MEG, magnetoencephalography; BOLD, blood-oxygen-level dependent; DTI, diffusion tensor imaging; SSP, strange situation paradigm; AQS, attachment Q-set.

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1. Introduction

Early relationships between infants and parents are of fundamental importance for the survival and development of one's own infant, and ultimately ensure the survival of the species (Darwin, 1872; Lorenz, 1943). Humanity is a very social species that invests heavily in nurturing and protecting the young. Accumulating evidence indicates that early life experiences have a major impact upon adult mental and physical health (Shonkoff et al., 2009).

These important early parent–infant interactions are central to understanding human nature and have over the years been the subject of a large body of behavioural research (e.g., Papousek and Papousek, 1983; Stern, 1985; Tomasello et al., 2005; Trevarthen and Aitken, 2001). However, it has only recently become possible to link aspects of these interactions to brain activity in both infants and parents using advanced neuroimaging techniques. Affective and social neurosciences have begun to emerge as exciting disciplines characterising the brain networks involved in the processing of reward, pleasure, emotion, empathy and related behaviours (Adolphs, 2003; Brothers, 1990; Cacioppo et al., 2007; Decety and Ickes, 2009; Dolan, 2002; Fiske and Taylor, 2008; Frith, 2007; Frith and Frith, 2007; Frith and Frith, 2010; Harris, 2003; Kringelbach and Berridge, 2009a; Lieberman, 2007). While a substantial volume of evidence has served to elucidate the intricacies of the social and affective brain in adults (Kringelbach, 2004), less is known about its development in the early years.

In this review, we focus on synthesising current knowledge about the development of the functional neuroanatomy of the evolving parent–infant relationship. We start by providing a coherent framework for describing and understanding the nature of early parent–infant interactions that has emerged from the behavioural literature. Using this behavioural framework, we describe what is known about the construction of the infant brain and the emerging abilities used to process uni- and multimodal sensory stimuli. Over time, these fundamental abilities allow infants to engage in complex social relationships with parents, caregivers and others. We also describe how the complementary parental responses change over the course of infant development, and the neural basis of such responses. We have chosen to focus largely on the human literature, since the translation between animal and human work remains speculative, and much of the

research on early non-human relationships has been reviewed elsewhere (e.g., Insel, 1997; Young et al., 2008).

Here, we focus on the first 18 months of life, since the middle of the second year is, in many respects, a developmental landmark which signifies the end of infancy. While the first few years are particularly important because vital development occurs across all domains, there is good evidence that major elements of the social and affective brain continue to develop well past early childhood (Meltzoff et al., 2009). The fundamental research presented here has important clinical applications because disturbances to normal early interactions, particularly in the context of parental psychological disorder, increase the risk of difficulties in child development (Squire and Stein, 2003; Stein et al., 2009). A better understanding of the development of the functional neuroanatomy of the early parent–infant relationship could thus have direct implications for enhancing affective development and experience (Kringelbach and Berridge, 2009b).

2. A behavioural framework for the early parent–infant relationship

From the existing behavioural literature, it is clear that there are a number of important components in the development of the parent–infant relationship. Based on current evidence, we have classified and further described six major components of the relationship: (1) orienting system; (2) recognition system; (3) intuitive parenting; (4) attachment relationships; (5) intersubjectivity; and (6) higher socio-emotional and cognitive functions (Fig. 1).

2.1. Orienting system

The early parent–infant relationship is defined by the immediate propensity of infants and parents to be attracted to and seek contact with one another. This *orienting system* serves to bring about close proximity between the two members of the dyad, thereby facilitating their interaction. On the part of the parent, there is attraction to infant characteristics, such as ‘cuteness’ (Darwin, 1872; Lorenz, 1943), which help to secure parental attentiveness. This orienting response of attraction to infants is present in adults who are not parents, and may be linked to evolutionary mechanisms ensuring survival of the species. From early postpartum, the orienting system helps to initiate interper-

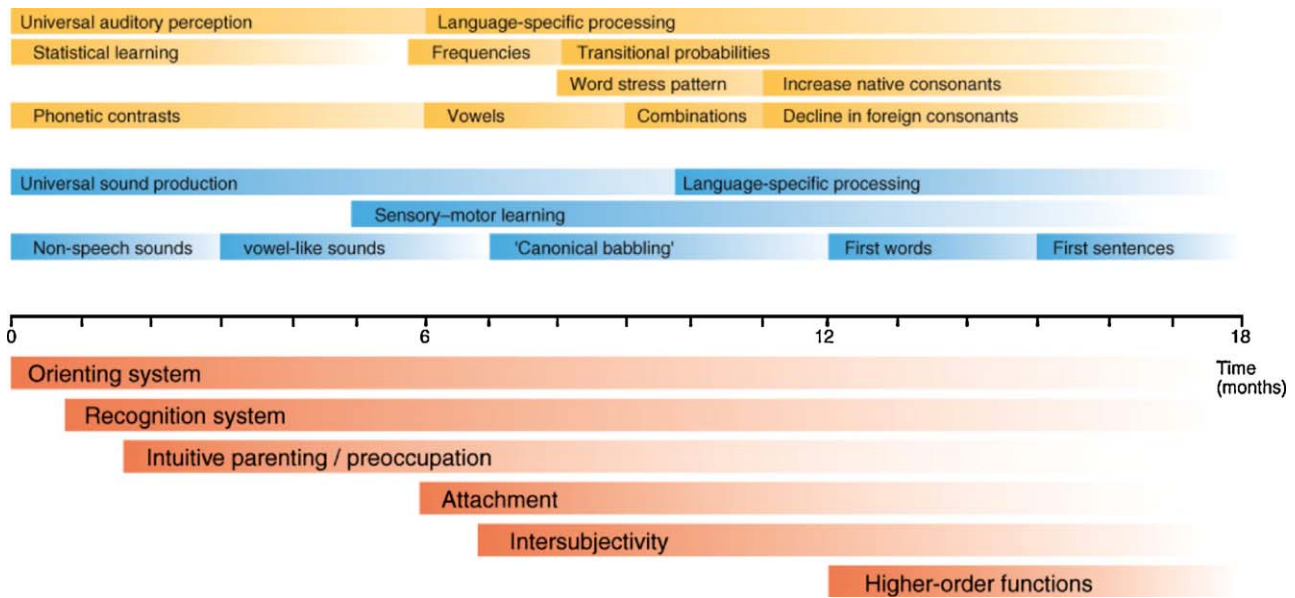


Fig. 1. Timeline of major infant development milestones. Timeline of the behavioural framework (red), and examples of the infant development of auditory perception (orange) and speech production (blue; Kuhl, 2004).

sonal contact; for example, the mother attempts to stay in the middle of the infant's visual field and makes direct eye contact. When eye contact is established, the mother immediately responds by making exaggerated facial expressions and vocalisations in greeting (Papousek and Papousek, 1983). On the part of the infant, there are social capacities far greater than previously appreciated (Trevarthen et al., 1981). Infants show a comparable orientation to, and preference for, human over non-human forms from birth, as evidenced by their preference for face-like over non-face forms (Johnson et al., 1991a) and their preference for speech over non-speech sounds of similar pitch and intensity (Vouloumanos and Werker, 2004).

2.2. Recognition system

The general orienting response is quickly superseded by a more selective, individuated, *recognition system*. Both parent and infant are selectively responsive to each other's unique characteristics, either from birth or very shortly thereafter. Mothers can accurately recognise their own infant early postpartum, even on the basis of single non-visual cues, such as smell, cry or touch (Cismaresco and Montagner, 1990; Kaitz et al., 1992; Porter et al., 1983; Russell et al., 1983). Within the first few days and weeks of life, infants in turn demonstrate clear preferences for their mother above other individuals. Infants preferentially orient to view the mother's face rather than the face of an unknown woman (Bushnell, 2001), show preference for the mother's voice (DeCasper and Fifer, 1980) and even preference for the smell of the mother's breast milk (Macfarlane, 1975). This recognition system is likely to ensure that the parent and infant seek each other out, thereby maximising contact and facilitating interaction.

2.3. Intuitive parenting

Over the early months of the infant's life, parents modify their multimodal communicative range to the infant's stage of perceptual, integrative and communicative abilities, a process referred to as 'intuitive parenting' by Papousek (2007). As time passes, the mother begins to leave a time lag between the infant's demands and their satisfaction, and progressively increases this

lag. Concurrently, the infant acquires the capacity to anticipate the mother's non-immediate responses, and accordingly becomes increasingly tolerant of delay.

Over the first two to three months, both parents and infants display responses that are remarkably attuned to each others' cues and signals (see Papousek and Papousek, 1975, for review). Through repeated interaction, parents rapidly come to know how to read and ascribe meaning to their infant's behaviour. From early postpartum, parents stay in the centre of the infant's visual field at exactly the infant's focal distance, and maintain eye contact (Papousek and Papousek, 1977, 1987). Parents also alter their speech when talking to their infant, speaking at a slower rate, in short sentences, repeating phrases, at a higher average pitch, elongating vowels and varying rhythms, often referred to as 'motherese' (Kuhl, 2004). These adjustments are common across cultures that differ widely in adult-directed speech (Grieser and Kuhl, 1988; Kuhl et al., 1997). This 'infant-directed speech' is important for infant language development and creates a communicative dialogue between parent and infant that aids familiarity, conveys emotional tone and helps establish contingent responsiveness in interactions (Marwick and Murray, 2008; Papousek and Papousek, 1983; Stern, 1985).

Intuitive parenting also includes the propensity to mirror infant expressions, vocalisations and even feeding movements, often expanding the infant's original communication to include other cues. For example, an infant 'pout' will be mirrored by the parent's mouth posture, but may also involve vocal changes, eyebrow and even shoulder movements (for review, see Stern, 1985). Such complex mirroring is part of a constellation of parental responses that are highly contingent on infant cues and expressions. By attending to infant facial expressions and vocalisations, the parent can imitate positive affective behaviour, and conversely contain and soothe negative affective behaviour (Brazelton et al., 1974; Papousek, 2007; Tronick and Gianino, 1986). Communication between infant and parent provides the context in which the infant begins to understand and organise affective experience. A parent's sensitive response will enhance the child's sense of efficacy in regulating affective states (Bell and Ainsworth, 1972). Consequently, when the parent responds sensitively to the infant's signals, the infant may experience the expression of affect as rewarding.

A considerable body of evidence has shown that, from early on, the infant is drawn to engage socially with others and has a rich repertoire of communicative behaviours. Such capacities allow the infant to partake in mutually responsive, conversation-like interactions with the parent (Bateson, 1975; Brazelton et al., 1974; Trevarthen, 1979; Tronick, 1979). Although parental imitation of the infant is more frequent than *vice versa*, the newborn has the capacity to imitate adult facial gestures and emotional expressions (Field et al., 1988; Meltzoff and Moore, 1977). By six weeks of age, infants show remarkable sensitivity to the qualities of adult communication (Brazelton et al., 1975; Murray and Trevarthen, 1985; Papousek and Papousek, 1975). They actively pursue certain kinds of social interactions, and react in striking ways if such interactions are not forthcoming (Cohn et al., 1986; Field et al., 1988). In studies where the mother's normal responsiveness is experimentally perturbed, infants rapidly show strong, specific reactions. For example, where the mother is asked to suddenly cease responding and adopt a 'still face' expression (Tronick et al., 1978), infants first protest, then become distressed and eventually withdraw. In paradigms that disrupt the contingency of the mother's behaviour, infants demonstrate puzzlement and confusion (Legerstee and Markova, 2007; Murray and Trevarthen, 1985; Nadel et al., 1999). Importantly, parents' interactive behaviour is also affected by disturbances in infant social responsiveness: if infant behaviour is experimentally made non-contingent on that of the mother, the mother will cease to show the normal verbal adjustments of speech addressed to infants (Murray and Trevarthen, 1986).

Over time, the structure of parent–infant interactions alters to accommodate improvements in the infant's key motor, cognitive and behavioural skills. From around 3 months, as infant vision and prehension improve, eye contact diminishes, and instead interactions begin to incorporate play with objects, and repetitive action games become routine (Trevarthen et al., 1981). Parents begin to facilitate the infant's growing awareness of the wider environment and scaffold the infant's activity with objects by demonstrating and teaching (Bruner, 1975; Carpenter et al., 1998; Vygotsky, 1978), and clearly delineating the significance of events (Gergely and Watson, 1996).

2.4. Attachment relationships

By about 5–6 months, the infant begins to show a strong specific attachment to a primary caregiver as described by Bowlby (1982). The infant starts to differentially direct certain behaviours, including orienting and signalling, to specific individuals in their environment. Such behaviours serve a protective function for the infant by promoting their caregivers' nurturing behaviour (Carter and Keverne, 2002; Miller et al., 2002). By the end of their first year, the infant demonstrates preference for their caregiver over others, seeking contact especially in times of stress, and reacting with distress upon separation (Bowlby, 1969; Bowlby, 1982). During the early years, the infant is highly dependent on the caregiver and develops a sense of security when confident that parental care will be available when needed. This secure attachment relationship provides a platform for the child's independent exploration of the wider world (Sroufe, 2005).

Behavioural sensitivity, generally defined as parental availability and appropriate, prompt, responsiveness to infant cues, has been shown in meta-analyses to be an important predictor of attachment outcomes (Bakermans-Kranenburg et al., 2003; De Wolff and Van Ijzendoorn, 1997). However, it appears that such parental sensitivity cannot account for all the variance in infant attachment security (Atkinson et al., 2000; De Wolff and Van Ijzendoorn, 1997; Goldsmith and Alansky, 1987). Accumulating evidence suggests that the parent's capacity to treat the child as a

psychological agent, known as 'mind-mindedness' (Meins, 1997), and the related concept of reflective functioning, are key aspects of parenting that are important for attachment (e.g., Lundy, 2003; Meins et al., 2001, 1998, 2003, 2002). Reflective functioning concerns the parent's capacity to think about the mental state and experiences of the infant, and is linked to the broader ability of mentalisation, or thinking about the mental states of others (Fonagy et al., 1991, 1998).

2.5. Intersubjectivity

From around the time when specific attachment relationships emerge, infants begin to develop an understanding of the subjective states of others and an ability to act jointly, a capacity referred to as *intersubjectivity* (Trevarthen, 1977). The first stage of this capacity, evident in the first 3 months, is termed 'primary intersubjectivity' and describes the infant's active and responsive appreciation of adults' communication (Trevarthen, 1979). At this early stage, these capacities reflect the infant's *implicit* awareness of others' feelings, attitudes and intentions. Linked to this capacity is the later ability to *explicitly* represent, explain and predict others' behaviours by attributing them to independent mental states such as beliefs and desires, referred to as 'theory of mind' (Frith and Frith, 2003; Gallagher and Frith, 2003).

At around 9 months, the infant becomes aware that their subjective experience can be shared with another person, termed 'secondary intersubjectivity'. Here, infants show awareness that their agency affects others, just as they are affected by the agency of others themselves. Around this time, precursors of 'theory of mind' become evident in the communication system (Stern, 1985; Trevarthen, 1979; Tronick, 1989). These precursors include: gaze following; using pointing to share reference to objects and events; and social referencing, whereby infants begin to appraise the affective expressions of their caregivers and modify their actions based on this appraisal (Campos et al., 1978). Experimental studies have shown that more reciprocal, symmetric roles in play develop, as does imitation of others' intentions and behaviours (e.g., Butterworth, 1991; Meltzoff, 1995; Tomasello et al., 2005). Notwithstanding the difficulties involved in studying spontaneous infant social behaviours, a number of naturalistic observations have found evidence for the emergence of nascent theory of mind skills, such as showing off, deceiving, cheating and teasing at this stage (Reddy, 2008). The development of a mature theory of mind arising from these skills has far-reaching consequences for social and affective interaction, and cooperation.

2.6. Higher functions

The structure and nature of parental responses changes to accommodate the infant's developing capacities. A key attribute of responsive interactions involves the parent treating the infant as an intentional agent who has representations of the wider environment. As the infant becomes gradually more independent of the parent towards the end of infancy, and more ready to engage socially with the wider world, the infant starts to show further precursors of important adult functions necessary for healthy coexistence. These include the related capacities of mentalisation, self-consciousness, episodic memory, theory of mind, empathy and sympathy, although some of these are not fully developed before the end of adolescence. These emerging higher socio-cognitive abilities are scaffolded by the parent, particularly during conversation, including reminiscences about the past and planning for future events, often using a narrative structure that informs the child about the wider social and cultural significance of their experience (Bruner, 1983; Dunn, 1988; Fivush and Nelson, 2006). As for earlier development, where parental behaviour changes in

response to the infant's developing capacities, the structure of the parent's child-directed speech is also highly responsive to developments in the child's linguistic and cognitive abilities (Lieven, 1978; Newport et al., 1977; Olsen-Fulero, 1982). While these parental functions that support the infant's socio-cognitive development have been described extensively, rather less is known about how parenting adjusts to the infant's developing sense of attachment.

3. Infant brain development

Physical brain development and the parent–infant relationship are inherently interlinked. In one direction, brain growth and the associated behavioural gains are vital to the development of the parent–infant relationship, and in the other direction, it is clear that the parent (and the environment created by the parent) has an impact on neurodevelopment. The brain of the newborn has largely the same number of neurons as the mature adult brain, but the connections between these neurons are not fully established (Nowakowski, 2006). The construction of the infant brain is heavily dependent on learning and the interaction of environmental factors with gene-expression (Caspi et al., 2002; Johnson et al., 2009; Meaney and Szyf, 2005; Shonkoff et al., 2009). During the first month after birth there is an overproduction of synapses (Bourgeois, 2010), followed by a process of 'pruning', whereby synapse numbers stabilise through learning. Measures of cortical thickness and neuronal density demonstrate that physical brain development is not complete until the third decade of life in some frontal areas, including the dorsolateral prefrontal cortex (PFC) and the orbitofrontal cortex (OFC; Gogtay et al., 2004; Sowell et al., 2004).

3.1. Early brain development

Neurochemical changes around the time of birth play a critical role in the shaping of the newborn brain (Herlenius and Lagercrantz, 2010). The healthy newborn starts continuous breathing movement and is aroused and awake within the first two hours after birth. This vigilance is likely to be related to activity

in the noradrenergic system, and in particular the locus coeruleus, the region from which noradrenergic neurons are distributed across the entire brain (Herlenius and Lagercrantz, 2010). Indirect evidence for a noradrenergic surge in the human infant comes from the finding of high plasma catecholamines after birth (Lagercrantz and Bistoletti, 1977). Around the time of birth, or shortly after, there is clear evidence for the presence of main fascicles of myelinated long-range connections, including the corpus callosum, cerebellar peduncles, corticospinal and spinothalamic tracts (see Fig. 2; Dubois et al., 2008, 2006). The corticobulbar pathways that regulate the striated muscles of the face are sufficiently developed at birth to allow the infant to signal to the caregiver in the form of facial expressions and vocalisations. Also at this time, there is evidence of basic brain functions such as dominant left-hemispheric activity to speech stimuli (see Fig. 2; Dehaene-Lambertz et al., 2006), and rudimentary face recognition in the fusiform cortex (Johnson, 2005). These abilities and their neural regulation function collectively to support the infant's social interaction and engagement with a caregiver (Porges, 2001).

3.2. Brain structural development after birth

While considerable brain development occurs prenatally, the most pronounced advances in brain structure and behaviour across the lifespan occur in the first two years of life (for reviews, see Anderson et al., 2003; Bell and Fox, 1992; Casey et al., 2000; Herschkowitz, 2000). A striking characteristic of human brain development is the relatively protracted period of postnatal development, increasing the extent to which the environment can shape the process. Synaptic plasticity is the most important mechanism that allows environmental factors to influence brain development throughout the lifespan (Lau and Zukin, 2007). Plasticity refers to changes that increase or decrease the strength, efficacy or number of synapses. The process of synapse overproduction and pruning appears to be under the control of both intrinsic programmes and environmental influences. Synapses are produced at a rapid rate in the postnatal period (Bourgeois, 2010), and reach a density that is twice the adult level by the age of 2 years, which then falls back to the adult level by early adolescence.

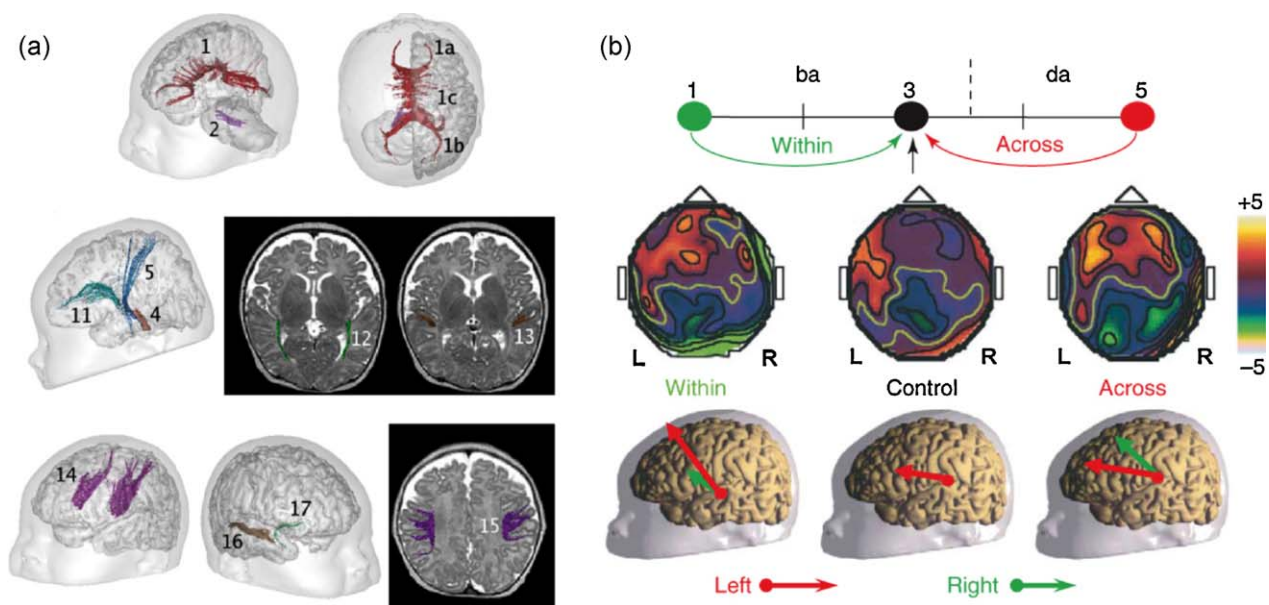


Fig. 2. Development of structure and function in the infant brain. More information is needed about the longitudinal structural changes in the infant brain. (a) An example is shown, using diffusion tensor imaging to track the development of the main fibre pathways (Dubois et al., 2006). Similarly more information is needed about the fine-grained temporal information of infant functional brain activity. (b) An example is shown from an ERP study of infants' phonetic processing (Dehaene-Lambertz et al., 2006).

The majority of cortical regions undergo a 'rise and fall' in synaptic density, with density becoming stable at adult levels at different points during later childhood and adolescence (e.g., Bourgeois, 2005; Goldman-Rakic et al., 1997; Huttenlocher, 1990). The rise and fall developmental sequence is also evidenced by other measures of brain physiology and anatomy.

At birth, subcortical structures are clearly defined and are similar to their adult forms. Although some of its key markers (sulci and gyri) are evident at birth, the cerebral cortex is considered relatively immature in terms of inter- and intraregional connectivity. It is generally accepted that brain structures resemble those of adults by two years of age, and all the main fibre tracts are present by 3 years of age (Matsuzawa et al., 2001). These changes in developmental structural patterns are mirrored by functional changes in brain activity. Using indirect measures, such as glucose uptake, studies of infant brain development have provided some important insights into functional activity. Glucose uptake has been shown to be highest in the sensorimotor cortex in neonates, and low over most of the remaining cerebral cortex (Chugani and Phelps, 1986). In comparison to the infant cerebrum, the cerebellum has a faster, but shorter growth spurt, starting later but achieving adult dimensions earlier (Dobbing and Sands, 1973). The cerebellum has been traditionally associated with motor control, physical coordination, and balance; more recently it has been suggested that distinct regions may have roles in cognition and learning (Diamond, 2000; Ito, 1993; Riva and Giorgi, 2000; Schmahmann and Sherman, 1998).

In the second and third months postpartum, glucose uptake starts to increase in the parietal, temporal and primary visual cortices. This coincides with improvements in motor and visual skills at this age (Amiel-Tison and Grenier, 1986; Bayley, 1993). By 6–8 months, glucose uptake has increased in the lateral inferior frontal cortex, and by 12 months in the dorsal and medial frontal cortex. Concurrently, infants exhibit improved cognitive and behavioural skills. At around one year, the pattern of glucose utilisation in an infant resembles that of an adult (Chugani, 1998; Chugani et al., 1987).

3.3. Developing a stable brain: a default mode?

Much recent interest has centred on the importance of the default dynamics of brain activity (the brain at rest) originally termed *default mode of brain function* (Gusnard and Raichle, 2001). A number of brain regions are implicated in this default mode network including the medial PFC, posterior cingulate cortex, lateral temporal cortex, inferior parietal lobule, and hippocampal regions. There is an emerging literature on the functional importance of this default network, which has been proposed to carry representations of self (Lou et al., 1999), internal modes of cognition (Buckner et al., 2008), and possibly states of consciousness (Laureys et al., 2004). On the basis of functional and connectivity analyses, the midline components of the default network have been divided into two functional sub-networks centred on a frontal and a parietal network (including precuneus and posterior cingulate cortex; Fransson and Marrelec, 2008).

We have previously proposed that this default network, or related neural circuits, contribute to computing relations between self and others, in evaluating eudaimonic meaning and interacting with hedonic circuits of positive affect (Kringelbach and Berridge, 2009b). Interestingly, it has been shown that the default network changes during early development (Fig. 3). It is not fully formed in pre-term babies (Fransson et al., 2007), or even at birth (Gao et al., 2009). At 2 years of age, activity begins to resemble the adult default network, with the medial prefrontal network starting to come online at 1 year (Fig. 4; Gao et al., 2009). Further refinements continue later in childhood (Fair et al., 2008). These findings are

significant, given that various parts of the medial PFC have been linked to reward processing, self-referential activity, mentalising and theory of mind, which the existing behavioural evidence suggests begin to emerge at around 1 year.

4. Orienting and recognition systems

At birth, the infant brain has developed to an extent that supports fundamental orienting behaviours; in turn, the parent is necessarily equipped with the social and affective responses required to orient and recognise the infant. Other components of the parent–infant relationship, and their neural substrates, develop through interaction and experience.

4.1. Processing social stimuli in infancy

Key elements of the social and affective brain emerge early in the postnatal life of an infant (Table 1). There is good evidence that the primary sensory cortices are the first to mature in the infant brain, helping the infant to process and filter sensory cues, particularly those relating to the parent. Activity across a wide range of cortical areas, including occipital, olfactory and temporal cortices, of the newborn brain has been demonstrated in response to basic sensory stimuli using near infrared spectroscopy (NIRS; e.g., Bartocci et al., 2000; Hoshi et al., 2000; Kotilahti et al., 2005; Pena et al., 2003; Taga et al., 2003). Activity in frontal regions in response to more complex social stimuli such as speech sounds has also been reported (Gervain et al., 2008; Saito et al., 2007a,b; Sakatani et al., 1999). Processing of social stimuli of increasing complexity, such as faces and eye gaze, has been shown to recruit multiple cortical regions (see Lloyd-Fox et al., 2010, for a review).

Faces communicate a wealth of social information, and are salient to infants even in their first days of life (Johnson et al., 1991a). One reason for this early predisposition to orient towards faces might be to facilitate bonding with parents. Another complementary effect is to bias the visual input to plastic cortical circuits. Biased sampling of the visual environment in the initial period after birth might guarantee the appropriate specialisation of the developing cortical circuitry (Morton and Johnson, 1991). In adults (and in other higher primates), the fusiform gyrus and superior temporal sulcus subserve face processing (Allison et al., 2000; Chao et al., 1999; de Haan et al., 2002a,b). In young infants, there is evidence to suggest that face processing is guided by both subcortical (De Schonen and Mathivet, 1989; Johnson, 2005; Morton and Johnson, 1991) and cortical regions (e.g., Grossmann and Johnson, 2007; Tzourio-Mazoyer et al., 2002). In the only published positron emission tomography (PET) study of infant face processing to date, the majority of brain areas implicated in adult face processing demonstrate some activity in 2 month old infants (Tzourio-Mazoyer et al., 2002). Infants exhibited significant activity in the right inferior temporal gyrus, an area thought to be the homologue of the adult fusiform face area (Gauthier et al., 1999; Kanwisher, 2000). Activity was also found in the inferior frontal and superior temporal gyri in infants, areas again implicated in adult face processing. In infants, these cortical areas are neuroanatomically immature (e.g., Huttenlocher and Dabholkar, 1997; Perrin and Huttenlocher, 2002) and demonstrate low levels of metabolic activity (e.g., Chugani and Phelps, 1986; Chugani et al., 1987). The question arises: to what extent can neuroanatomically immature regions with minimal functional activity influence visually-guided behaviour? One interpretation is that the subcortical visual route is more developed at birth relative to the cortical visual route (Atkinson, 2000; Born et al., 2002), and accordingly face processing may initially rely more heavily on subcortical structures.

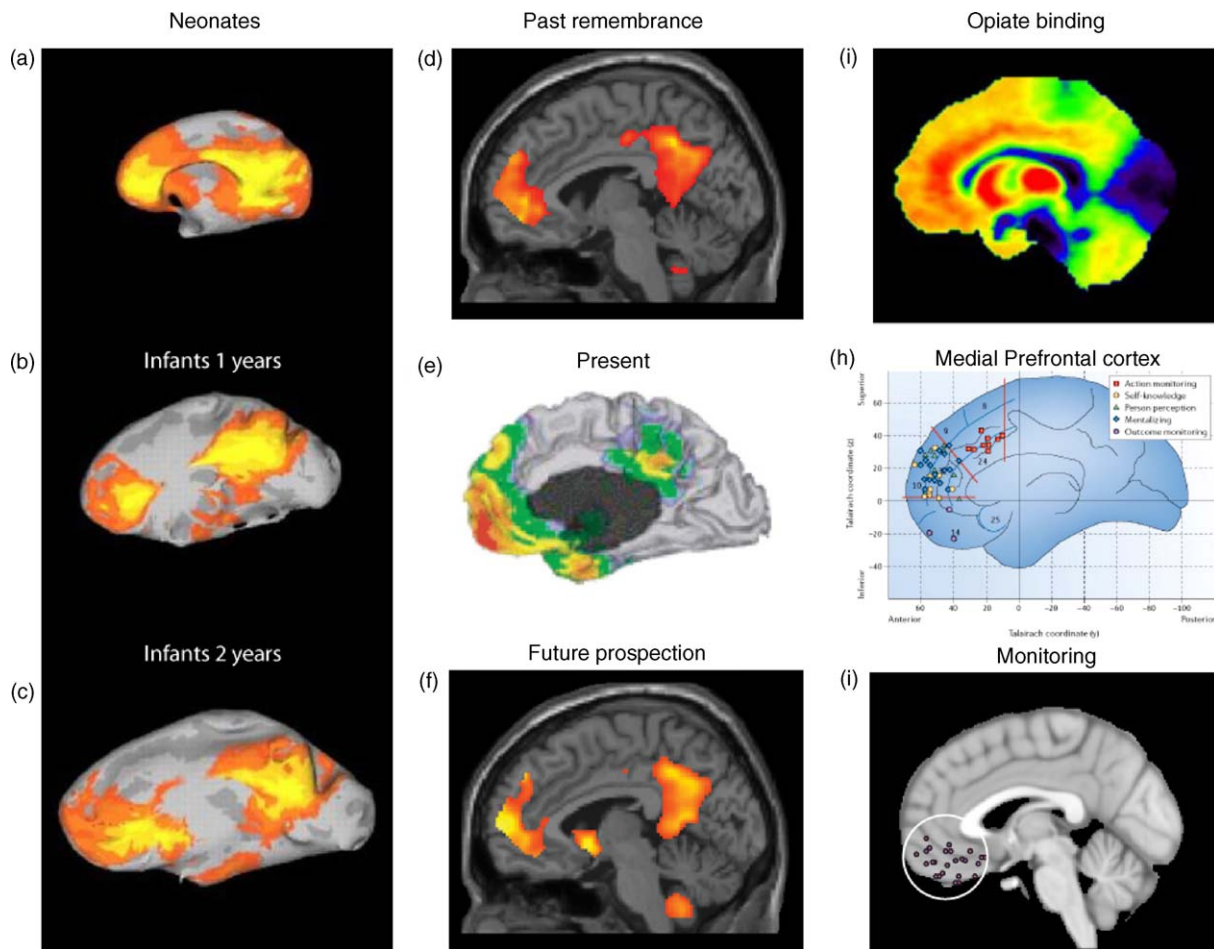


Fig. 3. Default brain modes. (a–c) There is recent evidence that the infant default resting state is not yet mature before birth (Fransson et al., 2007), at birth or at 1 years but only starts resemble the adult default mode by 2 years (Gao et al., 2009). (d–f) The adult brain's default network (Addis et al., 2007; Gusnard and Raichle, 2001) has in turn been linked to self awareness, remembering the past and prospecting the future (Addis et al., 2007). Some components overlap with networks involved in pleasure and reward, including midline structures such as the orbitofrontal, medial prefrontal and cingulate cortices. (g) Examples show key regions of the default network such as the anterior cingulate and orbitofrontal cortices that have a high density of opiate receptors (Willloch et al., 2004). (h) Subregional localisations of function link to self-knowledge, person perception and other cognitive functions (Amodio and Frith, 2006) and (i) are important in pleasure-related monitoring, learning and memory (Kringelbach and Rolls, 2004).

The cortical system involved in visual recognition more broadly has been estimated to emerge functionally between 2 and 8 months postpartum (De Schonen and Mathivet, 1989; Morton and Johnson, 1991; Nelson, 1995; Schacter and Moscovitch, 1984). Event related potential (ERP) studies suggest that the neural responses to faces found in infants, which roughly correspond to those found in adults, are less stimulus-specific in the first year of life (de Haan et al., 2002b; Halit et al., 2003), and processing becomes increasingly fine tuned (for review, see de Haan et al., 2003). There is good evidence for cortical involvement in face processing in infants aged between 6 and 9 months from a NIRS study demonstrating increased activity in the right fronto-temporal cortex in response to a mother's face, but not to an unknown face (Carlsson et al., 2008). At this age, infants demonstrate strong preferences for familiar caregivers, as evidenced by the emergence of stranger and separation anxiety. A related ERP finding in infants is an increased Nc (negative central) component in response to the mother's face compared to a stranger's face (de Haan and Nelson, 1997, 1999), which may also be associated with the increased salience of the primary caregiver around this age.

4.1.1. Infant processing of eye gaze and eye contact

Beyond relatively simple face processing, a more complex accomplishment of the adult social and affective brain is the

processing of information related to eyes and eye gaze. In the early postpartum period, infants are sensitive to another's gaze, reflected in their preference for looking at faces that have their eyes open rather than closed (Batki et al., 2000; Schacter and Moscovitch, 1984), and they orient towards direct eye contact from others (Farroni et al., 2002). An important communicative function of eye gaze is to direct attention to specific targets such as locations, events or objects. Comprehending the relations between eye gaze and target objects, 'referential gaze', is essential for elements of development such as word learning (Baldwin and Moses, 1996).

In an ERP study, Hoehl et al. (2008) demonstrated that by 3 months, infants exhibit different neural responses to objects dependent on others' eye gaze and facial expression. Infants attended more to objects cued by direct gaze and a fearful adult expression compared with objects cued by direct gaze and neutral facial expression, or averted gaze and either neutral or fearful expression. For the direct gaze and fearful expression condition, infants demonstrated increases in the Nc components compared to the other conditions. Further, in a study of infants at 4 months, Farroni et al. (2002) reported enhanced neural processing of faces with a direct gaze compared with an averted gaze, as evidenced by increased amplitude of the N290 component.

An ERP study of older infants at 9 months found that infants can encode the referential information of gaze in a comparable way to

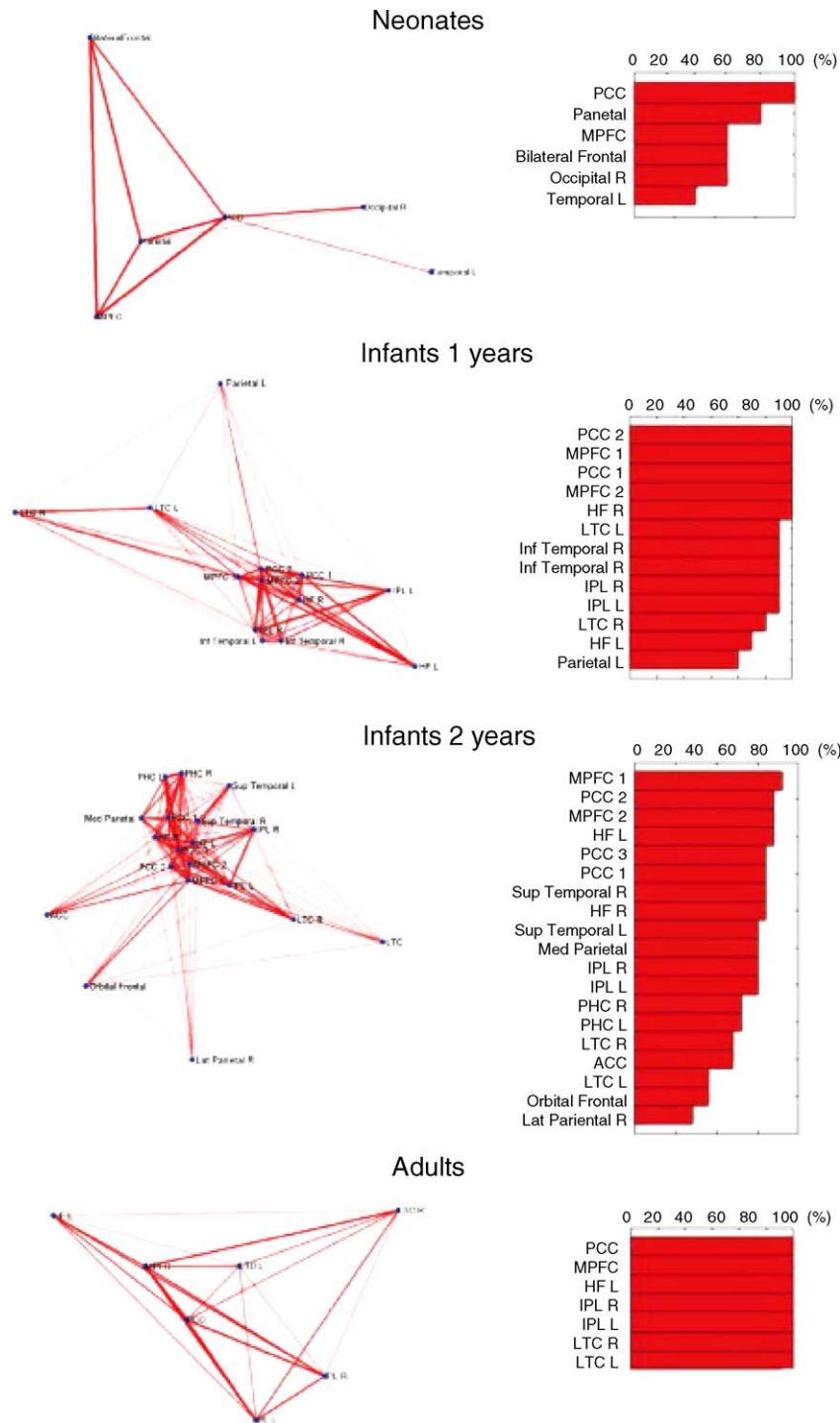


Fig. 4. Development of functional connectivity of default mode networks in infancy. On the left are shown the functional connectivity graphs and on the right degrees of connectivity of the default mode as present in neonates, in infants of 1 and 2 years of age and adults. In the graphs, more strongly connected regions are clustered near each other while weakly correlated regions are placed further away with the line width proportional to the connection strength. The degree of connectivity is listed in descending order. Note how the adult default mode network is very different from the networks present in infancy. Modified from Gao et al. (2009).

that of adults. Infants and adults watched a face whose gaze shifted either towards (object-congruent) or away from (object-incongruent) the location of a previously presented object (Senju and Hasegawa, 2006). In both adults and infants, object-incongruent gaze shifts elicited increased negativity at around 300msec compared with the object-congruent gaze shifts. However, only infants demonstrated an early frontal ERP component, that exhibited higher amplitude in response to the object-congruent gaze shifts. One interpretation is that in the infant brain, the

referential information provided by gaze is encoded in wider cortical circuits than those in adults, which become increasingly specialised (Grossmann and Johnson, 2007).

4.1.2. Infant responsivity to parental cues

Recognition of a parent or caregiver is an essential foundation for the evolving parent–infant relationship (Porter and Winberg, 1999). Infants are able to recognise a range of cues from a parent within the first few days of life and display stereotyped behaviours

Table 1
Behavioural framework and development of the infant social brain.

Age	Region	Functioning	Method	Study
Orientation and recognition				
Newborn	Sensorimotor cortex	Processing of primary sensory information	PET	Chugani and Phelps, 1986
Newborn	STG	Speech sound discrimination	MEG	Imada et al., 2006
Newborn	Left hemisphere	Discrimination of forward and reversed speech	NIRS	Pena et al., 2003
2–3 months	Increased glucose uptake in parietal, temporal and primary visual cortices	Improvements in visual and motor skills	PET	Amiel-Tison and Grenier, 1986; Bayley, 1993; Chugani and Phelps, 1986
2–8 months	<i>Subcortical</i> : right inferior temporal gyrus, left STG and left IFG <i>Cortical</i> : bilateral occipital, parietal and temporal regions	Face processing	PET, EEG	de Haan et al., 2002b; De Schonen and Mathivet, 1989; Schacter and Moscovitch, 1984; Tzourio-Mazoyer et al., 2002
3 months	Left angular gyrus, left precuneus	Discrimination of forward and reversed speech	fMRI	Dehaene-Lambertz et al., 2002
3–4 months	Central regions, N290	Processing of direct gaze and fearful expressions	EEG	Farroni et al., 2002; Hoehl et al., 2008
5–8 months	Right lateral area, bilateral superior temporal sulcus	Discrimination of upright and inverse faces	NIRS	Otsuka et al., 2007
6 months	STG and inferior frontal region of temporal lobe	Speech sound discrimination	MEG	Imada et al., 2006
6 months	Cortical midline structures	Distinct processing of mother's and stranger's faces	EEG	de Haan and Nelson, 1997
Attachment and intersubjectivity				
6–8 months	Increased glucose uptake in lateral inferior frontal cortex	Improvements in cognitive and behavioural skills	PET	Chugani, 1998; Chugani et al., 1987
7 months	Temporal regions	Discrimination of native and non-native speech sounds	EEG	Kuhl et al., 2008
7 months	Anterior cingulate and other prefrontal regions	Discrimination of happy and sad facial expressions	EEG	Nelson and De Haan, 1996; Reynolds and Richards, 2005
9 months	Occipito-temporal activity and fronto-central negative component	'Referential' gaze perception	EEG	Senju et al., 2006
11 months	Distributed activity (N200)	Discrimination of known vs. unknown words	EEG	Thierry et al., 2003
12 months	STG and inferior frontal region of temporal lobe	Temporally linked responses to speech sounds, infants begin to utter first words	MEG	Imada et al., 2006; MacNeilage and Davis, 2000
13–15 months	Left frontal regions	Changes in activity related to attachment security	EEG	Dawson et al., 2001
14–18 months	Left frontal and right central activity, bilateral medial frontal cortex, PFC	Ability to initiate joint attention	EEG, PET	Caplan et al., 1993; Henderson et al., 2002; Mundy et al., 2000
14–18 months	Parietal regions	Ability to respond to joint attention and attention switching	EEG	Mundy et al., 2000
Higher functions				
12 months	Medial prefrontal network	Emergence of the default mode, initial emergence of self-referential activity, mentalising and theory of mind precursors	fMRI	Gao et al., 2009
15–18 months	Temporo-parietal junction	Pass mirror test and evidence of self-representation	MRI	Lewis and Carmody, 2008
Further brain development				
2 years	Medial PFC, posterior cingulate cortex, lateral temporal cortex, inferior parietal lobule and hippocampal regions	Activity begins to resemble adult default mode network	fMRI	Gao et al., 2009

The timecourse of infants' emerging abilities and associated brain regions.

in response to such cues. For instance, sweet, pleasurable stimuli produce licking and tongue protrusions in infants, whilst bitter stimuli produce 'aversive gaping' (Berridge, 2003). Day-old infants make more licking and sucking mouth movements to breast milk odour than to other odours (Mizuno et al., 2004), and week-old infants preferentially orient to the smell of a breast pad of a lactating woman (Makin and Porter, 1989). Own-mother breast odour has been shown to have an analgesic effect on 5-day old infants (Nishitani et al., 2009). By 6 days after birth (and possibly before; Schaal et al., 1980) infants can identify their own mother's breast odour from that of other lactating women (Macfarlane, 1975), dependent on a critical amount of mother-infant 'skin-on-skin' contact (Mizuno et al., 2004).

By 3 days after birth, infants preferentially orient to view their own mother's face rather than the face of an unknown woman, an effect that is stronger in infants with greater previous exposure to their mother's face (Bushnell, 2001). One month-old infants have a preference for 'infant-directed speech' (Cooper and Aslin, 1990),

that is, exaggerated vocalisations aimed at the infant and that promote language learning (Burnham et al., 2002; Kuhl et al., 1997). A mother's voice has a 'soothing' effect on 1–4 day old infants, calming agitated motor movements (Hepper et al., 1993). Within 3 days after birth, infants preferentially suck on a non-nutritive nipple to hear their own mother's voice (DeCasper and Fifer, 1980).

Infants smile more in the context of dynamic, interacting touch compared with static touch in the *still face paradigm* (Stack and Muir, 1992). Touch can reinforce and maintain high rates of infant eye contact responses, vocalisations, and smiles during face-to-face interactions with the mother (Peláez-Nogueras et al., 1996). Skin-to-skin contact is widely reported to be beneficial to infant development. It has been shown to: aid infant motor, perceptual and cognitive development; support sensitive parent-infant interaction; aid the attachment process in pre-term infants; attenuate infants' physiological reaction to stress; and have an analgesic effect (Anderson, 1991; Feldman et al., 2010, 2003;

Ferber and Makhoul, 2004). Sensory saturation, where the infant experiences simultaneous visual, auditory, tactile, olfactory and gustatory stimulation, has been shown to have an analgesic effect on the pain response induced by the heel-stick procedure for taking blood in both full-term and pre-term infants (Bellieni et al., 2002; Freire et al., 2008; Gray et al., 2002, 2000).

4.2. Parental recognition of infant cues

Responsivity, defined as the parents' capacity to perceive infant cues and to respond to these cues promptly and appropriately (Ainsworth et al., 1974), has been identified as an important precursor of infant attachment security (e.g., Atkinson et al., 2005; De Wolff and Van Ijzendoorn, 1997; Nievar and Becker, 2008; Tarabulsky et al., 2005; van den Boom, 1994). Contingent parent–infant interactions promote infant survival and ultimately the development of higher social and affective functions. A body of neuroimaging studies has attempted to elucidate the neural correlates and mechanisms of this parental responsiveness. The approaches adopted to examine parents' neurobiological responses to the infant fall into two broad categories: (i) neuroimaging of the brain areas which are active in response to sensory cues from infants; and (ii) assessment of the neuroendocrinal changes around pregnancy in mothers and fathers.

4.2.1. Auditory infant cues

For the infant, vocalisations, such as cries, babbles and laughs, are the only means of communicating with the caregiver from a distance, and are therefore a vital component of early communication capacities. Infant vocalisations generally promote proximity to the caregiver and the initiation of caregiving behaviour. For the caregiver, infant vocalisations are alerting and communicate a wealth of information about the infant's current behavioural, physiological and affective state. From the first day postpartum, mothers and fathers become increasingly capable of reliably recognising their own infant's cry (Cismaresco and Montagner, 1990).

While functional magnetic resonance imaging (fMRI) is both noisy and relatively slow (on the scale of seconds), and thus not an ideal neuroimaging modality for studying auditory processing, Lorberbaum et al. (2002) found evidence for a role of thalamo-cingulate circuitry in maternal responsivity to infant cries. They reported increased activity in a wide range of areas, namely the medial thalamus, medial PFC, cingulate cortex, right OFC, the midbrain, hypothalamus, striatum and vicinity of the lateral septal region. It was also found that activity unique to the cry sound was predominantly right-sided. However, it should be noted that the white noise stimulus used by Lorberbaum et al was not frequency-matched with the cry stimulus.

There also appear to be a number of important factors impacting upon the neural responses to infant cries, such as past experience of parenting and possibly gender. Non-parents showed increased activity in the amygdala and bilateral insula in response to infant laughter, but not to infant crying, while parents showed the reverse pattern (Seifritz et al., 2003). For parents, activity in the right amygdala was correlated with measures of obsessive symptoms, such as anxious or intrusive thoughts and harm-avoidant behaviours (Swain et al., 2005). At 2 weeks postpartum, first-time parents responding to their infants' cries, compared with cries of other infants, showed bilateral activity in the amygdala and the insula. At 3 to 4 months, the activity pattern had changed, such that areas in the hypothalamus and the ventral tegmental area were activated. Neural responses in the experienced parents at two weeks, however, more closely resembled what was seen at 3 to 4 months in the first-time parents. These patterns of activity may reflect qualitative changes in parents' responses. In the initial

months after birth, the mother's neural response to infant cries might reflect 'alarm' and serve to mobilise engagement, whereas later on the response is more indicative of social engagement. Some gender differences in neural activity have also been suggested, although study sample sizes have been small. In men, but not women, infant vocal cues induced changes in activity in the anterior cingulate cortex and amygdala (although the direction of changes in activity is disputed; Sander et al., 2007; Seifritz et al., 2003).

Gender-specific differences in hormonal responses to infant cries have also been reported. Mothers with higher baseline levels of cortisol were shown to have greater feelings of sympathy when exposed to infant cries than mothers with lower baseline cortisol levels (Stallings et al., 2001). Fathers with higher baseline prolactin levels or lower testosterone were shown to have greater sympathy and 'need to respond' to infant cries than fathers with lower baseline prolactin or higher baseline testosterone (Storey et al., 2000). Parenting experience may also be a factor: new fathers demonstrate a greater cortisol response after hearing an infant cry compared to experienced fathers, who instead show a peak in prolactin levels not present in new fathers (Fleming et al., 2002).

4.2.2. Visual infant cues

Infant facial features and expressions are central to the intuitive parenting component of the parent–infant relationship. Recent work has begun to explore the neural basis of processing of infant faces, compared to adult faces. Both infant and adult faces elicit activity in the primary and dedicated higher visual areas such as the fusiform face area, but infant faces also appear to elicit activity in additional brain areas. One of the most consistent findings across neuroimaging studies is increased activity in the OFC in response to images of infants (Bartels and Zeki, 2004; Nitschke et al., 2004; Noriuchi et al., 2008; Ranote et al., 2004). Increased activity has also been reported in areas of PFC, substantia nigra, and insula (Bartels and Zeki, 2004; Noriuchi et al., 2008; Ranote et al., 2004; Strathearn et al., 2008); the cingulate cortex (Noriuchi et al., 2008; Strathearn et al., 2008), cingulate gyrus (Bartels and Zeki, 2004) and the striatum (Bartels and Zeki, 2004; Strathearn et al., 2008). In some studies, activity has also been reported in the periaqueductal gray, putamen, caudate nucleus, inferior frontal gyrus (IFG), thalamus, and superior temporal sulcus (Noriuchi et al., 2008); frontal eye fields, occipital cortex, fusiform cortex, caudate nucleus, mid-brain, reticular formation, locus ceruleus and raphe nucleus (Bartels and Zeki, 2004); the ventral tegmental area and the primary motor area (Strathearn et al., 2008). Although there are methodological differences across studies and some are difficult to interpret (e.g., functional MRI studies to date have employed passive viewing conditions, making it difficult to know what participants are doing) these discrepancies are insufficient to account for the variance in patterns of activity reported. However, taken together these studies indicate that infant faces induce activity in a wide variety of brain areas, including some previously associated with reward processing (Strathearn et al., 2008).

In order to assess the significance of activity in a given area within a network, it would seem important to establish that this activity is associated with a specific behaviour. Notably, increased activity in the OFC was found to correlate with self-reported increase in positive mood when a mother viewed a picture of her own infant, compared with an unfamiliar infant using both fMRI (Nitschke et al., 2004) and NIRS (Minagawa-Kawai et al., 2009). These studies do not test whether there is something special about infant faces *per se*, rather than one's own infant, partly because this type of comparison is likely to be confounded by familiarity. Nonetheless, such findings suggest that increased OFC activity is related to positive mood induced by viewing infant images,

Box 1. Neuroimaging methods

Early social relationships are not only inherently important, they are inherently difficult to study. At the simplest level, parent–infant interactions are built up from the mother and the infant recognising and responding to each other. Key aspects of the parent–infant relationship, namely recognition and responsivity of both parent and infant to one another are readily testable in neuroimaging contexts.

A variety of neuroimaging techniques such as positron emission tomography (PET), functional magnetic resonance imaging (fMRI), near-infrared spectroscopy (NIRS), electroencephalography (EEG) and magnetoencephalography (MEG) complement findings from genetic, clinical and animal studies by providing knowledge about patterns of brain activity underlying parental responsivity to infant cues. PET uses radioactive tracers to measure aspects of brain metabolism, providing very specific neurochemical information about the brain, but with poor spatio-temporal resolution. fMRI measures haemodynamic changes in response to neural activity and offers excellent spatial resolution, but poor temporal resolution. Some recent studies have employed NIRS, a portable optical imaging technique also based on second by second haemodynamic responses to neural activity. NIRS has the advantage of providing two haemodynamic signals (oxy- and deoxyhaemoglobin) while fMRI provides a measure of just one (deoxyhaemoglobin). The main drawback of NIRS is that it is only capable of picking up signals from the surface of the cortex in adults and has less spatial precision than fMRI (Wolf et al., 2008). EEG is a non-invasive technique, directly measuring electrical brain activity with excellent temporal, but poor spatial resolution. MEG measures magnetic signals induced by electrical activity in the brain and provides better spatial resolution than EEG, whilst maintaining high temporal resolution.

There are fewer techniques available for the examination of infant brain anatomy, development and functional activity. Post mortem analyses have been conducted, but usually with small sample sizes. Diffusion tensor imaging (DTI) is an MRI technique that measures the diffusion of water molecules in tissue. It produces images of white-matter tracts in the brain, allowing analysis of their density and maturation at different stages in development. The number of developmental PET, MRI and DTI studies is increasing, but these studies are typically limited to infants with suspected clinical symptoms because of the restrictive procedures of these methods. There is frequently disagreement over the interpretation of MRI images from infants in the initial 6 months after birth because of the relatively high water content of both grey and white matter at this stage. For a variety of reason, it is difficult to scan awake infants in fMRI paradigms that involve visual stimuli. EEG can also be readily carried out on infants, but as in adults, signals have poor spatial resolution. The use of MEG in infants is limited as standard scanners are too large to accommodate the infant brain and the field awaits development of suitably sized scanners.

NIRS has emerged as an important non-invasive technique for measuring the haemodynamic correlates of neural activity in infants in response to auditory, visual and tactile stimuli. It does not require the severe head-movement constraints of MRI and is well-suited for the study of the infant brain because of the permeability of the infant skull to infrared light, allowing examination of activity at a deeper level than in the adult brain. Innovative imaging paradigms will continue to provide a window into the emerging social brain in infancy.

consistent with previous research implicating the OFC in reward-related processing (Kringelbach, 2005).

While fMRI has excellent spatial resolution, it does not allow examination of the time course of brain activity (Box 1). Addressing this issue and that of the passive viewing conditions often used in fMRI contexts, Kringelbach et al. (2008) employed an implicit

paradigm to present infant faces to adults during magnetoencephalographic (MEG) imaging, which supports fine grained analysis of temporal neural activity. MEG revealed activity in the OFC within 130 ms when participants were presented with pictures of infant faces, a signal that was not observed for adult faces (see Fig. 5). Although the sample was too small to conduct

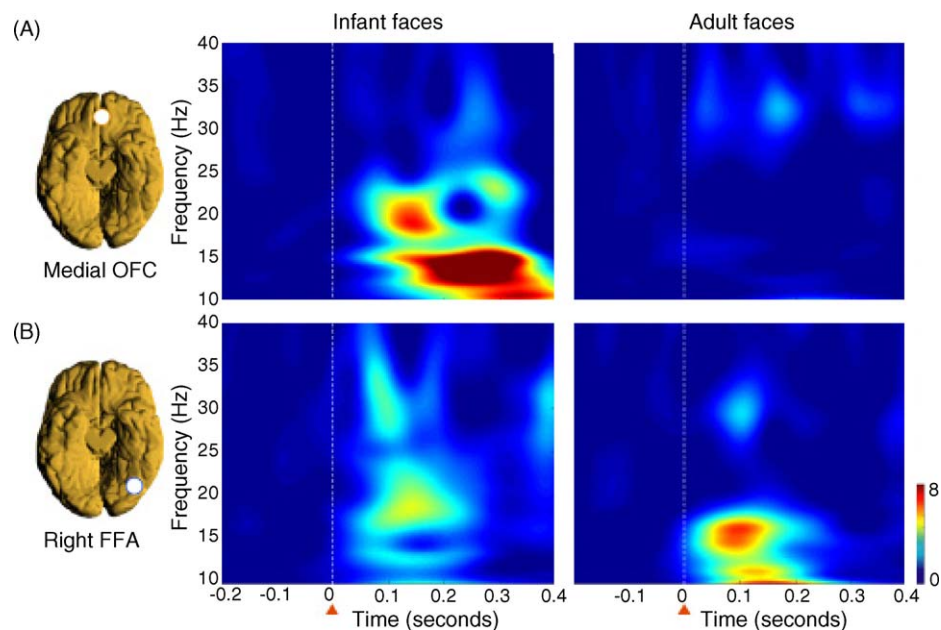


Fig. 5. A parental signature? Early adult brain responses to infant faces. Significant activity was present from around 130 ms in the right fusiform face area which did not discriminate between adult and infant faces, while the medial orbitofrontal cortex showed significant activity around the same time when viewing infant faces but not when viewing adult faces. The rows show time-frequency representations of the normalised evoked average group responses to baby and adult faces from the virtual electrodes show that the initial response to infant faces in the orbitofrontal cortex is present in the 12–20 Hz band from around 130 ms, and not present to adult faces (Kringelbach et al., 2008).

formal comparisons, this effect was evident in both adult males and females, and both parents and non-parents, possibly reflecting the neural basis for a caregiving response in adults.

4.2.3. Olfactory and tactile infant cues

The remaining unimodal infant cues, taste, odour and touch, have been studied to a far lesser extent. There is behavioural evidence that mothers can accurately recognise their infant by odour within as little as 10 minutes of postnatal contact (Porter et al., 1983; Russell et al., 1983). In mothers with several infants, those with higher baseline levels of cortisol performed more accurately on an infant odour recognition task than those with lower baseline levels (Fleming et al., 1997), suggesting that cortisol may be involved in olfactory sensitivity. In first-time mothers, higher baseline cortisol levels have been associated with greater affectionate touching of the infant (Fleming et al., 1997). Cortisol is the only hormone that has been related to accuracy in recognition, and pleasantness of infant stimuli.

While touch is a key social communication channel in other mammals, in humans it is typically limited to intimate relationships. Infant tactile behaviours can also elicit caregiving. For instance, infant rooting and sucking help obtain sustenance; the hand grasp reflex (palmar grasp) and reaching out of the arms (Moro reflex) help newborns establish contact and hold onto their caregivers (Eliot, 1999). After one hour of postnatal contact, blindfolded mothers can identify their own infant using tactile cues only, even when odour cues are controlled for (Kaitz et al., 1992), an ability which fathers demonstrate after an average of 6–7 h contact time (Bader and Phillips, 1999; Kaitz et al., 1994).

Early skin-to-skin contact between the mother and infant is beneficial to caregiving, supporting sensitive interaction and the development of attachment, particularly in pre-term infants (Anderson, 1991; Feldman et al., 2003; Ferber and Makhoul, 2004). Both fathers and mothers have been shown to touch their newborns in stereotyped ways, exploring the infant's arms and legs initially before moving onto the trunk (Parke and O'Leary, 1976; Parke et al., 1972). Parent–infant skin-to-skin contact has been shown to reduce the long-term stress response induced in infants by birth (Bystrova et al., 2003). A parent's touch can regulate their infant's arousal level and behavioural state as well as communicating information and discrete emotions (Hertenstein, 2002). Skin-to-skin (kangaroo) care is the most comprehensively documented developmental care intervention for preterm or low birth weight infants (Hamilton and Redshaw, 2009) and has been associated with both short- and long-term improvements in infant outcomes (Charpak et al., 2005; Feldman et al., 2002; Nirmala et al., 2006).

While there have been no neuroimaging studies to date examining the adult brain responses to infant touch, there have been some studies examining the affective components of touch likely to be relevant to future studies. A specific neural pathway of slow-conducting, C-afferent fibres that communicate information about pleasant, light touch to the insula could underlie processing of social somatosensory signals, such as a caress (Loken et al., 2009; Olausson et al., 2002). This links with findings of brain regions including the insular region (Olausson et al., 2002), the OFC and the cingulate cortex (Rolls et al., 2003) that have been associated with pleasant touch.

4.2.4. Multimodal integration: the importance of infant feeding

Nursing and feeding are the parental behaviours that are perhaps most associated with a new infant. It is widely assumed that breastfeeding has a positive impact upon the parent–infant relationship (e.g., Aguayo, 2001; Anholm, 1986; Leung and Sauve, 2005; Misri et al., 2000) and, indeed, breastfeeding has been shown

to help some mothers feel calmer (Uvnas-Moberg, 1996). In animal models, the hormones that affect milk stimulation and production have been shown to impact upon caregiving behaviour. There are also several non-nutritive features of breastfeeding and feeding more generally, including touch, close proximity and gaze that may be important for the attachment relationship.

Identifying the neurobiological responses underlying multimodal cues and contact such as those occurring in breastfeeding is even more challenging than for unimodal infant cues. The roles of cortisol, prolactin and testosterone have been investigated, but the mechanisms of their effects have not been described. Close contact with an infant, either through holding or breastfeeding, increases transient prolactin levels in mothers (Heinrichs et al., 2001). In addition, breastfeeding, but not holding, has a specific attenuating effect on cortisol stress responses and increases subjective ratings of 'calmness' in mothers (Heinrichs et al., 2001). Further, levels of oxytocin, a neurotransmitter purported to be essential for attachment in animal models (Insel, 1997) did not change before or after close contact with an infant. Fathers who were most responsive to infant cues had lower baseline and greater transient peaks in testosterone levels than less responsive fathers in a situational reactivity task (Storey et al., 2000).

4.2.5. Neuroendocrinal parental changes linked to birth

A considerable body of research has investigated the relation between neurotransmitters and caregiving behaviour. Many of the neuroendocrine studies are informative as to the normal neuroendocrine states of parent, prior to and during attachment formation. The precise role neuroendocrinal changes play in both short-term interactions and longer-term attachment formation is difficult to establish (for review, see Broad et al., 2006). Given the general success of adoption (Singer et al., 1985; van Ijzendoorn and Juffer, 2006), parturition-induced changes in neurochemistry are neither necessary nor sufficient for the initiation of attachment or unequivocal control of caregiving behaviour. Neurotransmitter systems influence each other in complicated, iterative and multidirectional ways, and unravelling relations between systems is difficult. Neurotransmitters can act as 'biological primes', facilitating the formation of an enduring emotional bond with offspring. The presence of specific neurotransmitters may predispose the brain's general reward-mediated mechanisms to facilitate mother–infant bonding at birth.

The birth of an infant is associated with numerous endocrinal changes in both mothers and fathers. While there is likely to be a complex relationship between multiple neuroendocrine systems, oxytocin has been ascribed a central role in maternal and social behaviour in animals (for reviews, see Carter, 1998; Insel and Young, 2001). Other key chemicals investigated in relation to caregiving behaviour are cortisol, prolactin, estradiol, progesterone, and testosterone. Pregnancy has a long-term effect on basal levels of hormones and neurotransmitters. Levels of cortisol, prolactin, estradiol and progesterone increase from baseline in women during pregnancy, as do levels of cortisol, prolactin and testosterone in men. Studies have found that cortisol levels peak during labour and decrease rapidly in the postpartum period (Storey et al., 2000). Changes in oxytocin levels are highly variable across women during pregnancy and in the first month postpartum: some women show increases from baseline, others decreases, and others still show relative stability (Levine et al., 2007). Low initial oestradiol to progesterone ratio in pregnant mothers, increasing in the 5–9th months of pregnancy followed by only small declines after birth have been associated with the strongest postnatal feelings of attachment to an infant (Fleming et al., 1997). While the physiological function of these hormones is well-established in animal models, there has been little investigation of the effects of hormonal changes around birth in humans.

In fathers, hormonal changes can be brought about by close contact with the mother (Storey et al., 2000). Short-term contact with an infant alters pulsatile levels of certain hormones, such as cortisol and prolactin in both mothers and fathers. Animal work and some preliminary human studies have implicated cortisol in short and long-term changes in emotional regulation in infant care. Elevated levels of cortisol have been observed in mothers with postnatal depression (Field, 1995) and have been found to predict elevated levels of cortisol in week-old infants (Lundy et al., 1999), indicating that hormonal changes in mothers have an impact on infant physiology. Studies of the human parent–infant relationship have relied on peripheral blood measures of oxytocin, which gives an imperfect index of the complexities of central oxytocin release. With this caveat in mind, in one study blood oxytocin concentration was found to correlate positively with the quality of maternal behaviour and maternal bond as measured by Yale Inventory of Parent Thought and Action (Levine et al., 2007). In recent work, blood oxytocin response to infant contact at 7 months was significantly higher in mothers whose own attachment status was secure, compared with mothers whose attachment status was insecure/dismissing (Strathearn et al., 2009). The oxytocin response was also correlated with activity in the hypothalamus/pituitary and ventral striatum regions 4 months later. It has long been theorised, but not empirically tested, that the physiological mechanisms supporting bond formation in non-humans may be comparable to that in humans. Clearly, the mechanism of action and role of each specific hormone varies as the parent–infant relationship develops from birth onwards.

5. Intuitive parenting and attachment

Beyond orienting and recognition, reciprocal interactions between the infant and parent must heavily depend on the social brain. One of the earliest reviews summarising the components of the adult social brain proposed roles for the OFC, amygdala, and the temporal poles in social behaviour (Brothers, 1990), broadly corresponding to the regions identified by affective neuroscience (Panksepp, 1991). Common affective networks involve key regions deep in the brain (nucleus accumbens, ventral pallidum, amygdala,

periaqueductal grey, hypothalamus, ventral tegmental area) and others in the cortex (see Fig. 6; OFC, mPFC, cingulate cortex and insular cortex; Amodio and Frith, 2006; Berns et al., 2001; Berridge, 1996; Cardinal et al., 2002; Everitt and Robbins, 2005; Krangelbach and Berridge, 2009a; Krangelbach et al., 2003; Krangelbach and Rolls, 2004; Watson et al., 2009). These hypothesised social and affective brain regions are likely to be recruited during the early parent–infant relationship because this is the most fundamental form of human social and affective behaviour.

The time surrounding pregnancy and childbirth is characterised by a preoccupation with the infant. While high levels of obsessive thoughts may be harmful at another point in life, in early postpartum these are not only typical, but may be critical to the formation of healthy maternal attachment. Such preoccupation may involve the same brain circuits assumed to underlie anxious and obsession-like thoughts namely networks involving the dorso-lateral PFC and orbito-striatal areas (Abramowitz et al., 2009).

5.1. Attachment

Social attachment is a universal process, provided that opportunities to interact regularly with a caregiver exist. While nearly all infants become attached to parents, not all become securely attached (Box 2). Parents generally experience heightened arousal and responsiveness in the period after childbirth, in which infant cues are especially salient (Fleming and Corter, 1988). Heightened responsiveness to infant cues may be a requisite for 'parental sensitivity', affording optimal attunement to the infant's needs. However, heightened sympathetic nervous system activity (heart rate increase and cortisol secretion) has been established as a feature of insecure infant attachment (Spangler and Grossmann, 1993; Spangler and Schieche, 1998).

Parents' representations of their own early attachment experiences have been shown to have an impact on their infant's attachment security (Fonagy et al., 1991; Steele et al., 1996; Van Ijzendoorn et al., 1991). Behavioural genetic studies have attributed the majority of variance in attachment security to environmental rather than genetic factors (Bokhorst et al., 2003). The neural underpinnings of human adult *attachment style* are not

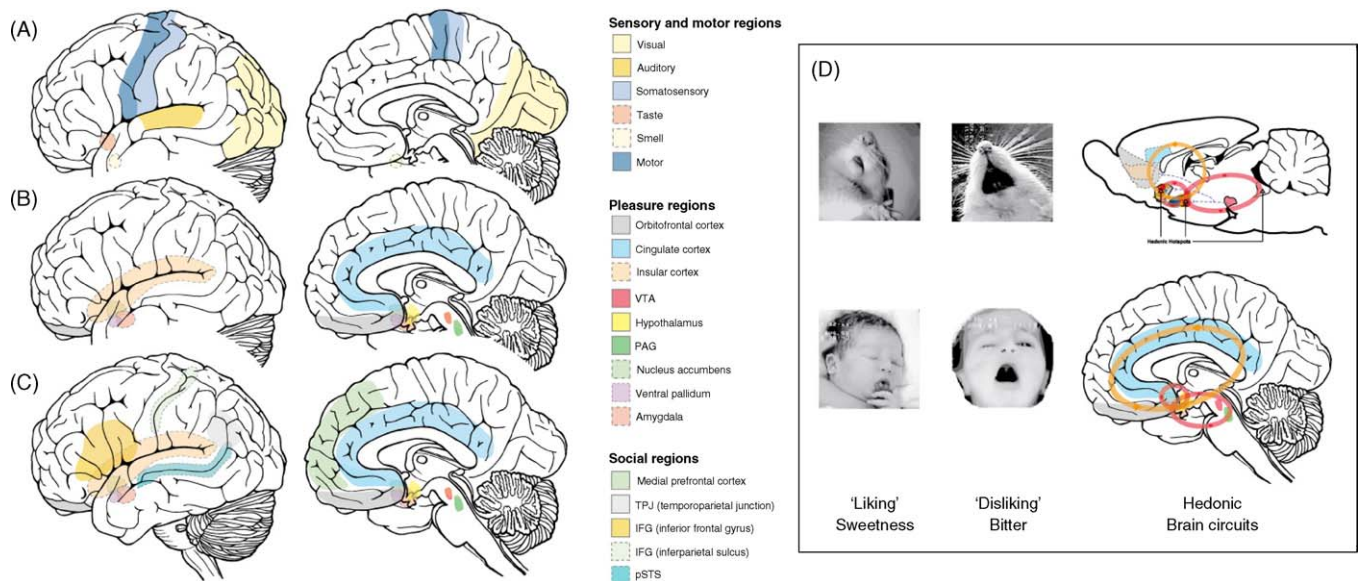


Fig. 6. Adult brain systems from sensation to basic pleasures and higher-order social processing. The schematic figure shows the approximate sensorimotor, pleasure and social brain regions in the adult brain. (a) Processing linked to the identification of and interaction with stimuli is carried out in the sensorimotor regions of the brain, (b) which are separate from the valence processing in the pleasure regions of the brain. (c) In addition to this pleasure processing, there is further higher-order processing of social situations (such as theory-of-mind) in widespread cortical regions. (d) The hedonic mammalian brain circuitry can be revealed using behavioural and subjective measures of pleasures in rodents and humans (Berridge and Krangelbach, 2008).

Box 2. Behavioural measures of attachment

The ‘strange situation’ paradigm (SSP; Ainsworth et al., 1978) is the most widely used instrument for assessment of infant attachment security (Solomon and George, 1999). The SSP is a structured 20 min procedure designed to examine by observation whether the infant uses the caregiver as a secure base under conditions of mild, increasing stress, from the entrance of a stranger to separation from the caregiver. The paradigm has good reliability and predictive validity (Teti and Nakagawa, 1990). Four discrete categories of attachment can be determined from the procedure: ‘secure’, and three ‘insecure’ attachment types. Within this coding system, secure infants are all treated as equally secure, whereas it seems more likely that infants will vary in their degree of security (Rutter, 1995).

Another widely used instrument in the measurement of infant attachment is the Attachment Q-set (AQS; Waters and Deane, 1985). The AQS is a continuous measure, thereby circumventing the categorisation issue of the SSP. The AQS is conducted in a natural setting instead of in a laboratory, and is considered to be more ecologically valid than the SSP (Rutgers et al., 2007). A further advantage of the AQS over the SSP is that it does not include separation or reunion of the infant and caregiver and is therefore less distressing. Van Ijzendoorn et al. (2004) reported that the observer AQS, but not the self-reported AQS, shows sufficient validity to be considered an appropriate measure of the attachment security of infants and toddlers. However, unlike the SSP, the AQS is not informative as to the type of attachment insecurity the infant presents with. There is no cut-off point dividing secure from insecure children. Both the AQS and the strange situation are designed for use after attachment is established, and are not designed for use within first year of life.

There are a number of measures currently used to assess the emotional aspects of the caregiver’s bond to an infant, including: Parental Bonding Questionnaire (Brockington et al., 2001; Papousek and Papousek, 1983), Parenting Stress Questionnaire (Loyd and Abidin, 1985), and self-report (e.g., Wojnar, 2004). Questionnaire-based measures are problematic because of social desirability effects on responding and may also be confounded by maternal mood or psychopathology.

While all of these measures have provided useful information about aspects of the parent–infant relationship, none are readily amenable to neuroimaging contexts. Neuroimaging techniques such as fMRI, MEG, NIRS and EEG have the potential to elucidate the neural mechanisms that underlie parental responsiveness to infant cues, and also infant responsiveness to parent cues.

yet well defined (e.g., Shaver and Clark, 1994). Animal models have implicated the amygdala and ventral striatum in mammalian attachment (Insel, 1997; Loup et al., 1991). Adult attachment anxiety has been associated both with increased activity in the anterior temporal pole, an area possibly associated with low mood (Levesque et al., 2003), and with lower activity in the OFC, a region associated with emotion regulation (Beer et al., 2004; Kringelbach, 2005; Levesque et al., 2003). Using a broad measure of adult attachment (the adult attachment projective) and fMRI, Buchheim et al. (2006) examined neural activity in women when presented with line drawings used to activate the attachment system (depicting illness, solitude, separation and abuse). Women with secure compared to insecure attachment patterns showed increased activity in the right amygdala, left hippocampus and right IFG, suggesting these regions are important in the attachment system.

In a study examining the neural basis of attachment security, Lemche et al. (2006) found strong positive correlations between levels of activity within bilateral amygdala, autonomic activity and measures of attachment insecurity during a stress prime condition. They suggested that the amygdala has a key role in mediating autonomic activity associated with human attachment insecurity. An electroencephalography (EEG) study in infants found that insecurely attached infants exhibited relatively reduced left frontal brain activity (Dawson et al., 2001).

6. Intersubjectivity

Communication in infancy develops in a domain of intersubjective learning (Stern, 1985; Trevarthen, 1979). For the newborn infant, communication involves interaction with a parent who intuitively modifies facial expressions, prosody of speech and related behaviours. Of these modes of early communication, the neural basis of infant speech perception has been most extensively studied.

6.1. Infant speech perception and production

In the majority of adults, the left hemisphere of the brain is specialised for speech processing (Binder et al., 1997; Szafarski et al., 2002). This hemispheric specialisation has been observed in infants within the first few days of life using NIRS (Pena et al.,

2003). By 3 months, normal and reversed speech elicits similar patterns of cortical activity in infants to that seen in adults (Dehaene-Lambertz et al., 2002). Using fMRI, Dehaene-Lambertz et al. found both types of speech stimuli were associated with activity in the left superior temporal gyrus (STG), but only normal speech was associated with activity in the left angular gyrus and left precuneus. These findings suggest that the cortical areas involved in adult speech perception are already active and to some degree functional at 3 months of age, well before the onset of speech production. In another study of 3-month-old infants using NIRS, bilateral activity was found in the frontal, temporal and temporoparietal regions in response to normal speech and ‘flattened’ speech, whereby the variations in pitch contour were removed (Homae et al., 2006). The right temporoparietal region exhibited more prominent activity in response to normal speech compared with flattened speech, demonstrating that this region is sensitive to pitch information in continuous speech, at least at the age of 3 months.

Between 4 and 10 months, infants start to produce a variety of vocal sounds (‘babbling’) and can differentiate between sounds in words (Kuhl, 2004; Oller and Eilers, 1988). A MEG study by Imada et al. (2006) found that newborns, six and 12 month old infants all exhibited activity in the STG (a sensory region associated with speech perception) specifically to speech stimuli. Activity in the inferior frontal region of the temporal lobe (a motor area implicated in speech processing) was found only in 6 and 12 month old infants. Finally at 12 months only, the responses of the inferior frontal region and STG appeared to be linked temporally. It is around this time that normally developing infants utter their first words (MacNeilage and Davis, 2000). ERP studies have started to identify the developmental time points at which the brain becomes differentially responsive to speech-related stimuli. At 7 months, there is distinct processing for native and non-native speech sounds (Kuhl and Rivera-Gaxiola, 2008; Kuhl et al., 2008; Rivera-Gaxiola et al., 2005) and at 11 months, known and unknown words (Thierry et al., 2003).

6.2. Processing of emotional expressions

Within the first few days of life, infants are able to imitate simple facial gestures, such as mouth opening and tongue protrusion (Meltzoff and Moore, 1983). From as early as 2 months,

infants can discriminate between smiling and frowning facial expressions (Barrera and Maurer, 1981), and by 5 months, fearful and angry expressions (Schwartz et al., 1985). By 7 months of age, infants recognise the same facial expression across individuals (e.g., Kotsoni et al., 2001). In adults, recognition of facial expressions recruits a wide range of brain regions, specifically, the amygdala, fusiform face area, insula, OFC, superior colliculus, striate cortex, STG and thalamus (for review, see Adolphs, 2002). Less is known about the neural substrates of facial expression processing in infancy. In one ERP study examining infants' processing of facial expressions, an enhanced Nc component was found in response to fearful faces that was not present in response to happy faces (Nelson and De Haan, 1996). Dipole modelling suggested that the cortical sources of the Nc component are located in the anterior cingulate and other prefrontal regions (Reynolds and Richards, 2005). There is some evidence that affective experience has an impact upon the infant's developing neural and behavioural responses to facial expressions. One study reported that infants with mothers who smiled a lot were found to look longer at fearful rather than happy faces, and those infants rated as having a positive temperament also demonstrated a larger Nc component to fearful faces (de Haan et al., 2004).

6.3. Infant development of joint attention

One of the major landmarks in early social, affective and cognitive development is the capacity to systematically engage in joint attention exchanges. Joint attention is a three-way social interaction that requires monitoring: a) another individual's attention in relation to the self; b) another object or event, and c) the other individual's attention toward that other object. It is widely accepted that by 18 months, children are capable of engaging in true joint attention (Bakeman and Adamson, 1984; Frith and Frith, 2003; Tomasello, 1995). In adults, the dorsal part of the medial PFC has been identified as underlying joint attention (e.g., Frith and Frith, 2003; Saxe, 2006b). A PET study by Caplan et al. (1993) found that glucose metabolism in the PFC positively correlated with later rates of change in the children's ability to initiate joint attention. EEG studies have also implicated frontal regions (Henderson et al., 2002; Mundy et al., 2000). In a longitudinal EEG study, left frontal and left and right central activity was associated with ability to initiate joint attention in both 14 and 18 month old infants (Mundy et al., 2000).

Henderson et al. (2002), using dense array electrodes for their EEG recordings, found that medial frontal cortical activity in both hemispheres was associated with improved ability to initiate joint attention. Responding to joint attention has been associated with slightly different regions than initiating joint attention, namely increased activity in the left parietal area and decreased activity in the right parietal area (Mundy et al., 2000). These areas have also been linked behaviourally to tasks that tap early attention shifting capacities in 4–6 month-old infants (Johnson et al., 1991a,b).

7. Higher functions

Social behaviours including joint attention, social referencing and cooperation are evident towards the end of the first year of life (Moore and Corkum, 1994). These behaviours have been interpreted as evidence for significant social understanding (Trevarthen and Hubley, 1978) and the beginnings of theory of mind (Bretherton, 1991).

7.1. Parent mentalisation about their infant

Research on the neural basis of thinking about other minds (Pelphrey et al., 2005; Saxe, 2006b) suggests that specific regions in

the medial PFC and temporal cortex mediate aspects of emotional empathy and collaborative behaviours. Understanding one's own behaviours and understanding those of others are abilities subserved by the same set of neural mechanisms (Frith and Frith, 2003; Gallagher and Frith, 2003). Components of the mentalising system need to supply the content of these thoughts, feelings and beliefs and their relation to people's actions. This knowledge is acquired partly from an understanding of the world based on past experience applied to the current situation, and partly from observations and predictions about people's current behaviour. Both types of knowledge contribute to the understanding of mental states and their relation to actions, and may be accessible via the temporal poles and superior temporal sulcus (Frith and Frith, 2003). Parental empathy requires understanding and predicting an infant's mental states and behaviours and experiencing appropriate emotions. Candidate neural circuits that could support parental empathy include a variety of cortical regions, specifically the OFC, inferior frontal, premotor, insular, temporo-parietal and cingulate cortices (Decety and Grezes, 2006; Saxe, 2006a).

7.2. Development of theory of mind

Neuroimaging studies of adults have reported a consistent set of cortical regions associated with thinking about other people's thoughts, or "theory of mind": the bilateral temporo-parietal junction, the medial PFC and the posterior cingulate cortex (Frith and Frith, 2003; Gallagher et al., 2000; Saxe and Kanwisher, 2003). At present, it is difficult to link the large body of behavioural studies of theory of mind in infants and young children to neuroimaging studies with adults because of our lack of knowledge of the developing human brain in terms of structure and function. The theory of mind system of the brain is generally accepted to be in operation by approximately 18 months of age, supporting implicit attribution of intentions and other mental states (Frith and Frith, 2003). Explicit theory of mind behavioural capacities appear to emerge between the ages of 4 and 6 years.

The inferior parietal lobule, the IFG and premotor cortex are thought to be involved in the detection of agency of an action (Rizzolatti and Craighero, 2004) and consequent purposeful imitation (Buccino et al., 2004). Single neuron recordings from these regions in primates suggest that they contain 'mirror neurons' that fire in the same way to both the observation and execution of a motor action. The hypothesised mirror neuron system has attracted interest as it has been suggested to underlie or serve as a rudimentary component of theory of mind (Gallese and Goldman, 1998). However, research in humans has been limited: single neuron recordings in humans are restricted to clinical purposes, and human studies have therefore relied on indirect neuroimaging techniques that have, to date, failed to identify a robust set of true 'mirror neuron' regions. Neuroimaging studies have employed 'repetition suppression' paradigms that assume activity in a region decreases with repeated performance of the same process. In theory, a mirror neuron region should demonstrate decreased activity with subsequent observation then execution, or execution then observation, of an action. The majority of fMRI studies to date have generally reported suppression in activity in particular regions during observation and then execution, or during execution and then observation of an action, but not both (e.g., Chong et al., 2008; Lingnau et al., 2009). However, there is some recent evidence that suppression in both conditions is found in the IFG (Kilner et al., 2009), although the relationship between the blood-oxygen-level dependent (BOLD) signal and underlying individual neuronal activity remains controversial, and further research in this area is required.

Critical components of theory of mind emerge in early infancy. Even so, infants do not pass the mirror test of self-recognition or

show fully self-conscious behaviours until they are about 18 months old (Frith and Frith, 2007; Lewis and Carmody, 2008; Rochat, 2003). Feelings of ownership and identification with movements and emotional gestures reflected in a mirror are possible only with a mental representation of a sentient self. While young infants display abilities characteristic of what may be termed as basic consciousness, they still have to undergo substantial maturation to achieve adult levels of consciousness (Zelazo, 2004). Conscious reflective capacity is necessary to formulate beliefs about the mental states of others, central to theory of mind. According to one prominent model of mature consciousness, there must be a global 'space or scene' where some kind of synthesis between past, present and future takes place in a dynamic flow of consciousness (Changeux and Dehaene, 2008; Lagercrantz and Changeux, 2009). There are many alternative views of the neural substrates that are involved in consciousness. The right anterior insular cortex may represent 'interoceptive cues', the sensory cues from inside the body that contribute to self awareness (Craig, 2002). The anterior cingulate cortex, along with other components such as the OFC, is thought to be involved in self-awareness in relation to motivation and goal-directed behaviour (Devinsky et al., 1995). More broadly, the anterior cingulate cortex and OFC are thought to play a role in the working memory component of consciousness (Dehaene and Naccache, 2001; Kringelbach and Berridge, 2008). The roles of these neural components, and their development in infancy, remain difficult to specify.

8. Conclusion

The evolutionary imperatives of survival and procreation are well-served by the social and affective nature of the early parent–infant relationship. Brain growth and maturation in infancy support the formation of the early parent–infant relationship; yet remarkably little is known about the underlying functional neuroanatomy in the early years. In this review, we have presented a behavioural framework for describing the development and timing of the various components and processes involved in the early parent–infant relationship. We have reviewed the existing evidence for its neural substrates in adults, while concurrently presenting a coherent picture of the brain basis of infants' abilities that allow them to initiate appropriate behaviours towards their parent or caregiver (Table 1). We have highlighted the difficulties involved in examining the interface between brain and behaviour in development. Brain–behaviour relationships are complex and challenging, and the early parent–infant relationship is likely to rely on networks dispersed across the brain, rather than a distinct circumscribed region.

We have presented evidence to suggest that the same adult brain networks involved in emotional and social interactions are already present in immature and incomplete forms in the infant. These networks involve key regions deep in the brain (nucleus accumbens, ventral pallidum, amygdala, periaqueductal grey, hypothalamus, ventral tegmental area) and others in the cortex (OFC, mPFC, cingulate cortex and insular cortex; Amodio and Frith, 2006; Berns et al., 2001; Berridge, 1996; Cardinal et al., 2002; Everitt and Robbins, 2005; Kringelbach and Berridge, 2009a; Kringelbach et al., 2003; Kringelbach and Rolls, 2004; Watson et al., 2009). Activity in the default resting state network emerges slowly and begins to resemble the adult default network at about 2 years of age, with one of the two central hubs in the medial prefrontal network starting to come online at 1 year (Gao et al., 2009), consistent with several developmental milestones. Further refinements continue to take place in later childhood (Fair et al., 2008) and it is not yet clear when the adult system is fully in place.

Future research might focus on the timing and changes in the connectivity between areas across development. Techniques that allow us to trace neural connectivity will also be extremely useful in this domain, as it is likely that the networks used in the development of a skill will be different from those seen in the mature brain. The use of advanced neuroimaging techniques, such as diffusion tensor imaging, with fine-grained behavioural tasks should enable investigation of the developmental time course of early relationship formation (Fig. 2; Dubois et al., 2008; Dubois et al., 2006; Paus et al., 2001; Ulug, 2002). In addition to this longitudinal structural information, we will also need more fine-grained temporal and spatial information about the functional neuroanatomy of infant brain activity. Much brain processing occurs on the scale of milliseconds rather than seconds, and thus methods such as EEG or MEG are more appropriate than haemodynamic methods such as fMRI.

Finally, it is important to interpret with caution correlations from neuroimaging studies with the complexities of the early parent–infant relationship. While these findings are important in the understanding of the mechanisms underlying early relationships, their causal significance remains to be demonstrated. A number of conditions, such as postnatal depression, disturb specific aspects of the evolving parent–infant relationship (Murray et al., *in press*). These naturally occurring perturbances alter one facet of the evolving relationship, allowing the study of its consequences for the developing parent–infant dyad. Postnatal depression, occurring in approximately 13% of mothers after birth (O'Hara and Swain, 1996), compromises measurable aspects of parental caregiving such as contingent responsiveness. Randomised clinical trials, which involve treating depression, and improving key parenting capacities, provide another window into the complex evolution of the parent–infant relationship, and infant development. Treatment trials provide the opportunity for a quasi-experimental elucidation of the brain mechanisms underlying the development of the parent–infant relationship. Neuroimaging studies of mothers before and after treatment for postnatal depression and other perturbances would allow strong inferences to be made about the putative neural requisites for early parent–infant interactions.

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