

Review

Understanding the human parental brain: A critical role of the orbitofrontal cortex

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The bond between a parent and an infant often appears to form effortlessly and intuitively, and this relationship is fundamental to infant survival and development. Parenting is considered to depend on specific brain networks that are largely conserved across species and in place even before parenthood. Efforts to understand the neural basis of parenting in humans have focused on the overlapping networks implicated in reward and social cognition, within which the orbitofrontal cortex (OFC) is considered to be a crucial hub. This review examines emerging evidence that the OFC may be engaged in several phases of parent–infant interactions, from early, privileged orienting to infant cues, to ongoing monitoring of interactions and subsequent learning. Specifically, we review evidence suggesting that the OFC rapidly responds to a range of infant communicative cues, such as faces and voices, supporting their efficient processing. Crucially, this early orienting response may be fundamental in supporting adults to respond rapidly and appropriately to infant needs. We suggest a number of avenues for future research, including investigating neural activity in disrupted parenting, exploring multimodal cues, and consideration of neuroendocrine involvement in responsivity to infant cues. An increased understanding of the brain basis of caregiving will provide insight into our greatest challenge: parenting our young.

Keywords: Parenting; Infants; Orbitofrontal cortex; Caregiving; Neuroimaging.

Given the extent and complexity of human infant needs, parenting represents one of our greatest social and practical challenges (Konner, 2010). We are intrinsically motivated by the pleasures of social interaction, of which the parent–infant relationship is arguably the strongest (Parsons, Young, Murray, Stein, & Kringelbach, 2010). This social relationship is of fundamental importance to the survival of the infant, and ultimately to ensure the survival of the species (Darwin, 1872). Even when survival is ensured, it has been shown that early experiences can have lasting effects on later cognitive and emotional development (Shonkoff, Boyce, & McEwen, 2009). Parenting of infants therefore reflects a biological necessity, and the

systems underlying parental behavior appear to be conserved to a significant degree across species (Numan & Insel, 2003).

A large amount of previous research behavioral, neuroimaging, and neuroendocrinal studies points toward core brain networks and neurotransmitters regulating parenting in mammalian species (Barrett & Fleming, 2011; Swain, Lorberbaum, Kose, & Strathearn, 2007). The human parental brain, studied to a far lesser extent than in other mammals, may share many of these features. Given the numerous features unique to human infancy, such as a prolonged dependency on a caregiver (Konner, 2010), direct comparisons across species are challenging. While

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core components may be shared across mammals, there are species-specific features of parental care and the underlying brain networks (Parsons et al., 2010; Swain et al., 2007). Recent growing evidence has suggested that the orbitofrontal cortex (OFC), a comparatively large brain area in humans and primates, may be crucially implicated in different phases of human caregiving behavior (Lorberbaum et al., 2002; Parsons, Young, Mohseni et al., 2013). This is consistent with current understanding of OFC function; in humans, the region acts as a nexus of reward-related processing (Kringelbach, 2005; Rakic, 2009; Zald & Rauch, 2006), and the parent–infant bond is inherently rewarding.

In this review, we consider the evidence for the OFC as a hub facilitating parenting; in particular, by allowing state transitions between the brain networks for predicting, evaluating, and responding to infant stimuli. First, we review the fundamental human parental capacities involved in caregiving. We show that the parent–infant interaction is a privileged subset of social interactions, and suggest that these interactions draw upon the overlapping brain networks for processing social and other rewards. Specifically, we focus on the role of the OFC in facilitating the early parental focus of attention, as exemplified by the evidence from behavioral and neuroimaging studies for neural processing of infant visual and auditory cues. These studies demonstrate multiple roles for the OFC in parenting, specifically related to (1) infant-specific cortical sensitivity, with early differential OFC activity in response to infant communicative cues (Parsons, Young, Kringelbach, & Stein, 2013), (2) social learning, and (3) domain-general functions such as prediction, processing of visual and affective cues, and reappraisal processes in responses to infants as social rewards.

HUMAN PARENTAL CAPACITIES

Parenting is a complex behavior that varies across cultures (Bornstein et al., 2012) and demands significant resources on the part of the adult (Konner, 2010). The provision of optimal care first requires the parent to focus attention to infant signals, and respond contingently and appropriately to these signals. Parenting is multicomponential, comprised of, but not limited to physical behavior patterns, supporting regulation of infant emotion, and consideration of the infant’s agency and intentions. In terms of what is immediately amenable to neuroscientific exploration, a clear starting point concerns the basic mechanisms of parental focus of attention to infant signals.

While parenting capacities form one side of the dyad, the relationship between a parent and an infant is bidirectional in nature. With this in mind, we have described a behavioral framework in which the parent–infant relationship can be considered (Parsons et al., 2010). As the postnatal period proceeds, interactions become increasingly complex and sophisticated, beginning with simple orienting to infant cues and culminating in prolonged interactions such as play, involving narrative structure and mentalizing aptitude. Our behavioral framework describes six major components of the parent–infant relationship over the first 18 months: (1) orienting system; (2) recognition system; (3) intuitive parenting; (4) attachment relationships; (5) intersubjectivity; and (6) higher socio-emotional and cognitive functions. Our main emphasis here, the parental focus of attention to child signals, draws mostly on the first three of these components.

Early interactions between a parent and an infant are characterized by an immediate propensity for each to 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 cues, such as “cuteness” (Darwin, 1872), which help to secure parental attentiveness. From the early postnatal period, the orienting system helps to initiate interpersonal 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 vocalizations in greeting (Papousek & Papousek, 1983). Infants show a comparable orientation to, and preference for, human over nonhuman forms from birth, as evidenced by their preference for face-like over non-face forms (Johnson, Dziurawiec, Ellis, & Morton, 1991) and their preference for speech over nonspeech sounds of similar pitch and intensity (Vouloumanos & Werker, 2004).

The general orienting response is superseded by a more selective *recognition system*. Both parent and infant become increasingly responsive to each other’s specific features, from birth or shortly thereafter. Mothers can accurately recognize their own infant early postpartum on the basis of single nonvisual cues, such as smell, cry, or touch (Cismaresco & Montagner, 1990; Kaitz, Lapidot, Bronner, & Eidelman, 1992; Porter, Cernoch, & McLaughlin, 1983; Russell, Mendelson, & Peeke, 1983). Within the first few days and weeks of life, infants also demonstrate preference for their mother’s face (Bushnell, 2001), voice (DeCasper & Fifer, 1980), and even

breast milk smell (Macfarlane, 1975). Crucially, therefore, the infant must be viewed as a dynamic participant within the dyadic, and often triadic, parent–infant relationship, with rapidly expanding interactive capabilities over the course of development. By about six weeks of age, infants show remarkable sensitivity to the qualities of adult communication (Brazelton, Koslowski, & Main, 1974; Papousek & Papousek, 1975). They actively pursue social interaction with a caregiver, and react in striking ways if such interactions are not forthcoming (Cohn & Tronick, 1983; Field et al., 1988). Therefore, the reciprocal recognition system functions to ensure prolonged parent and infant proximity, facilitating further interaction.

The processes underlying parental orienting and recognition have been conceptualized as instinctive or “intuitive,” forming a distinct class of social behavior (Papousek, 2000; Papousek & Papousek, 1987). These responses are hypothesized to occur too rapidly to be under conscious control and therefore referred to as “intuitive.” Evidence for such rapid, intuitive responses to infant cues comes from a number of human neuroimaging studies, using temporally sensitive methods. Two studies have demonstrated early differential responses to infant faces within one-seventh of a second, occurring in the OFC (Kringelbach et al., 2008; Parsons, Young, Mohseni et al., 2013). Other recent work has demonstrated rapid differential responses to infant vocalizations, within about 80 milliseconds, occurring in the periaqueductal gray (PAG) (Parsons, Young, Joansson et al., 2013). Taken together, these studies suggest that specialized caregiving responses to infant cues can occur early in time, and therefore may be considered as nondeliberate or intuitive.

In this review, we focus on two powerful elicitors of social attention for the infant: visual cues, including the face, facial features and expression, and vocal cues. In addition to being the most oft-studied infant cues to date, these two domains of infant cues appear vital to orienting, in that they initiate approach behavior and subsequent interaction. The basic orienting response to infant cues appears to be present among adults, regardless of parental status (Parsons, Young, Parsons, Stein, & Kringelbach, 2012; Sprengelmeyer et al., 2009), although the extent to which orienting to infant cues is modulated by parental experience is currently being explored. In one study, parents and nonparents showed similar face-specific neural activity and sensitivity in response to infant faces, as indexed by the N170 event-related potential (Noll, Mayes, & Rutherford, 2012). However, other studies have demonstrated more robust effects of parental status on responding to infant cues (Nishitani, Doi, Koyama, & Shinohara, 2011;

Proverbio, Brignone, Matarazzo, Del Zotto, & Zani, 2006).

Although nonparents appear to have a similar propensity for perceiving and orienting to infant cues as parents do, it is clear that parenting leads to greater sensitivity to cues from one’s own infant. It is probable that this sensitivity is supported by differential patterns of neural activity in response to a range of infant cues (e.g., Seifritz et al., 2003). Longitudinal studies of adults before and after becoming parents would be especially informative in this regard, although most studies have, to date, used cross-sectional comparisons of parents and nonparents to provide insight into the mechanisms through which parental experience affords such attunement. Nevertheless, we can capitalize on the conserved ability of nonparent adults to rapidly orient to infant cues to explore such capacities, while eliminating the mediating effects of parenting experience.

BRAIN NETWORKS UNDERLYING SOCIAL INTERACTION: RELEVANCE TO PARENTING

Interacting with an infant is considered to be inherently rewarding. Lorenz (1943) first proposed that infant cues have a high intrinsic reward value, which naturally attracts adults and motivates the provision of care. Indeed, adults typically respond to images of infants with the most conspicuous of pleasure responses: a smile (Hildebrandt & Fitzgerald, 1979). The pleasure of social interaction, alongside other adaptive pleasures such as food and sex, has also been proposed as intrinsically motivating, ensuring species survival (Kringelbach & Berridge, 2009). Pleasurable experience has been proposed to consist of a complex set of processes, each with distinguishable neurobiological mechanisms (Kringelbach & Berridge, 2009; Leknes & Tracey, 2008). These include at least the three psychological components, referred to as “wanting,” “liking,” and “learning,” and each has both conscious and nonconscious subcomponents. While “liking” represents the hedonic impact of a reward, “wanting” refers to a type of incentive motivation that promotes the approach toward and consumption of the reward. In the context of social interaction, an initial expectation and “wanting” for a reward (i.e., the inherent pleasure of a friendly interaction) often results in behavior to attain the reward (i.e., beginning a conversation), which is subsequently “liked.” Lastly, once reward-related cues are learned, the brain is able to represent predictive associations and cognitions, underpinned by prediction-error monitoring

in the OFC. The human neuroimaging evidence has demonstrated a significant overlap in the brain systems involved in the phases of wanting, liking, and learning of the pleasure cycle for the fundamental rewards (Georgiadis & Kringelbach, 2012; Kringelbach, Stein, & van Hartevelt, 2012; Parsons et al., 2010). In conceptualizing parent–infant interaction as a privileged subcategory within the broader field of social interaction, we can also consider aspects of this relationship in terms of a temporal distinction between “wanting,” “liking,” and “learning.”

Our understanding of parent–infant interaction can be informed by the progress made in understanding social cognition more generally. Social cognition is considered to be of such fundamental importance that some have argued that it may represent the “default mode” of cognizing in humans (Schilbach et al., 2006), emphasizing the importance of continuous attunement to the social environment in order to prioritize attention to biologically relevant stimuli. Previous research has made substantial progress in describing the brain networks underlying social interaction. Up to now, much of this research has not investigated different phases of social interaction, such as orienting, monitoring, or evaluation, but instead has grouped these together. This corpus of knowledge has thus implicated a vast network of regions in social cognition and interaction, although the extant literature has tended to be fairly “amygdala-centric,” following earlier research exploring social interaction in nonhuman primates (Prather et al., 2001). Some of the major brain structures involved in social cognition include the superior temporal gyrus and fusiform gyrus, superior colliculus and primary sensory cortices; premotor cortex, OFC, amygdala and ventral striatum; the anterior cingulate cortex, as well as regions involved in higher-level processes such as social reasoning, theory of mind, empathy, and moral cognition (for reviews, see Adolphs (2003), Eslinger (1998), Fiske and Taylor (2008), Frith and Frith (2010), Frith (2007), Lieberman (2007), and Moll and de Oliveira-Souza (2007)).

Within this extensive network, the OFC has been described as a crucial cortical relay, uniquely placed as a nexus for sensory integration, the modulation of autonomic reactions, and participation in learning, prediction, and decision-making for emotional and reward-related behaviors (Kringelbach, 2005). Furthermore, the OFC is specifically active at phase transitions, often alongside the anterior cingulate cortex; for example, when an individual is required to adapt their behavior to rapidly changing social cues (Kringelbach & Rolls, 2003). Given that human behavior is often unpredictable, flexible behavioral responses in a social situation are a key part of

successful interaction. This may be achieved by the unique ability of the OFC to integrate associative content from different domains, such as identity and affect, in order to generate predictions based upon the affective salience of stimuli (Chaumon, Kveraga, Barrett, & Bar, 2013). The link between affect and identity may allow the OFC to rapidly detect biological salience in the environment and identify it for further privileged processing. Indeed, in the context of infant-specific cues, the OFC appears to represent a rapid “neural signature of parenting,” reflected in its early, specific activity in response to infant cues.

It has been shown that the OFC appears to become active and engaged when inputs have enough information to allow object identification, compared to meaningless information such as gratings (Chaumon et al., 2013). Early information therefore reaches the OFC, having already been identified in terms of basic stimulus salience by primary sensory and subcortical regions. For instance, the PAG, a region of the brainstem closely connected with regions in the early visual pathways such as the superior colliculi, has been found to be active in studies where mothers view own-infant images or videos (Bartels & Zeki, 2004; Noriuchi, Kikuchi, & Senoo, 2008). The precise role of the OFC therefore appears to be related to cortical coordination of resources relevant to processing of domain-specific, biologically salient stimuli such as infant cues, but may also be involved in later processing in a more domain-general manner.

Although the orienting of adults to infant cues appears effortless and spontaneous, parenting also involves the need to make decisions, such as how to interact with an infant. When making decisions, the brain must predict and evaluate the reward values of stimuli and various behaviors interacting with them (Kringelbach, 2005; Rangel, Camerer, & Montague, 2008). The OFC is crucially involved in such processes, with functional subregions subserving different roles (see Figure 1). Whereas the medial OFC (mOFC) has been suggested to relate to monitoring, learning, and memory for reward, the lateral (lOFC) is suggested to relate to evaluation of punishers, which can lead to changes in behavior (Kringelbach & Rolls, 2004). Responsive caregiving is likely to draw upon a range of these functions, requiring ongoing monitoring, learning, and memory for infant cues, and also evaluation of these cues in order to adapt behavior. In addition, a region in mid-anterior OFC is thought to track changes in subjective pleasure (Kringelbach, O’Doherty, Rolls, & Andrews, 2003). This region may therefore provide a neural correlate of subjective pleasure considered to be inherent in interactions with an infant. The medial–lateral hedonic gradient may

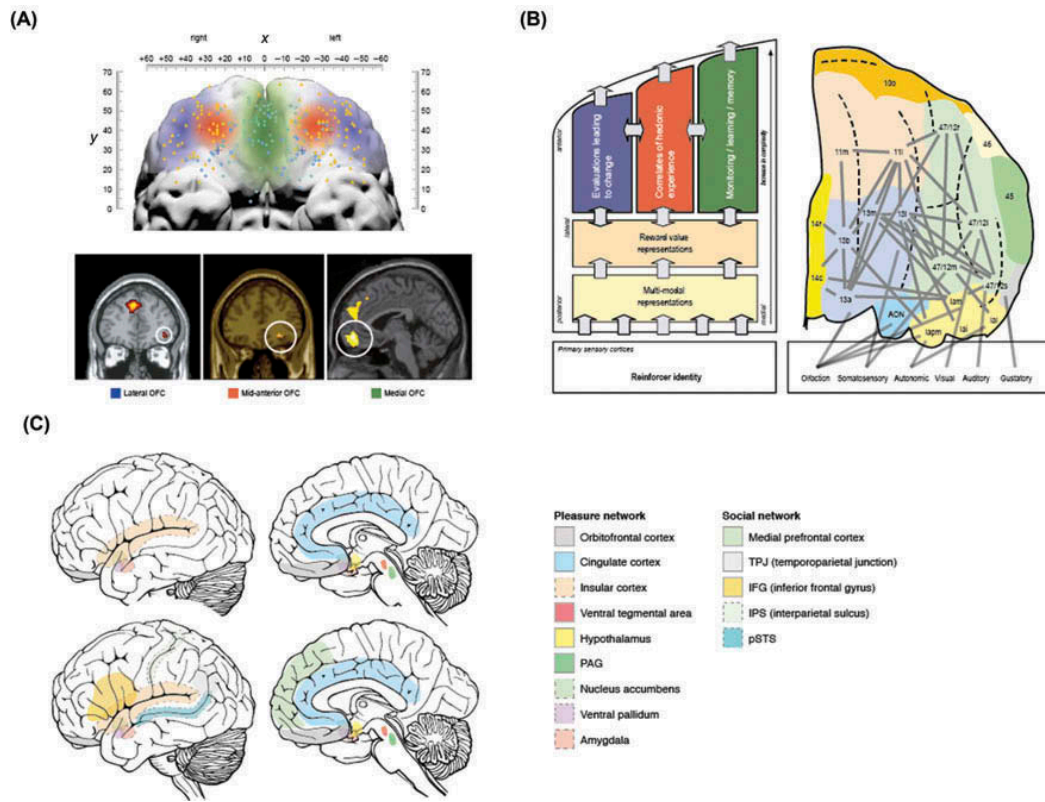


Figure 1. The functions of the orbitofrontal cortex; and the overlapping networks involved in social interaction and pleasure.

be considered alongside an abstraction-concreteness gradient in the posterior–anterior dimension, so that more complex or abstract reinforcers (such as monetary gain and loss) (O’Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001) are represented more anteriorly in the OFC than less complex sensory rewards (such as taste) (Small, Zatorre, Dagher, Evans, & Jones-Gotman 2001). Whether this distinction can be meaningfully applied to infant cues, which have complex sensory and abstract elements, is an issue for future work.

Despite ongoing dispute about the precise functional split of labor between the mediolateral distinction (e.g., Walton, Behrens, Noonan, & Rushworth, 2011), it is clear that choice behavior in uncertain environments, and the information gleaned from prediction-based learning in social interactions must feature within dynamic parent–infant contact. Learning through prediction-making and subsequent analysis of error, therefore, may provide the process of individuation involved in the parenting experience, allowing for optimization of “intuitive parenting” responses. It follows that the ability to explore OFC activity in response to infant cues might exemplify

how the brain coordinates a seemingly “cognitively impenetrable” orienting response (Fodor, 1983).

This review therefore considers three potential roles of the OFC in parenting. First, we consider an infant-specific cortical sensitivity, driven by findings indicating very early differential activity to infant faces and voices (e.g., Kringelbach et al., 2008; Parsons, Young, Mohseni et al., 2013). Second, domain-general functions of the OFC may be subsequently involved in responding to infants as socially rewarding beings. These include prediction-making, associative processing of visual and affective cues (Bar, 2004, 2007), and reappraisal processes (Kanske, Heissler, Schönfelder, Bongers, & Wessa, 2011). The third consideration concerns how the OFC may be a key region in the process of social learning, and therefore may be uniquely poised to provide insights into how parenting experience can lead to functional changes in the brain.

INFANT VISUAL CUES: FACES

The unique facial configuration of infants is thought to attract attention and evoke caregiving in adults.

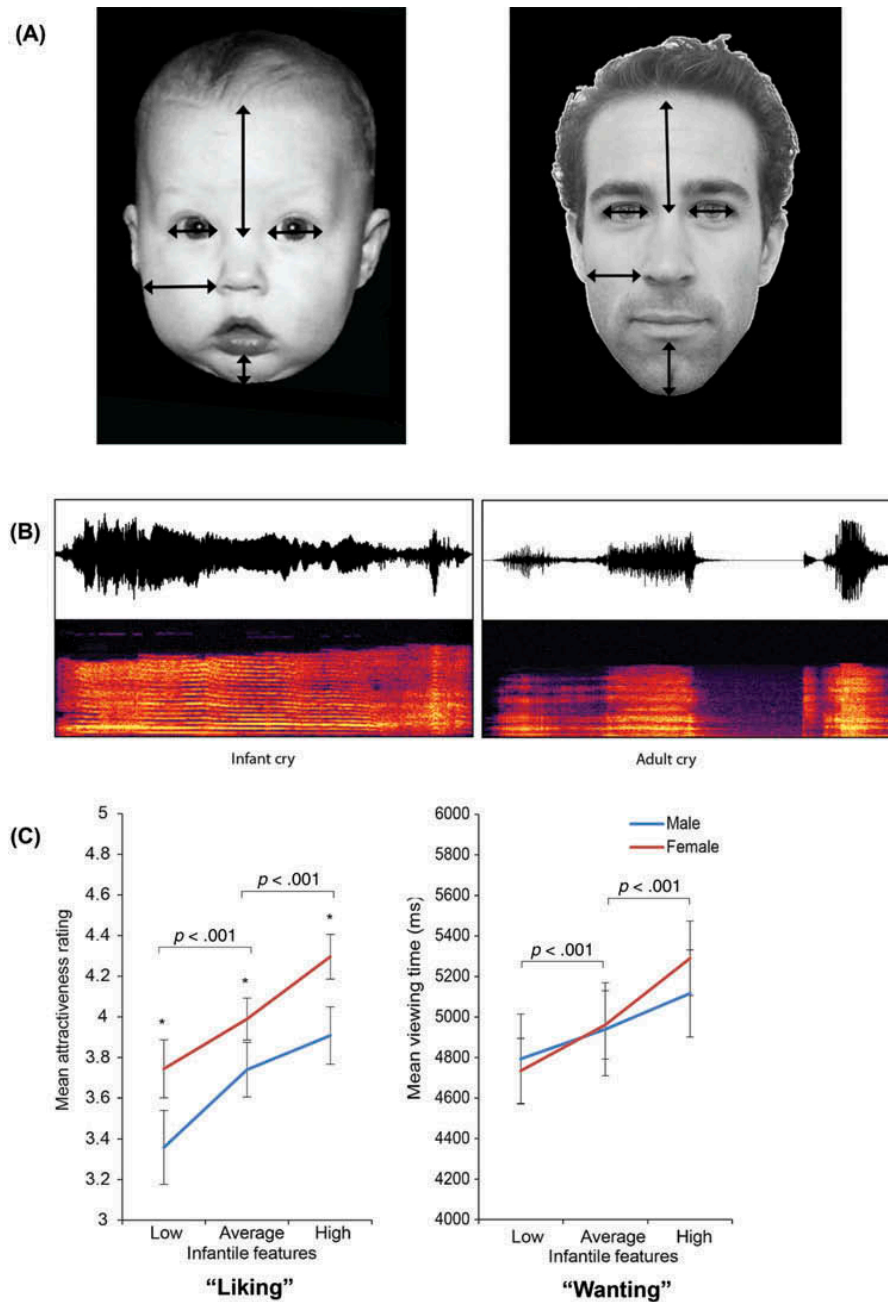


Figure 2. Physical differences between infant and adult faces and voices; and gender differences in perception. (A) Different facial configurations characterize infant and adult faces. Features typically described as “cute” include large eyes and pupils, small noses and mouths, a large forehead and cheeks. Left, image taken from Parsons et al. (2011); right, image taken from own database. (B) Typical features of an infant cry compared to an adult cry. Infant cries are characterized by high and variable pitch within the range of 200–600 Hz, and a longer duration of cry bursts and pauses. (C) “Liking” and “wanting” responses to infant faces of different levels of “cuteness,” separated by gender, taken from Parsons et al. (2011). Left, “liking” as indexed by adults’ attractiveness ratings of infant faces. Right, “wanting” as indexed by mean viewing times for the infant faces. Both men and women rated infant faces with more “infantile features” as significantly more attractive than infant faces with less “infantile features.” Despite a discrepancy between male and female “liking” ratings, both genders demonstrated comparable “wanting” to view the infant faces.

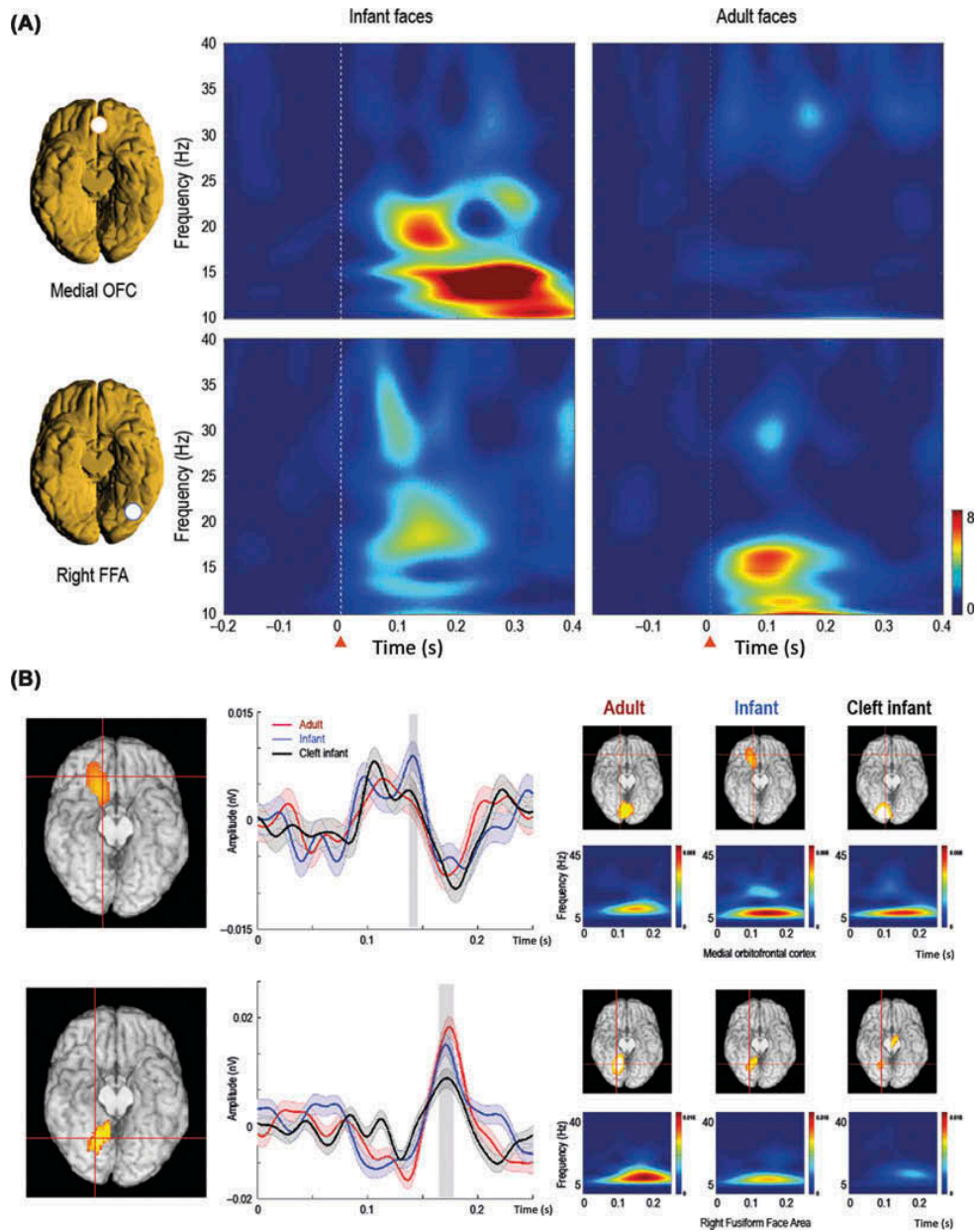


Figure 3. Evidence for privileged brain activity in response to infant cues. (A) Rapid, specific brain responses to infant cues. Using MEG, significant activity was present from around 130 ms in the medial OFC when viewing infant faces but not when viewing adult faces. Activity in the fusiform gyrus at around 170 ms did not discriminate between adult and infant faces. This shows time–frequency representations of the normalized evoked average group responses to baby and adult faces from the virtual electrodes show that the initial response to infant faces in the OFC is present in the 12–20 Hz band from around 130 ms, and not present to adult faces (Kringelbach et al., 2008). (B) Brain responses to infant, infant with cleft lip, and adult faces, using MEG from Parsons, Young, Mohseni et al. (2013). Left: transverse slices with group source reconstruction are shown. Right OFC activity (thresholded at $z > 3.1$) was present in response to infant faces but diminished for the infant faces with cleft lip or the adult faces. Middle: MEG waveforms, determined from beamforming analysis, from the OFC, averaged for the three different face categories, show a clear peak in response to typical infant faces at 140 ms. Right: the time–frequency plot shows greater alpha band activity seen in response to the typical infant faces compared with the other faces. The face-selective M170 in the right FFA was similar for the adult and typical infant faces, but substantially lower for the infant faces with cleft lip (left: transverse slices with group source reconstruction). Averaged group waveforms (middle) and time–frequency plots (right) illustrate the magnitude of this difference.

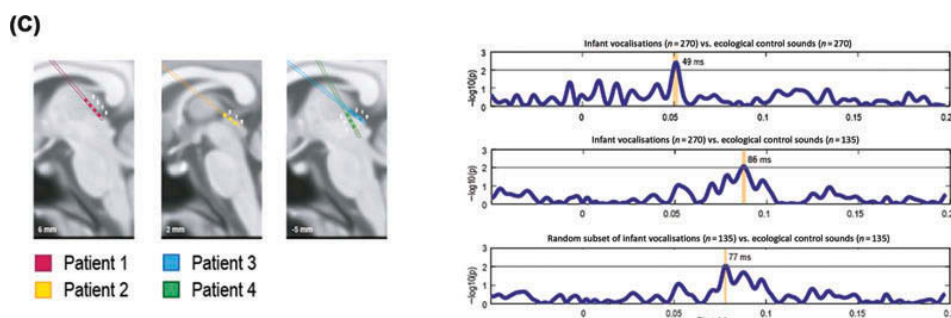


Figure 3. (Continued). (C) Very early response of midbrain (PAG) to human infant vocalizations measured by local field potentials from macroelectrodes implanted during deep brain stimulation (Parsons, Young, Joansson et al., 2013). Left, three sagittal slices of the averaged standard brain in MNI space (-5 , 2 , and 6 mm) showing the approximate locations of the implanted PAG/PVG electrode placements in each of the four patients (color-coded), with each contact point numbered. Each electrode had four contact points (those points that can be shown in the present slice are in filled color). Right, early differential response to infant vocalization sounds in local field potentials recorded from the midbrain (PAG).

Such features are viewed as pleasant and rewarding, and are often referred to as “cuteness,” including large eyes and pupils, small noses and mouths, and a large forehead (see Figure 2; Hall Sternglanz, Gray, & Murakami, 1977; Hildebrandt & Fitzgerald, 1979). There is a seemingly universal and spontaneous preference for infant facial features, conserved across multiple species (Sato, Koda, Lemasson, Nagumo, & Masataka, 2012). In humans, the heightened responsiveness and activity in brain networks implicated in communicative, infant-directed behavior is present in both parents and nonparents and specific to human infant faces, but not to faces of other infant mammals or adult faces (Caria et al., 2012). This reflects the specificity of infant-related responses, and indicates that specialized responses to infants can transcend the biological relationship between an adult and an infant.

Infant faces: Behavioral findings

It is hard to imagine a class of visual stimuli with greater biological salience than infant faces. Both children and adults consistently prefer pictures of infants over pictures of adults (Berman, Cooper, & Mansfield, 1975; Fullard & Reiling, 1976). Adults are also highly sensitive to even subtle changes in infant facial features (Sprengelmeyer et al., 2009). Perhaps the most convincing evidence for the importance of infant facial features in eliciting care comes from instances of facial anomaly, signaling compromised health. Cleft lip in infants has been associated with disruption of parental care (Field & Vega-Lahr, 1984; Murray et al., 2008), particularly in the case of severe disfigurement (Murray et al., 2008). Adults who are not parents have

also been shown to react negatively to both specific and global changes to the infant face, such as in cleft lip, fetal alcohol syndrome, and prematurity (Frodi, Lamb, Leavitt, & Donovan, 1978; Parsons et al., 2011; Waller, Volk, & Quinsey, 2004).

The attentional magnetism of “cute” infant attributes has so great a pull that *neoteny*, the process of giving human or nonhuman stimuli childlike, juvenile features, has even been used in a vehicular manner for use as a marketing tool. For instance, the Japanese culture has embraced the concept of “kawaii,” whereby toys, cartoon characters, entertainment, and fashion have become coveted by means of their “cute” and “charming” infantile attributes. Similarly to infant “cuteness,” items with “kawaii” attributes have similarly been shown to afford an advantage for tasks requiring focused attention (Nittono, Fukushima, Yano, & Moriya, 2012) due to heightened approach motivation and systematic processing. Such usage therefore capitalizes upon the capacity of baby schema to guide attention at early stages of visual and affective processing (Kringelbach et al., 2008). Infantile characteristics also activate reward systems in the brain and may induce more positive feelings for such stimuli, as has been demonstrated with baby-faced men (Zebrowitz, Luevano, Bronstad, & Aharon, 2009).

Not only do adults display a greater esthetic appreciation of infant visual cues, but they also display a greater “wanting” or incentive salience to view infant stimuli too, compared to images of adults, suggesting an inclination for further interaction. This parallels findings in other animals that reward consists of the distinct processes of wanting and liking, which in turn involve distinct yet partly overlapping brain and neurotransmitter systems (Berridge, 1996).

Crucially, whereas “liking” is frequently measured by explicit ratings of stimulus attractiveness, behavioral paradigms have measured “wanting” by implicit measures, where participants have control over how long they can view each image for. This hedonic stratification is important to consider when exploring responsiveness to biologically relevant cues. Essentially, it highlights the importance of assessing both the reward value of stimuli (“liking”) in the context of behavioral response (“wanting”), not unlike the proposed role of the OFC as a crucial “hub” of synthesis for identity, affect, and action (Bar, 2007; Chaumon et al., 2013).

Experience with one’s own infant may also serve to alter parental attraction and responsiveness to visual cues, relating to the third reward component, “learning.” This selectivity may function to enhance human parents’ capacity to seek out their own infant, in contrast to the nonselectivity seen in other species such as rodents (Swain et al., 2007). Mothers are able to recognize their own infants just by looking at their pictures, following between half an hour and five hours of exposure after childbirth (Kaitz et al., 1992; Kaitz, Good, Rokem, & Eidelman, 1988), and also demonstrate more positive emotions toward their own infants compared to unknown infants (Doi & Shinohara, 2012). The importance of experience with an infant is clear even in nonparents and exemplifies how learning both follows from, and shapes, future social interaction. For instance, a brief period of learning about experimentally manipulated infant temperament can change perception about physical parameters, such as the cuteness of an infant (Parsons, Young, Bhandari, Stein, & Kringelbach, *in press*).

Are women more attuned to infant cues than men?

Bowlby (1969) proposed that children are born with a biological predisposition to form one exclusive attachment relationship to aid survival, unique to their mother. However, Bowlby’s ardent emphasis on the mother as the focus of the monotropy has left a legacy of inequality in the literature surrounding parent–infant interactions, with fathers typically “kept in the wings” (Solantaus & Salo, 2005). A comprehensive study of parenting, therefore, requires consideration of both genders in interaction with infants. Exploring whether visual cues elicit caregiving behaviors differentially in men and women is first contingent upon understanding whether the motivational salience of infant faces is comparable for both genders, and in this domain, findings have been mixed.

The literature on gender differences in responsiveness to infants exemplifies the importance of considering behavioral data relating affect to action. For instance, women have been found to display greater overt positive appraisals of infant facial features, giving significantly higher attractiveness ratings than men (see Figure 2; Parsons et al., 2011; Sprengelmeyer et al., 2009). However, there have been inconclusive results concerning gender differences in the incentive salience to view “cute” infants. Men do generally appear less “attuned” to infant cuteness when asked explicitly (e.g., Lobmaier, Sprengelmeyer, Wiffen, & Perrett, 2010). Yet, although some studies have shown women to be more sensitive to infant cuteness than men when giving “liking” responses, others have found men not to differ on measures of “wanting” or incentive salience in response to infant cues (Parsons, Young, Kumari, Stein, & Kringelbach, 2011; see also Hahn, Xiao, Sprengelmeyer, & Perrett, 2012). One crucial difference in the distinction between “liking” and “wanting” is the element of conscious processing. It may be that men are less conscious of, or less willing to admit, the extent of their “liking” of infant cues. The reasons underlying these findings remain to be explored, for example, lower explicit ratings of infant attractiveness in males might be a consequence of societal expectations concerning gender roles in parenting (Lamb, 1975). Potential differences between the genders warrant investigation, but may not be as robust or as great in magnitude, as previously thought.

Infant faces: Neuroimaging evidence

Activity within the OFC in response to infant faces but not adult faces has been documented across multiple imaging methods, including: electroencephalography (EEG) (Proverbio, Riva, Zani, & Martin, 2011), magnetoencephalography (MEG) (Kringelbach et al., 2008; Parsons et al., 2013), and functional magnetic resonance imaging (fMRI, Baeken et al., 2009; Glocker et al., 2009; Leibenluft, Gobbini, Harrison, & Haxby, 2004; Montoya et al., 2012; Nitschke et al., 2004; Ranote et al., 2004; Strathearn, Li, Fonagy, & Montague, 2008). Given that faces are socially salient stimuli, any activity specifically in response to the infant faces is taken to reflect privileged processing of infants. In general, these findings have converged upon a set of key structures centered around the OFC and dopaminergic reward systems, and are suggestive of infant-specific activity early on in processing.

Parental orienting to infant cues is hypothesized to instigate processing that prioritizes infant stimuli as “attentional magnets,” re-allocating brain resources

to focus on caregiving behaviors. Localized activity has been found in the medial OFC within a seventh of a second following stimulus presentation, to infant (but not adult) faces. This activity was found in adults of both genders, in parents and nonparents, suggesting a general caregiving instinct amongst all adults. These findings, although tantalizingly indicative of a neural basis for orienting to infant cues, remain some distance from a comprehensive understanding of the connectivity and time course of activity between regions and corresponding behavior. Little evidence exists regarding how such neural markers of responsivity actually relate to caregiving behavior. It may be helpful therefore to consider activity in the mOFC as a potential biological basis for the orienting stage or “innate releasing mechanisms” initially posited by Lorenz (1943), *promoting* but not *determining* caregiving in response to infant cues. Seemingly, the differential activity seen for infant and adult faces is indicative of the rewarding value of “cute” infant faces, a view which is reinforced by evidence from other key reward regions, such as the nucleus accumbens, that show-modulated activity by subtle graded manipulation of the cuteness of infant faces (Glocker et al., 2009).

Our understanding of how “learning,” as a crucial outcome and component of reward, may alter the functional neuroanatomy underlying parenting is currently limited. Neuroimaging data complements behavioral findings of enhanced responsivity to own-infant cues and an “own-infant preference” among parents. For instance, mothers display a unique response to their own infant faces compared to unknown infant faces in key dopamine-associated reward-processing brain regions including the OFC, anterior cingulate and insular cortices (Strathearn et al., 2008). Rather than this being an effect of familiarity alone, as one would display with any previously acquainted social partner, differential neural activity in mothers to images of their own versus *familiar* infants can also be differentiated in regions relating to reward, including the OFC (Bartels & Zeki, 2004). This suggests that processing of own-infant stimuli leads to a progressive attunement of brain networks involved in processing of such rewarding, biologically and personally salient stimuli.

Sensitivity to infant cues, therefore, is flexible as demonstrated by the effects of experience in adults when they become parents. While nonparents’ experience with infants as social partners may serve to alter their perception and responsivity to infant cues, the learning involved in the rewarding aspects of parenting may also be privileged. Evidence to date is limited concerning whether and how the brain may

undergo functional changes in response to the experience of parenting, although animal studies are suggestive of functional changes in many areas, including prefrontal regions related to the expression of parenting behaviors (e.g., Lonstein, Simmons, Swann & Stern, 1998). One human study using structural imaging has reported gray matter changes during the early postpartum period in new mothers (Kim et al., 2010), although many important questions remain. For example, structural changes in the OFC, associated with parenthood, may occur as a consequence of repeated changes in functional activity after accumulated experience with infant cues. Further, whether such proposed functional changes are a consequence of orienting responses or reward-related processing is an open question.

What happens when infant visual cues are disturbed?

A critical question concerns the possible impact upon parent–infant interaction in circumstances where the configuration of the infant face is naturally altered. Conditions where the infant is born with an altered facial configuration provide a strict test of whether the infant facial structure elicits specialized processing in adults. Behavioral studies of adults responding to unfamiliar infants with and without facial abnormalities have demonstrated that changes to the infant facial configuration can compromise adult responsivity.

Cleft lip in infancy has been the most studied facial abnormality with reference to adult motivational processing, and is associated with raised risk for difficulties in mother–infant interactions (e.g., Field & Vega-Lahr, 1984; Koomen & Hoeksma, 1993). It is also the most common congenital condition affecting the face and cranial bones, with an incidence of 1 in 700 live births in the United Kingdom (Goodacre & Swan, 2008). Such a condition affects specific features of the typical infant schema, although global facial features may remain unaffected. Compelling evidence for the importance of these facial features in parent–infant interactions comes from a study of infants with cleft lip undergoing early or late surgical cleft lip repair. In this study, infants who had “late” cleft lip repair (at 3–4 months, compared to early neonatal surgical repair) displayed poorer cognitive outcome at 18 months. These outcomes were shown to be mediated by difficulties in parent–infant interactions (Murray et al., 2008), which were marked in infants with more severe cleft lips.

Functional neuroimaging using MEG of adults viewing healthy infants and infants with cleft lip was used to test the causal relationship between infant facial configuration and OFC activity (Parsons, Young, Mohseni et al., 2013). Significant activity was found in the right OFC at around 140 ms in response to typical infant faces, replicating previous results by Kringelbach et al. (2008). However, diminished activity in the same region was found for the cleft lip infant faces or adult faces, suggesting that early OFC responses are remarkably sensitive to the typical structural configuration of infant faces. Furthermore, one fMRI study found evidence of an interaction among adult personality traits (in this case, harm avoidance) and appraisal and arousal in response to infant faces that were either happy, or sad-looking with corresponding facial disfigurement (Baeken et al., 2009). Here, OFC activity was again evident in response to processing of infant faces, although the nature of fMRI data prevents us from telling whether this OFC activity was found early on (indicating orienting) or later in processing, possibly related to reward monitoring and evaluation.

INFANT AUDITORY CUES: VOCALIZATIONS

For an infant, communicative cues comprise both facial and vocal components. Vocalizations, particularly distress cries, allow the infant to capture the attention of a caregiver from a distance. While crying is present from birth, other communicative signals such as laughter and babbling are gradually added to the infant's vocal repertoire, both of which appear at around four months (Oller, 1980). The ability to respond to infant vocalizations, universal in mammalian species, is fundamental to parental responsivity (MacLean, 1990).

Infant distress cries: Behavioral findings

One of the most conspicuous infant cues communicating a need for care is the "biological siren" of crying. Put simply, infants will cry when in distress, and stop crying when their needs are fulfilled, but how best to characterize infant cries has been hotly debated. Attempts to divide infant cries into acoustically distinct categories, such as pain, hunger, or separation, have had only mixed success, and researchers now tend to describe cries as "graded signals" (Soltis, 2004). It has also been argued that caregivers may

use acoustic information, together with other cues, to guide caregiving behavior (Young, Parsons, Stein, & Kringelbach, 2012).

A distressed infant's cry, characterized by a high and variable pitch (see Figure 2), can elicit autonomic arousal in the listener, as demonstrated by physiological measures including heart rate, blood pressure, skin conductance (Boukydis & Burgess, 1982; Zeskind & Collins, 1987), and even in handgrip force (Bakermans-Kranenburg, van Ijzendoorn, Riem, Tops, & Alink, 2012). Such changes may serve to prepare adults to react rapidly to infant needs. Certainly, there is a link between the magnitude of physiological response and parental responsivity, as parents who exhibit greater physiological arousal are more likely to respond swiftly (Del Vecchio, Walter, & O'Leary, 2009).

These physiological changes in arousal after hearing an infant, if functionally important, should translate into altered or improved behavioral responsivity. Indeed, it has been demonstrated that participants show improvements in fine motor performance after listening to infant distress vocalizations, compared to adult distress or bird vocalizations (Parsons et al., 2012). Combined with evidence that hearing infant cries disturbs normal performance on simple cognitive tasks (Morsbach, McCullough, & Clark, 1986), this finding suggests that infant cries may both orient people away from less biologically salient tasks, and afford an advantage in subsequent motor movements (Parsons et al., 2012). The immediate improvement in participant motor performance may reflect a readiness to address the distressed infant.

The ability to respond appropriately to infant cries is also associated with the ability to respond to other infant cues (Frodi & Lamb, 1980), suggesting that responsivity is not purely modality-specific, but reflects a more general mechanism. Indirect evidence for the notion of modality-independent responsivity to infant cues comes from instances of disrupted parenting. In postnatal depression, problems in both processing of facial cues and vocalizations have been documented (Stein et al., 2010). Mothers with depression have been shown to be less sensitive to pitch differences in infant cries than healthy mothers (Donovan, Leavitt, & Walsh, 1998), although there may be protective factors in the relationship between depressed mood and auditory discrimination of infant cries, such as musical training (Young et al., 2012). Sensitivity to an infant's cries has been found to distinguish reliably between mothers with and mothers without postnatal depression (Murray & Cooper, 1997). Indeed, it may be that key infant communicative cues undergo largely similar processing, independent of modality.

Infant vocalizations: Neuroimaging evidence

Infant cry vocalizations convey important affective and physiological information, and have been shown to elicit specialized activity in a host of brain regions. One fMRI study with healthy, breastfeeding, first-time mothers found more activity in several brain regions specifically related to infant cries and not white noise, including the medial thalamus, medial prefrontal, and right OFCs (Lorberbaum et al., 1999, 2002). Subsequent studies have confirmed these regions as prime candidates for the brain networks contributing to human maternal behavior, vital for mammalian emotional response and regulation to infant cues (e.g., Seifritz et al., 2003). What remains unclear is whether the OFC is also sensitive to differences in the infant cry, such as graded acoustic information. Furthermore, recent evidence suggests that differential brain activity in response to infant distress cues in mothers must also be viewed alongside neuroendocrine system activity. Indeed, peripheral levels of the “neurohormone of attachment,” oxytocin, have been found to be higher in mothers who demonstrate secure attachment to their infant compared to mothers who demonstrate unstable attachment patterns. Crucially, those “high oxytocin” mothers also showed correspondingly higher levels of activity in reward-related brain regions (Strathearn, Fonagy, Amico, & Montague, 2009). Associating endocrinal factors alongside both behavioral differences (such as attachment) and brain activity promises to elucidate the functional properties of “parenting networks” by affording further variables that may moderate the parent–infant relationship.

“Learning,” as a component and consequence of reward again, appears to affect the OFC and more general brain responses of parents to infant vocal cues. Similar to the findings regarding visual infant cues, parenthood appears to lead to functional changes in parental brain circuitry when processing infant vocalizations such as crying. When mothers were played video clips of their own distressed, crying infant without sound, the OFC, PAG, anterior insula, and dorsal and ventrolateral putamen were all specifically active in response to one’s own infant (Noriuchi et al., 2008). Here, a differential pattern of activity in the dorsal OFC was found for videos of one’s own infant when smiling, compared to the crying video clips, suggesting a strong and specific brain response for own-infant distress.

While the OFC may function as an early cortical hub responding preferentially to infant-specific cues such as crying, subcortical regions may also be

implicated in early processing of infant cues. One region of the brainstem, the PAG shows differential responses to infant vocal cues relative to other salient and acoustically similar sounds, within 80 ms (Parsons, Young, Joensson et al., 2013). Such findings indicate fast subcortical processing of infant stimuli, likely to complement OFC processing. While they can act as important clues as to the infant’s affective and physical needs, there is much ambiguity inherent in the cries of infants (Soltis, 2004). Uncertainty is also inherent in parental behavior toward their infant. For example, an adult will typically open their arms wider to pick up an infant crawling toward them unsteadily, compared to an infant sitting down, as they cannot predict whether the crawling infant may falter or change direction. Similarly, when responding to infant cries, the parent does not typically know the reason behind the infant’s distress, or the optimal behavioral response, if one exists. Therefore, the OFC might have greater involvement in further processing to resolve the “uncertainty” about infant needs and the appropriate caregiving behavior. One such view characterizes the OFC as involved in decision-making under ambiguity (Bach & Dolan, 2012). Paralleling earlier explanations of OFC function in terms of monitoring and evaluation, Bach and Dolan (2012) consider the OFC as involved in representing and resolving uncertainties regarding rules (for example, the probability of an infant cry meaning either hunger or illness) and outcomes (even if the adult knows the precise odds of their infant being hungry, they still ultimately don’t know whether they are or not). Such processing may be particularly pertinent to resolution of the variable and ambiguous infant cry signal.

Infant laughter: Behavioral and neuroimaging findings

Communicating a very different affective state to crying, infant laughter emerges reliably at around four months after birth (Ambrose, 1963; Darwin, 1872). An earlier ontogenesis of smiling perhaps also contributes to paternal responsivity to infant affective communication, with infant smiles becoming contingently linked to maternal talk and smile, by the second and third months postpartum (Lavelli & Fogel, 2002). Positive affective expression, be it laughter or smiling, elicits warmth and care in adults, and crucially attracts their attention (Bowlby, 1969).

The neural processing of infant laughter has been studied far less, in comparison to infant distress cries, and yet it is an important infant cue in maintaining interaction with a caregiver and facilitating

attachment. For instance, the incentive salience of infant laughter appears to be elevated by oxytocin administration in nulliparous women (Riem et al., 2012), which is hypothesized to enhance parent–infant bonding. Furthermore, the motivational tendencies of adults and the valence of the infant cue (i.e., happy compared to sad faces) may also modulate the neural response (Montoya et al., 2012). The next step is to translate differences in neural activity as a function of affective expression to specific parenting behavior and learning. For instance, the OFC has been implicated in the detection and evaluation of reward valence in addition to monitoring reward values (Kringelbach, 2005). Specifically, it has been suggested that where a punishment is conceivable, the lateral portion of the OFC is involved in responding to counteract negative reinforcement. It is therefore conceivable that cues may be both processed differently, and responded to differently in parents.

Emerging evidence has demonstrated a number of significant differences between parents and nonparents, when directly contrasting their responsivity to different vocalizations such as crying compared to laughter. One fMRI study found distinct patterns of neural activity in parents compared to nonparents in response to infant vocal cues in the amygdala and other limbic regions. Parents showed stronger activity in these regions in response to infant cries, whereas nonparents showed stronger activity to infant laughter (Seifritz et al., 2003). Evidence from event-related potentials also suggests that motherhood may lead to enhanced efficiency in processing of infant cues, but only at later cognitive evaluation stages (Doi & Shinohara, 2012).

SUMMARY OF ADULT RESPONSE TO INFANT CUES

Both infant visual and auditory cues have been shown to elicit OFC activity, which may support efficient orienting of adults' attention to infant needs. Infant cues indeed act as "sign stimuli" to communicate biological salience and motivate adults to provide care through reward-based and affective associations. Yet, although the literature on the affective and rewarding nature of parenting is enormous, (e.g., Bowlby, 1969; Lorenz, 1943; Papousek & Papousek, 1987) the advent of functional neuroimaging and the integration of parenting within the domain of social neuroscience offers unparalleled opportunity to understand the parent–infant bond.

The parent–infant bond is undoubtedly imbued with emotional salience, and typically forms with little

conscious effort. Given that emotions consist of a physiological and neurological reaction leading to specific voluntary and involuntary patterns of behavior (Ledoux, 2012), emotion is one source of exogenously or endogenously cued information that guides us in decision-making. The OFC is an obvious potential region for coordinating the link between stimulus identity, reward value, and affective processing (Bar, 2004; Kringelbach & Rolls, 2004). Social signals, and especially biologically salient social signals such as infant cues, are represented in terms of both sensory and affective information, and these components of stimulus identity are not easily separable. The need for rapid processing and categorization of stimuli in terms of their affective value, as well as identity, provides an adaptive mechanism to ensure that what is important is oriented to and guaranteed immediate attention.

Yet, what is also clear from our exploration of the literature is that infant cues do not just orient the adult to the infant, but also convey a wide range of information, including affective expression. Here again, the overlapping neural circuitry for reward and affective processing provide an important link to understanding motivational factors underlying parental behavior. In addition to "liking" being a useful characterization of parental responsivity to infant cues, "wanting" also represents a hedonic dimension characterized by motivation to act.

As a uniquely placed cortical area, the OFC functions to integrate sensory and affective information to modulate motor responses. Following orienting, separable patterns of activity may mediate different types of parental behavior. For instance, it has been suggested that whereas descending connections may modulate basic reflexive caregiving behaviors such as grooming, ascending connections involving mesocortical and mesolimbic dopamine systems may be more involved in motivational and flexible behavioral responses to infant cues (Lorberbaum et al., 2002). This distinction potentially parallels the mediolateral trend in the OFC with regard to monitoring and evaluation (Kringelbach & Rolls, 2004), with monitored reward values of reinforcers perhaps being available for further sentient processing to guide behavior, and the lateral evaluative function leading to more pre-scient activity in motor regions to induce appropriate behaviors.

FUTURE DIRECTIONS

Early parental influences have far-reaching consequences on the infant's development in a range

of domains, such as behavioral, social, cognitive, and even physical development (Downey & Coyne, 1990; Goodman, Brogan, Lynch, & Fielding, 1993; Rahman, Iqbal, Bunn, Lovel, & Harrington, 2004). Understanding the brain basis of how adults come to raise their children, therefore, is an enormous, but worthy, challenge. We highlight four routes that are promising for investigation.

First, it would be of great clinical importance to further our understanding of the circumstances in which parent–infant interaction is compromised. Conditions affecting either the infant or the adult can have profound consequences for the parent–infant relationship. On the part of the infant, conditions affecting the local or global facial structure, such as cleft lip, William's or Down's syndrome, impact the parent–infant relationship, in different ways, and for different reasons (Montirosso et al., 2012; Sarimski, 1996; Slonims, Cox, & McConachie, 2006). Understanding whether and how these conditions affect parents' processing of infant signals at the neural level may inform how best to support interactions between parents and infants.

Conditions affecting the parent, such as postnatal depression which affects substantial numbers of mothers and fathers (15% of mothers, Murray et al., 2010; 5–10% fathers, Paulson & Bazemore, 2010), have been shown to disrupt parental responsiveness to infant cues. While some studies have begun to investigate the effects of postnatal depression on brain processing of general emotional cues (Moses-Kolko et al., 2010), and responses to infant emotional faces (Barrett et al., 2012; Laurent & Ablow, 2013), a comprehensive investigation awaits. Since a substantial proportion of mothers with postnatal depression remit within a few months (Cooper & Murray, 1998), longitudinal studies of maternal brain responsivity hold particular promise.

The second potential route for further work is to extend current understanding of responses to infant cues beyond infant faces and voices, into other modalities, such as olfaction and tactile responses. Although a body of knowledge has emerged describing the parental response to infant cries and infant facial features, these only represent a small fraction of the wide repertoire of infant communicative cues. For instance, infant cues are rarely presented unimodally in naturalistic settings, so a significant challenge remains to explore adult responsiveness to multimodal cues. Some studies have begun to use dynamic video stimuli (e.g., Noriuchi et al., 2008), although such examples represent a small minority.

Furthermore, examining how parents come to understand and differentiate the wealth of infant affective expression is clearly warranted. It could

be speculated that there is a hierarchy of biological salience within infant cues with those cues carrying negatively valenced information, such as crying or the unpleasant smell of a soiled nappy, prioritized above positively valenced cues such as a smile or laughter. Given its role in domain-general processing of reinforcer value, it seems likely that the OFC may play a role in differentiating between infant affective states, in addition to a role in initial orienting of attention.

The third line of promising research, for which the experimental literature has been extensively pursued with other animals (e.g., Champagne & Meaney, 2001; Fleming & Corter, 1988; Fleming, Corter, Stallings, & Steiner, 2002), but is lacking in humans, concerns the functional changes associated with becoming a parent (Kim et al., 2010). Future studies may be able to use advances in MRI techniques, such as diffusion tensor imaging, to examine changes in the connectivity of networks supporting parenting. Relating potential anatomical changes to behavioral changes in responding to infant cues will ultimately bring us closer to determining biological markers of parental sensitivity.

Finally, the study of neuroendocrinal factors underlying human parenting might be fruitfully integrated with studies of brain responses to infant stimuli. The nonapeptide stimulating perhaps the greatest research momentum of all, oxytocin, has been strongly implicated in animal models of parenting (Carter, 1998; Insel, 2010) and evidence is accumulating in humans (Galbally, Lewis, Ijzendoorn, & Permezel, 2011). An important aim would be to increase our understanding of how oxytocin and other hormones act to modulate brain responses to infant stimuli. Future work on oxytocin in human parenting will require measures of both central and peripheral levels. Extension to the study of oxytocin's role in fathers, as well as alloparenting, may provide fruitful next steps. Parenting presents a considerable challenge to those who find themselves becoming mothers and fathers each day, yet a comprehensive scientific understanding of the parenting relationship has never been more promising.

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