THE NEURAL BASIS OF FACE PROCESSING IN INFANCY AND ITS RELATIONSHIP TO THE DEVELOPMENT OF EMPATHY

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ABSTRACT
Faces are a salient part of the visual social environment, providing important signals including emotional expression and direction of eye gaze that inform us about other people’s feelings and intentions. In this paper, we review the development and neural bases of infants’ perception of emotion and eye gaze from faces. Building from the idea that the same or similar brain network responds when we see another person experiencing an emotion as when we actually experience it ourselves, we go on to speculate how the neural system underlying infants’ abilities to perceive social information in the face might provide the brain bases for emerging empathy abilities. We conclude by providing suggestions as to how developmental cognitive neuroscientists can bridge the gap between how infants’ perceptions are used to give rise to the semantic meaning of emotions and also the understanding of how the emotions displayed reflect the feelings of others.

KEYWORDS: faces, emotion, eye-gaze, event-related potentials, infancy.

INTRODUCTION
Empathy involves the ability to share and understand other people’s emotions and feelings. Faces play an important role in this process, since they provide directly observable information about the emotions other people are experiencing and about the focus of their attention; from this perceptual information we can infer their mental and emotional states as well as possible behaviours and actions. This reciprocal form of non-verbal communication permits successful social interaction and is a skill that infants develop over time. In this paper, we will review the neural
bases and development of face processing in infants, with the view that the emergence of the abilities to perceive and understand social information from faces is an important basic component in the development of empathy. We will mainly focus on infants’ abilities to perceive emotion and direction of eye gaze from faces, because there is a growing literature in this area and because the ability to correctly perceive this social information from the face provides some initial input for sharing and understanding other people’s feelings. We will also discuss the more limited literature on brain bases of the development of infants’ abilities to connect this perceptual information to its social meaning. We will conclude by discussing implications of this work for our understanding of how the mental and emotional concept of empathy develops.

**Empathy, Face Processing and the Social Brain in Adults**

To set the background for understanding the development of face processing and its links to emerging empathy skills in infants, we will first give a brief overview of what is known about the brain underpinnings of these skills in adults.

In adults, a network of interconnected brain regions involving subcortical, frontal cortical and temporal cortical regions has long been implicated in social cognition. In recent years a number of specific brain regions within this broad network have been identified as components of the ‘social brain’ including the amygdala, orbital frontal cortex, temporopolar cortex, anterior cingulate cortex, superior temporal sulcus and fusiform gyrus (Johnson, 2005a,b; Payne & Bachevalier, 2009).

With respect to processing information in faces, a dominant framework proposes that visual information about faces is initially passed along two neural pathways. In the subcortical pathway, information travels from the retina directly to the superior colliculus, then to the pulvinar and on to the amygdala (de Gelder, Frissen, Barton, & Hadjikhani, 2003; Johnson, 2005b). This system is involved in detecting faces and directing visual attention to them. In the core cortical pathway, information travels from the retina via the geniculo-striate pathway, and includes the inferior occipital gyrus (encompassing the lateral occipital area, of which the ‘occipital face area’ is a subregion), fusiform gyrus (including the ‘fusiform face area’) and posterior superior temporal sulcus/gyrus. The inferior occipital gyrus mediates the early perception of faces and passes this information to two areas: (a) the fusiform gyrus and (b) the superior temporal sulcus/gyrus. There is evidence that the fusiform gyrus is primarily involved in the interpretation of the static components of facial expressions and identity (Kanwisher, McDermott, & Chun, 1997), while the superior temporal gyrus contributes to the recognition of the dynamic properties of facial expressions and eye gaze (Allison, Puce, & McCarthy, 2000). Both the subcortical and core cortical pathways interact with the extended cortical-subcortical system. It encompasses a variety of regions involved in the...
further processing of these inputs to allow activities important in emotion processing such as conscious emotional appraisal and interpretation of the intentions of others. The paralimbic and higher cortical areas such as the medial prefrontal cortex, somatosensory cortices and the anterior cingulate are involved in longer-latency processing of the conscious representations of emotional states, in controlling behavior in social situations and in the planning of actions and goals (Gobbini & Haxby, 2007; Haxby, Hoffman, & Gobbini, 2000; Johnson, 2005b). The right medial prefrontal cortex has been linked to perception of eye gaze directed at the self (Schilbach et al., 2006).

A magnetoencephalography (MEG) study by Streit et al. (1999) illustrates the structures and time sequence involved in the recognition of facial expressions of emotion. The following areas displayed activation during facial emotion recognition; right superior temporal cortex, the right inferior occipitotemporal cortex, the middle temporal cortex, the amygdala, the left inferior frontal cortex and the right anterior cingulate gyrus (Streit et al., 1999). Activation was first noted at 160 ms after presentation in the right superior temporal cortex and inferior occipitotemporal cortex. This was followed by activation in the middle temporal cortex at 200 ms, the amygdala region 20-40 ms later and the anterior cingulate gyrus 240 ms after stimulus onset. Subsequently activation was noted in the left inferior frontal cortex. This study demonstrates not only the distributed neural system involved in processing emotional faces but also the time sequence involved in the process. This time sequence of activation noted adds support to the above proposal of the subcortical and core cortical pathways initial involvement in face processing with later latency interaction with the extended cortical-subcortical system and the neural structures proposed to underlie these abilities.

Within this general network, there is also evidence that different basic emotions activate different patterns of brain activity. For example, functional imaging studies have demonstrated that the amygdala is disproportionately activated by facial expressions of fear (reviewed in Vuilleumier & Pourtois, 2006). There is also evidence that the prefrontal cortex has a particular role in the recognition of anger with activation in this region when compared to both happiness and sadness (Blair, Morris, Frith, Perret, & Dolan 1999; Harmer, Thilo, Rothwell, & Goodwin, 2001). The perception of facial expressions of disgust is regulated by both the insula and the basal ganglia. Patient studies have shown that damage to the left insula and basal ganglia prevent correct identification of the facial expression of disgust, and additionally an inability to experience the emotion itself (Adolphs, Tranel, & Damasio, 2003; Calder, Keanes, Manes, Antoun, & Young, 2000). The perception of happiness has been linked to activation of the ventral striatum, an area believed to be important also in processing reward (Lawrence, Chakrabarti, & Calder, 2004).
Understanding the brain areas activated when we see facial emotion is also relevant for understanding the brain bases of empathy, as one influential idea is that the same or similar brain network responds when we see another person experiencing an emotion as when we actually experience it ourselves. For example, Preston and de Waal (2002) proposed a perception-action model of empathy which theorises that, when we perceive another person, we automatically create an internal representation of that person’s current emotional state. These authors suggest that it is in this manner that infants learn the meaning of emotions expressed by their caregiver. This enables the infant through experience to understand their parents and also to develop a social referencing system whereby they can also learn about novel or ambiguous objects, people or situations from their parent and use this information to govern their behavioural responses accordingly.

An fMRI study by Singer et al. (2004) looked at the perception-action model as applied to empathy responses in adults. In this experiment subjects underwent an fMRI to examine the brain activity elicited while they received a painful stimulus or watched their partner receive the same painful stimulus. The anterior insula and anterior cingulate cortex were activated when the subject experienced pain and when they watched their partner receive the painful stimulus. Other research also shows similar neural responses when people observe pictures of people showing particular emotions (e.g., disgust) and when they experience that emotion themselves (e.g., smell a disgusting smell; Wicker et al., 2003). While such responses are considered automatic in that they do not require conscious or effortful processing, it is believed that adults can inhibit or control such responses. It is important to note that, in spite of these similarities, additional activity does occur when people experience emotions themselves as compared to viewing them in others. For example, in the study of pain mentioned above, the posterior insula, the sensorimotor cortex, and the caudal anterior cingulate cortex were activated in the self-pain but not other-pain condition. This demonstrates that some, but not all, of the neural areas associated with a specific emotional response are activated during an empathic experience of that emotion, more specifically the affective areas are activated in empathic responses but not the sensory areas (Singer et al., 2004).

Carr, Iacoboni, Dubeau, Mazziotta, and Lenzi (2003) also hypothesized that empathy involves the representation of those same emotions internally. In their study subjects imitated or observed facial expressions of emotions. The results indicated that similar neural circuits were activated in the observation and imitation of emotions. Activation in the superior temporal sulcus was greater in response to imitation than observation, as was activation in the anterior insula, inferior frontal cortex and amygdala. The authors suggest that this is evidence of how “action representation is a cognitive step towards empathy” (p. 5501).
Perceiving Emotion and Eye Gaze: Development and Neural Correlates in Infants

How Well Can Infants Perceive Emotion and Eye Gaze?

If one way infants learn about other’s emotions through links between their perceptions of those emotions and the automatic triggering of corresponding internal states, then an important first step in this process is the development of their abilities to perceive emotional information in faces.

*Emotion*: Infants show early sensitivity to emotional information in the face, with a few studies showing that newborns are able to discriminate, and even imitate, facial expressions of emotion (Field, Woodson, Cohen, Greenberg, Garcia, & Collins, 1983; Field, Woodson, Greenberg, & Cohen, 1982). Certainly, by the end of the first half-year of life, infants are able to discriminate at least some of the features of the face that to adults denote different expressions (reviewed in de Haan & Groen, 2006). The results are most extensive and most consistent with respect to the ability to discriminate happy from other expressions. With only one exception (Schwartz, Izard, & Ansul, 1985), the results of several studies are in agreement that during the first few months of life infants are able to discriminate happy from surprised, angry and fearful expressions (Barrera & Maurer, 1981; Field et al., 1982; Field et al., 1983; Kotsoni, de Haan, & Johnson, 2001; LaBarbera, Izard, Vietze, & Parisi, 1976; Nelson & Dolgin, 1985; Nelson, Morse, & Leavitt, 1979; Soken & Pick, 1999; Walker, 1982). However, in several studies infants had difficulty discriminating happy from sad expressions (Oster, 1981; Young-Browne, Rosenfeld, & Horowitz, 1977) even by 7 months of age (Soken & Pick, 1999; but see Caron, Caron, & MacLean, 1988; Walker, 1982). Interestingly, one study has demonstrated that infants as young as 3.5 months of age can discriminate between happy and sad expressions, but only when posed by the mother and not when posed by a stranger (Kahana-Kalman & Walker-Andrews, 2001), suggesting that a familiar facial context might facilitate infants' abilities to tell apart expressions.

*Eye Gaze*: The direction of another person’s eye gaze is an important social cue, as it can provide important information both about that person’s intentions and about significant events in the environment. In fact, it has been argued that one factor contributing to the development of infants’ abilities to process direction of gaze is their learning that monitoring their caregiver's direction of gaze allows them to predict the locations of interesting objects or events in their environment (Moore & Corkum, 1994). Shifts in eye gaze are such a powerful cue that they can influence the viewer’s attention in an automatic, reflexive manner (Driver, Davis, Ricciardelli, Kidd, Maxwell, & Baron-Cohen, 1999; but see Vecera & Rizzo, 2006).
Infants are sensitive to direction of eye gaze from the first days of life, preferring to look at faces with direct than averted gaze (Farroni, Csibra, Simion, & Johnson, 2002). Viewing faces with direct gaze also influences how infants process and react to them. For example, young infants can only effectively use a gaze shift to guide their own looking if it is preceded by at least a brief period of mutual eye contact (Farroni, Mansfield, Lai, & Johnson, 2003). In addition, 4-month-olds (Farroni, Massaccesi, Menon, & Johnson, 2007a), like adults (Mason, Hood, & Macrae, 2004), are better at recognising facial identity when they have studied faces with direct gaze than when they have studied faces with averted gaze (see Blass & Camp, 2001 for a similar type of result). Four-month-olds also show enhanced processing of information about objects cued by an adult’s gaze relative to objects that were not cued (Reid, Striano, Kaufman, & Johnson, 2004). The later effect is similar to ERP studies of adults showing that a reflexive shift of attention following the observation of a dynamic or static eye gaze cue enhances and speeds up early visual processing of a target presented at the gazed-at location (Schuller & Rossion, 2004). While infants’ abilities to process direction of eye gaze is impressive, development of this skills continues for some years, as 6- and 8-year-olds are still worse than adults at matching faces according to eye gaze direction, but 10-year-olds are adult like (Mondloch, Geldart, Maurer, & LeGrand, 2002).

Neural Bases of Emotion and Eye Gaze in Infants and its Links to Empathy

Core Cortical System: Fusiform and STS

Neuroimaging studies of infant populations are rare as the methods used are often not suitable for typically developing infants due to task demands, risks, and restrictions involved. A small literature using positron emission tomography (PET) and near-infra-red spectroscopy (NIRS) has examined regions of the brain activated by faces in infants. For example, one study conducted by Tzourio-Mazoyer et al. (2002) looked at the neural correlates of face processing in 2 month old infants using Positron Emission Topography (PET). The infants were shown static photos of unknown women. Activation was noted in the fusiform face area and inferior occipital cortex, the same cortical areas to show activation in adult populations when processing faces. No activation was seen in the superior temporal sulcus which could reflect slower functional development of this region or could be the result of the use of static rather than dynamic facial images.

Other studies do suggest a role for the STS in face processing in infants. Near infra red spectroscopy is an imaging technique that can provide localization information about brain activation in infants by measuring haemodynamic changes noninvasively. Results from such studies implicate the right frontal and temporal cortex in face processing in infants in the first postnatal year under a variety of tasks. The right temporal cortex is more active for upright compared to inverted faces in 5- to 8-month-olds (Otsuka, Nakato, Kanazawa, Yamaguchi, Watanabe, &
Kakigi, 2007), the right fronto-temporal cortex is more active for the mother’s face than a stranger’s face in 6- to 9-month-olds (Carlsson, Lagercrantz, Olson, Printz, & Bartocci, 2008; this study only measured on the right side and not on the left), and the right superior posterior temporal cortex and right temporopolar cortex is more active for mutual gaze than for baseline or averted gaze in 4-month-olds (Grossmann et al., 2008).

Together, the results from PET and NIRS studies suggest that two key components of the core cortical network, the fusiform gyrus and superior temporal sulcus, are active during face processing by at least 2-4 months of age (the youngest ages studied). Limitations of this work are that the NIRS studies sampled only limited regions of the scalp thus may not have identified additional regions involved, and none of the studies directly compared patterns of activation in infants and older children or adults within the same study to document any differences in the strength, specificity or spatial distribution of the neural responses with age.

Event-related potentials (ERPs) have also been used to examine development of the core cortical systems. Work with infants has been based on findings in adults identifying a face-sensitive ERP component, the N170. This component is typically larger in amplitude and shorter in latency to faces compared to other non-face images (Bentin, Allison, Puce, Perez, & McCarthy, 1996). The N170 is thought to reflect the structural encoding of face information as the amplitude and latency are affected by disruption to the configural aspects of faces but not objects or animal faces (Bentin et al., 1996; de Haan, Pascalis, & Johnson, 2002). Components of the Core System contribute to the generation of the adult N170, including regions of the fusiform gyrus (Shibata et al., 2002), the posterior inferior temporal gyrus (Bentin et al., 1996; Shibata et al., 2002), lateral occipito-temporal cortex (Bentin et al., 1996; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002), and the superior temporal sulcus (Henson et al., 2003; Itier & Taylor, 2004).

Infant ERP studies have not shown this same N170 response as seen in adults. However infant ERPs display N290 and P400 components that have similar properties to the N170. For example, a study by Halit, de Haan, and Johnson (2003) showed that 12-month-old infants display an N290 with greater amplitude to inverted human faces compared to upright human faces, as does the adult N170, but that this inversion effect does not occur for monkey faces, again like the adult N170. This pattern of inversion effect is not seen in 3-month-old infants and the authors suggest that this is because the N290 increases in its specificity to human faces during development (Halit et al., 2003). Source analyses in 3- to 12-month-olds show that the generators of the infant N290 include similar regions to those identified for the adult N170, including the lateral occipital area bilaterally, and the fusiform gyrus and superior temporal sulcus particularly on the right (Johnson et al., 2005). The lateral occipital area showed left and right hemisphere activation from 250-500 ms after stimulus onset and was active in face processing at all ages tested.
The response from this area discriminated between upright and inverted faces but was not sensitive to eye gaze. The right STS and fusiform regions were both sensitive to inversion as well as direction of eye gaze. However, the fusiform area was more sensitive than the STS to direction of eye gaze direction. As the authors point out, this is contrary to results in adults which propose the STS to be involved in dynamic aspects of face processing and the fusiform in the static components (Allison et al., 2000; Kanwisher et al., 1997).

The infant P400 component has also been functionally linked to the adult N170, as 6 month old infants show a shorter latency P400 for faces compared to objects (de Haan & Nelson, 1999). The adult N170 is typically larger amplitude to fearful faces than happy or neutral faces (e.g., Leppanen, Moulson, Vogel-Farley, & Nelson, 2007; Rigato, Farroni, & Johnson, 2009), a result which has been interpreted as reflecting amygdala enhancement of cortical processing. In 7-month-old infants, the P400 is also larger in amplitude to fearful than happy or neutral expressions, a finding that may reflect a similar mechanism of enhancement of cortical processing (Leppannen et al., 2007). This larger amplitude to fearful than happy or neutral expressions is not seen in 4-5 month olds (Peltola, Leppanen, Maki, & Hietanen, 2009; Rigato et al., 2009), however the latency of the P400 and N290 to happy faces is quicker than for fearful faces, as is the latency of the N170 in adults (Rigato et al., 2009).

Johnson et al. (2005; Johnson, 2005a) propose an interactive specialization (IS) approach to the development of face processing and other abilities of the social brain network. The IS theory suggests that brain regions are initially poorly defined in their functionality and it is over time and through experience with the external environment that they become more functionally localized and specific. This process is due to interregional interaction between different cortical areas and it is the changes in interactions between cortical regions that leads to the development of abilities and reduces the stimuli to which a region is activated by. The IS theory is in opposition to the maturational viewpoint which suggests that the development of abilities is due to the maturation of specific brain regions that have been prewired to specific functions. The IS theory is supported by the source localization and neuroimaging studies mentioned previously, as the same brain regions are active in the adult social brain network as that of the infant. Furthermore, as the IS theory suggests, brain regions become more specific in their activation over time as seen by the absence of the face inversion effect in 3 month olds on the N290 waveform and its presence by 12 months (Johnson et al., 2005). Applied to understanding links between face processing and empathy, one prediction might be that these systems have an even greater overlap in infancy but the distinctions between processing of different emotional states and self versus others’ emotional states might become more differentiated with age.
Subcortical System: Amygdala

The amygdala is one subcortical structure believed to be particularly active in the processing of emotional stimuli. While activation of the fusiform gyrus can be modulated by attentional resources available, the amygdala displays activation to emotional face stimuli even when attentional demands are high (Vuilleumier, Armony, Driver, & Dolan, 2001). Adolphs, Tranel, and Damasio (2003) suggest that although the amygdala shows rapid activation in response to emotional stimuli, this neural structure may also be involved in later cognitive processes with emotional stimuli not just in the perceptual processing stages. This suggests that the amygdala plays a role in face processing not only as part of the subcortical system but also as part of the extended cortical-subcortical system which is thought to be involved in emotional interpretation.

There is indirect evidence from the eyeblink startle response for amygdala involvement in emotion processing in infants. The eyeblink startle response is a reflex blink initiated involuntarily by sudden bursts of loud noise. In adults, these reflex blinks are augmented by viewing slides of unpleasant pictures and scenes, and they are inhibited by viewing slides of pleasant or arousing pictures and scenes (Lang, Bradley, & Cuthbert, 1990, 1992). Based on work in animals, it has been argued that fear potentiation of the startle response is mediated by the central nucleus of the amygdala, which in turn directly projects to brain stem centers that mediate the startle and efferent blink reflex activity (Davis, 1989; Holstege, Van Ham, & Tan, 1986). One study has shown that five-month-old infants' blinks were augmented when they viewed angry expressions and were reduced when they viewed happy expressions, relative to when they viewed neutral expressions (Balaban, 1995). These results suggest that by 5 months of age, portions of the amygdala circuitry underlying the response to facial expressions may be functional.

Another line of evidence that points to the importance of the amygdala in emotion processing in infants comes from studies of patients with paediatric mesial temporal lobe epilepsy. It has been documented that adult patients with frank unilateral and bilateral amygdala lesions show impairments in the recognition of basic emotions such as fear and happiness and to an even greater extent more complex social emotions such as guilt and boredom (Adolphs, Baron-Cohen, & Tranel, 2002). Meletti et al. (2003) studied the impact of mesial temporal lobe epilepsy on the ability of subjects to recognise emotions from facial expressions as the amygdala is one structure that is often damaged in this form of epilepsy. The authors found that only those subjects with right mesial temporal lobe epilepsy demonstrated impairments in facial emotion recognition and not subjects with seizure foci presenting in other cortical areas. The degree of difficulty in emotion recognition was related to age of onset with a greater impairment in earlier onset seizure subjects. These results add support to the role of the amygdala in facial...
emotion processing, the right hemisphere dominance in face processing and also the importance of the amygdala early in life for forming emotion recognition abilities.

**Extended Cortical-subcortical System: Anterior Cingulate/Prefrontal**

In adults the paralimbic, medial prefrontal cortex, somatosensory cortices and the anterior cingulated are thought to be involved in the extended cortical-subcortical system. Preston and de Waal (2002) suggest that activation of prefrontal cortex, specifically the dorsolateral and ventromedial regions, reflects the maintenance and manipulation of emotional information in working memory, and that this is necessary for cognitive empathy processes. Emotional information is held in working memory while feedback from other cortical areas such as somatosensory and limbic regions provide input to permit the appropriate emotional appraisal and response.

There is little direct information about the development of the extended cortical-subcortical system in emotion and eye gaze processing in infants.

Johnson et al. (2005) source localisation study of infant ERP response to face stimuli found that prefrontal regions were active from 3 months of age, and their activity increased with age. The frontal regions did not differentiate upright from inverted faces but did show a differential response to direct versus averted eye gaze. Though the prefrontal areas may not be involved in the N170/290 component, it is thought to play a role in later latency components such as the Negative component (Nc). Another source localisation study indicated that the generators of this Nc component in infants can be found in anterior cingulate and lateral prefrontal regions (Reynolds & Richards, 2005).

Studies in infants do show that emotion and eye gaze influence the Nc component. In an experiment by Hoehl, Reid, Mooney, & Striano (2008) the effect of eye gaze direction on 4 month old infant’s Nc was investigated. In this study 4-month-old infants viewed an adult face with eye gaze either directed at an object or averted from the object. The latency of the Nc was shorter and the amplitude smaller in the object-directed eye gaze condition. The authors suggest that the object-directed eye gaze results in faster processing while the averted eye gaze requires more attentional resources and takes longer to process. The amplitude of the positive slow wave (PSW) that follows the Nc was greater for the object-directed eye gaze. The PSW is believed to reflect memory processing and as a result this enhanced PSW is interpreted as a stronger memory representation created for the object that was cued by eye gaze. Overall these findings suggest that object directed eye gaze facilitates faster processing and a stronger memory representation for the object. The infants in this study at 4 months used the social information of eye gaze to direct their attentional resources to an object in the environment.

The Nc appears to be not only sensitive to eye gaze direction but also to emotional content. Several studies have shown that in the 7-month-old infants, the
Nc is larger for fearful compared to happy faces (de Haan, Belsky, Reid, Volein, & Johnson, 2004; Nelson & de Haan, 1996; Peltola et al., 2009). While 7-month-olds demonstrate a larger amplitude Nc to fearful than happy faces and also longer looking times to fearful expressions, 4-5 month olds do not demonstrate this increased attention allocation (Peltola et al., 2009; Rigato et al., 2009). This overall pattern of findings suggests that the cognitive interpretation of fearful expression of emotions might be emerging around 7 months. Rigato et al. (2009) did find that 5-month-olds can discriminate happy and fearful expressions and that they process happy expressions more quickly. This might indicate an earlier development of the ability to process happy faces, an interpretation consistent with behavioural evidence suggesting that infants prefer to look at faces with direct gaze and happy facial expressions (Farroni et al., 2007b).

Several studies have also examined the combined influence of emotion and eye gaze on the Nc component. A study by Hoehl, Palumbo, Heinisch, and Striano (2008) combined facial expression with direct eye gaze towards the infant or averted eye gaze towards an object, creating a triadic context. Images of faces expressing neutral or fearful expressions averted towards an object or directed towards the infant were shown to 7-month-old infants. The results showed an enhanced Nc in the fearful expression and averted eye gaze towards an object condition while no difference was found between fearful and neutral expressions directed towards the infant. The fearful expression with eye gaze averted towards the object contains the most socially explicit information – a threat in the environment – compared to the other three conditions. This suggests that by 7 months of age, infants demonstrate increased attention processing in socially meaningful situations. This could possibly represent the beginning of empathic cognitive processing.

In a further experiment by Hoehl and Striano (2008), again eye gaze direction was examined in combination with fearful and angry facial expressions. 7 month old infants were shown images of faces with eye gaze directed towards them or averted to the side with fearful or angry expressions. Angry facial expressions with direct eye gaze showed an increased Nc than the angry expression with eye gaze averted. The fearful expressions with both direct and averted eye gaze did not display any variation in neural response as measured by ERP. This discrepancy between this and the previous experiment showing the effect for fearful expressions in combination with eye gaze may be due to the fact that in this experiment the fearful averted eye gaze was not directed to any object.

Overall these results combined suggest a relation in facial expression and eye gaze direction at 7 months with angry expressions with eye gaze directed towards the infant and fearful expression averted to an object both producing an enhanced NC. Both of these conditions communicate more socially relevant information than the other conditions in these experiments and this may explain the increased attentional processing noted.
Linking Faces to Emotions in the Infant Brain

There is relatively limited information as regards to how the infant brain links the percepts of emotional information in the face to their semantic meanings. Perceptually, infants may be able to discriminate physical differences in facial configuration but the cognitive awareness leading to recognition of emotions is thought to develop later.

One mechanism that may be involved in this process is imitation. Gallese, Fogassi, and Rizzolatti (1996) first noted how we perceive the actions of others through the mirror neuron system of the motor cortex. Gallese, Keysers, and Rizzolatti (2004) suggests that a similar mirror system operates in understanding others’ emotions. As mentioned previously, the perception-action model suggests that infants learn through internal representation of seen emotions. Studies have suggested that infants as young as 36 hours demonstrate imitation of facial expressions of emotions including happy, sad and surprised (Field et al., 1982). Newborns also show auditory-oral matching behaviour by showing significantly more mouth opening after hearing the vowel sound /a/ and more mouth pursing after hearing the consonant sound /m/ (Chen, Striano, & Rakoczy, 2004). In spite of these impressive results, studies of infants beyond the newborn period suggest that such matching responses are not a common occurrence in young infants. Several studies show that, while parents imitate their children at a high rate in the first postnatal year, infants’ rate of behavioural or vocal imitation was low (summarised in Jones, 2007). Infants’ behavioural matching increases in the second half of the first year, but, during this period, vocal cues to behaviours play an important role in eliciting matching behaviours: infants match behaviours with vocal cues before they match silent behaviours (Jones & Yoshida, 2006). Thus, while newborns’ imitation of facial expressions provides intriguing evidence of early emergence of basic components of empathy, evidence suggests that such newborn responses may not be continuous with imitation observed later in infancy (Jones, 2007). Parents’ own tendency to imitate their infants may contribute more to infants linking percepts to internal states during the first months.

There is some relevant evidence from infant EEG studies regarding the pattern of brain activity triggered by emotional stimuli. In one of the first studies examining EEG while infants perceived emotions, 10-month-olds showed greater activation of left than right frontal areas in response to videos of an actress showing a happy expression (Davidson & Fox, 1982). Newborn infants also show greater activation of left frontal and parietal areas when they experience a sweet taste compared to water (Fox & Davidson, 1986), a stimulus also shown to produce a distinct facial response of relaxation (though not smiling) in other studies (Rosenstein & Oster, 1988; Zhang & Li, 2006). These studies together hint at an overlap in infant brain regions involved in experiencing and viewing positive emotions. Though such studies have limitations, such as the limitation of spatial

resolution of the EEG, they provide a possible way of investigating the relation between brain bases of the perception and experience of different emotions in infants.

Electrophysiological studies have also been used to investigate how infants use the emotional information they perceive to guide their behaviour. A study by Hoehl, Wiese, and Striano (2008) demonstrated social referencing abilities in 3-month-old infants. In this study an adult displayed fearful or neutral expressions directed towards an object followed by immediate presentation of the object on its own. Objects that were cued by a fearful expression demonstrated an increased Nc, increased attention, but not the objects cued by neutral expressions. When novel objects were presented immediately following the fearful/neutral expressions and object parings no effect was found on the Nc. Finally, when eye gaze was averted from the object with fearful/neutral facial expression followed by immediate presentation of the object, again no increased effect was found on the Nc. This experiment shows that at 3 months infants use eye gaze along with facial expression to socially reference novel objects and govern attention. A similar pattern has been reported for 12-month-old infants, who show a larger Nc response to objects associated with an adult’s negative emotion than neutral or positive emotion (Carver & Vaccaro, 2007).

However, there is still a question about how long such information is retained. Hertenstein and Campos (2004) used a social referencing paradigm to examine adult emotional display towards a novel object effect on infants’ behaviour towards that same object after a 60 minute delay. Fourteen-month-olds demonstrated regulation of their behaviour based on whether the adult expressed a negative or positive emotion towards the object. Eleven-month-olds did not display this effect after the 60 minute delay but did so after a 3 minute delay. The results suggest that 14-month-olds effectively use social information displayed by an adult to govern their behaviour and that they retain this information but that this retention of information is not displayed by 11 month olds. The difference in the delay period might explain the variation in results between this study and the Hoehl et al. (2008) study mentioned previously which demonstrated social referencing effects in 3-month-olds. Infants in this study were shown the target object directly after the adult referencing, that is no delay was involved. Infants may be capable of discriminating the emotional information displayed by adults at different ages but it is the ability to retain this information that varies.

Furthermore the difference in results between these two studies could be explained for by the source localisation analysis by Johnson et al. (2005). The prefrontal regions in this study were active from 3 months but activity increased with age. Perhaps it is the increase in prefrontal activity within the first year of life that accounts for the ability of the older infants to maintain and act on socially meaningful information cued by adults and might reflect the emerging cognitive empathic processing abilities.
SUMMARY & CONCLUSIONS

Emotions and direction of eye gaze are two important social cues perceived from faces that are salient to an observer and that provide information as to the mental and emotional state of another person. It is the ability to process this perceptual information and to cognitively and emotionally interpret it that leads to empathic experiences. The spatial and temporal components of the neural networks underlying the ability to process this information in adults have been well documented through neuroimaging and neurophysiological studies. In adults it is the extended cortical-subcortical system that is believed to mediate higher cognitive processes of empathy, though the core cortical and subcortical systems clearly feed information into this system. The occipito-temporal lobe areas of the cortical system and the subcortical structures such as the amygdala appear to be involved in the initial perceptual and attention orienting responses, while later activation within the prefrontal cortex and anterior cingulate, part of the extended cortical-subcortical system, give rise to the social cognitive processes. As suggested by a number of these studies empathy involves not only a cognitive awareness and understanding of another person’s thoughts and feelings but also part activation of those same emotions in oneself.

Overall, studies of infants suggest that similar neural structures that are involved in these processes in adults are also active in infants: the lateral occipital gyrus, the superior temporal sulcus/gyrus, fusiform gyrus, amygdala, anterior insula, anterior cingulate gyrus and prefrontal regions all demonstrate activation to emotional face stimuli and/or eye gaze in both adults and infants. However, these brain structures and their interconnections mature along different timelines and become increasingly integrated during infancy and adolescence to support more complex and controlled use of facial social information.

The Perception-Action model and imitation studies indicate that the same neural networks involved in expressing an emotion are also activated when we see another person expressing that emotion and that this imitation occurs within the first months of life. However the ability to imitate an emotion does not necessarily imply a cognitive awareness of its social meaning. Changes in the brain structure over childhood and growing specialisation of different neural regions along with experience, through viewing emotional faces and the behaviours and actions associated with these through the process of social referencing is likely to gradually bring about this cognitive understanding of emotional expressions. We argue that there is some suggestion that the initial cognitive functions involved in this process might be functioning from 7 months.

Studying empathy development in infancy is challenging due to the limited behavioural and communicative repertoire of infants as the limited number of methods available to research these processes in infants compared to adult populations. Much of the research on face and eye gaze processing in infants has
focused on event-related potential methods. ERPs provide good temporal resolution but poor spatial resolution. Near infrared spectroscopy (NIRS) could be a useful method in future research examining empathic processes in infancy and childhood as this can provide good temporal information along side a greater spatial resolution than ERP studies allow. In particular, future studies with infant populations could focus on the functions of the extended cortical-subcortical system as currently there is strong evidence to suggest that emotional face processing occurs within a specific neural network in the infant brain. However, there is a need to bridge the gap between how this perceptual information is then used to give rise to the semantic meaning of emotions and also the understanding of how these emotions displayed reflect the feelings of others.

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