Social development

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Introduction

Humans are an exquisitely social species. We are constantly reading each other’s’ actions, gestures and faces in terms of underlying mental states and emotions, in an attempt to figure out what other people are thinking and feeling, and what they are about to do next (Blakemore et al. 2004). Social and emotional functioning is a critical component of educational attainment. There is a rapidly expanding literature on social cognitive development during the first two years of life, and it is here that we start our review. Much less is known about the neurodevelopment of social skills in mid-childhood and adolescence. Nevertheless, the second half of this chapter focuses on the development of social understanding during this period of life and on possible contributions of an improved understanding for education.

Early development of the social brain

The earliest stage of postnatal development, infancy (0-2 years), is the time of life during which enormous changes take place- the ‘helpless’ newborn seems almost a different creature from the active, inquisitive 2-year-old. During this period, human infants develop in a world filled with other people, and developing an understanding of other people and their actions is one of the most fundamental tasks infants face in learning about the world. In this section, we present empirical findings from several areas of social information processing in early development: (1) face and gaze processing, (2) joint attention, (3) biological motion, and (4) understanding human action. The findings discussed are mainly based on electroencephalography (EEG)/event-related potential (ERP) methods, which are the most commonly used methods with this age group. These EEG/ERP methods, which provide precise information on the timing of brain and cognitive processes, have more recently been complemented
by functional near-infrared spectroscopy (fNIRS) (see Chapter 2) that enables us to better localise cortical activation in infants (see Lloyd-Fox et al., 2010 for a review).

**Face processing**

Human faces in particular provide a plethora of social information, including the identity, the emotional state and the attentional focus of a conspecific (via the direction of eye gaze). Behavioural work with newborn infants has revealed that newborns attend preferentially to face-like patterns within hours of being born (Morton & Johnson, 1991; Johnson, 2005) providing evidence for a mechanism to bias the input that is processed by the newborn's brain. The face preference observed in newborns is thought to be guided largely by subcortical brain structures, while it has been proposed that the maturation of visual cortical areas is necessary for the emergence of the more sophisticated competencies underlying identity recognition from faces (for a discussion, see Johnson, 2005). Newborns first recognise their mother’s face on the basis of information from the outer contour of the head, hairline, and the internal configuration of eyes, nose, and mouth (Bushnell, Sai, & Mullin, 1989). But it is not until 6 weeks of life that they become able to do this recognition solely on the face’s internal configuration (de Schonen & Mathivet, 1990).

Investigations of brain areas involved in face processing in infants have been limited mainly by technical issues (de Haan & Thomas, 2002; Grossmann, 2008). One exception has been a study by Tzourio-Mazoyer and colleagues, who took advantage of the opportunity to perform positron emission tomography (PET) on infants in an intensive care unit as part of a clinical follow-up (Tzourio-Mazoyer et al., 2002). In this small-scale study, a group of six 2-month-olds were imaged while they watched a face...
or an array of coloured diodes used as a control stimulus. The results revealed that faces activated a network of areas in 2-month-old infants’ brains similar to that described as the core system for face processing in adults (Haxby, Hofman, & Gobbini, 2000; Kanwisher, 2000; Gauthier et al., 2000). It is interesting to note that a cortical region that at the age of 2 months is neuroanatomically immature (Huttenlocher & Dabholkar, 1997; Huttenlocher, 2002) and has only a low level of resting metabolic activity (Chugani & Phelps, 1986; Chugani, Phelps, & Mazziotta, 1987) can be functionally activated. In addition, viewing faces activated bilateral inferior occipital and right inferior parietal areas in infants. The former has been implicated in early perceptual analysis of facial features, whereas the latter is thought to support spatially directed attention in adults (Haxby et al., 2000). In contrast to what is known from adults, face processing in 2-month-olds also recruited areas in the inferior frontal and superior temporal gyrus, which have been identified as a part of the adult language network. One possible interpretation of this is that the co-activation of face and future language networks has a facilitatory effect on social interactions guiding language learning by attention toward the speaker’s face and mouth (Tzourio-Mazoyer et al., 2002).

However, most studies of infant face perception rely on the more readily applicable recording of EEG measures. We now discuss briefly the empirical evidence available on infants’ face processing using event-related brain potentials (ERPs; for a more detailed review, see de Haan, Johnson, & Halit, 2003). In adults, human faces elicit an N170 response (a negative component, which occurs at around 170 ms post stimulus presentation), which is most prominent over posterior temporal sites and is larger in amplitude and longer in latency to inverted than to upright faces (Bentin et al., 1996;
de Haan, Pascalis, & Johnson, 2002). This component is not modulated by the inversion of monkey faces (de Haan et al., 2002), nor when upright objects are compared to inverted objects (Bentin et al., 1996). This selective inversion effect for human faces has been taken as evidence for a face-related processing mechanism generating the N170.

On the basis of waveform morphology and some of its response properties, it has been suggested that the infant N290 is a precursor to the adult N170, in that it shows similar stimulus sensitivities and scalp distribution patterns. In these studies, infants’ and adults’ ERPs were measured in response to upright and inverted human and monkey faces (de Haan et al., 2002; Halit, de Haan, & Johnson, 2003). As the adult N170, the infant N290 is a negative-going deflection observed over posterior electrodes whose peak latency decreases from 350 ms at 3 months to 290 ms at 12 months of age (Halit et al., 2003). This is consistent with the latency of many prominent ERP components reducing with increasing age during childhood. The results of these studies indicate that at 12 months of age the amplitude of the infant N290, like the adult N170, increases to inverted human but not inverted monkey faces when compared to the upright faces. However, the amplitude of the N290 was not affected by stimulus inversion at an earlier age (3 and 6 months).

The development of the face-related brain processes reflected in the N170/N290 continues well beyond infancy (for a review, see Taylor, Batty, & Itier, 2004). While latency of the adult N170 is delayed by face inversion, no such effect is observed for the latency of the infant N290 at any age (de Haan et al., 2002; Halit et al., 2003). There is evidence that suggests that this latency effect is not apparent until 8 to 11 years of
age (Taylor et al., 2004). Furthermore, while the amplitude of the adult N170 is larger to monkey faces, infants’ N290 shows the opposite pattern. A completely adult-like modulation of the amplitude of the N170 has not been reported until 13 to 14 years of age (Taylor et al., 2004).

In summary, evidence available from PET and EEG/ERP studies suggests that most of the brain areas and mechanisms implicated in adult face processing can be activated within the first few months of postnatal life. However, this should not be interpreted as meaning that these cortical areas are specialised for processing faces at this stage, nor function in the same way as they do in adulthood, as considerable further tuning of these areas continues into childhood (Johnson 2011, see later sections).

**Gaze processing**

An important social signal encoded in faces is eye gaze. The detection and monitoring of eye gaze direction is essential for effective social learning and communication among humans (Csibra & Gergely, 2009). Eye gaze provides information about the target of another person’s attention and expression, and it also conveys information about communicative intentions and future behavior (Baron-Cohen, 1995). Eye contact is considered to be one of the most powerful modes of establishing a communicative link between humans (Kampe, Frith, & Frith, 2003). From birth, human infants are sensitive to another person’s gaze as reflected in their preference to look at faces that have their eyes opened rather than closed (Batki et al., 2000). Furthermore, newborns look longer at faces with direct/mutual gaze as compared to faces with averted gaze (Farroni, Csibra, Simion, & Johnson, 2002). Eye gaze has also been shown to effectively cue newborn infants’ attention to spatial locations,
suggesting a rudimentary form of gaze following (Farroni et al., 2004). The question that arises is how the behaviorally expressed preference for direct gaze and the capacity to follow gaze are implemented in the infant brain.

By 4 months, the infant brain manifests enhanced processing of faces with direct gaze as indexed by an increased amplitude of the N290 when compared to averted gaze (Farroni et al., 2002). This finding is obtained even when the head is averted but direct mutual gaze is maintained (Farroni, Johnson, & Csibra, 2004). However, enhanced neural processing of faces with direct gaze is only found when eyes are presented in the context of an upright face. Moreover, in a recent study, 4-month-old infants watched two kinds of dynamic scenarios in which a face either established mutual gaze or averted its gaze (Grossmann et al., 2008). Hemodynamic responses were measured by NIRS, permitting spatial localization of brain activation. The results revealed that processing mutual gaze social interactions activates areas in the infant right superior temporal cortex (STS) and prefrontal cortex (PFC) that correspond to the brain regions implicated in these processes in adults (Kampe et al., 2003; Pelphrey et al., 2004) (see Figure 1). The ERP and NIRS results reviewed above support the notion the mutual gaze is processed in the brain from early in development.

Another communicative function of eye gaze is to direct attention to certain locations, events, and objects. In an ERP study, 9-month-old infants and adults watched a face whose gaze shifted either towards (object-congruent) or away from (object-incongruent) the location of a previously presented object (Senju, Johnson, & Csibra, 2006). This paradigm was based on that used in an earlier fMRI study (Pelphrey, Singerman, Allison, & McCarthy, 2003) and was designed to reveal the neural basis of
“referential” gaze perception. When the ERPs elicited by object-incongruent gaze shifts were compared to the object-congruent gaze shifts, an enhanced negativity around 300 ms over occipito-temporal electrodes was observed in both infants and adults. This suggests that infants encode referential information of gaze using similar neural mechanisms to those engaged in adults. However, only infants showed a fronto-central negative component that was larger in amplitude for object-congruent gaze shifts. It is thus possible that in the infant brain the referential information about gaze is encoded in more widespread cortical circuits than in the more specialized adult brain. We return to this interesting finding on referential gaze in the next section in which the neural basis of a very closely related social-cognitive phenomenon called joint attention will be discussed.

**Joint Attention**

The process by which two people share attention towards the same object or event is called joint attention. Joint attention is considered to be one of the most fundamental social cognitive skills that develop during infancy. Besides attending to an external object or event herself, the ability to jointly attend with another person requires the infant to monitor (a) the other person’s attention in relation to the self and (b) the other person’s attention toward the same object or event. Behavioral studies suggest that triadic representations between two minds and a shared object of attention emerge around 9 months of age. They are also thought to be uniquely human representations supporting shared attention and collaborative goals (Tomasello, Carpenter, Call, Behne, & Moll, 2005). The dorsal part of the medial prefrontal cortex (mPFC) has been identified as a critical region to support joint attention in the adult brain (Frith & Frith, 2006; Saxe, 2006; Schilbach et al., 2010; Williams et al. 2005).
Striano, Reid, and Hoehl (2006) examined the ERP correlates of joint attention in 9-month-old infants by having an adult interact live with the infant in two contexts. In the joint attention context the adult looked at the infant and then at the computer screen displaying a novel object, whereas in the non-joint attention context the adult only looked at the chest of the infant and then at the novel object presented on the screen. Objects presented in the joint attention context compared to objects in the non-joint attention context were found to elicit a greater negative component (Nc) peaking around 500 ms with a maximum amplitude over frontal and central channels. The Nc is thought to be generated within the prefrontal cortex and may indicate the allocation of attention to a visual stimulus (Reynolds & Richards, 2005). Therefore, Striano et al. (2006) suggested that infants benefit from the joint attention interaction and thus devote more attentional resources to those objects presented in this context. Recently, this ERP paradigm has also been used to examine joint attention in younger infants (see, Parise et al., 2008). This study found that by 5 months infants show an increased allocation of attention to the cued object in a joint attention condition.

Despite these insights from using ERP methods, it still remains unclear which brain regions are involved in engaging in triadic interactions. However, in a recent study, NIRS was used to localize infant brain responses during triadic interactions (Grossmann & Johnson, 2010). In this study, 5-month-old infants showed increased left prefrontal cortical responses when engaged in joint triadic interactions compared to two (non-triadic) control conditions, in which either no eye contact was established or the person looked away from the object (see Figure 2). These findings are in line with previous fMRI work with adults implicating left prefrontal regions in joint
attention (Schilbach et al., 2010). Thus, 5-month-olds infants seem to engage similar prefrontal regions during triadic social interactions as adults.

Further support for the notion that left prefrontal cortex plays a critical role in joint attention comes from a clinical study in which cortical metabolism in infants was measured using PET (Caplan et al., 1993). In this study, higher rates of preoperative glucose metabolism in frontal cortical regions, especially left frontal region, was a positive predictor of the postoperatively assessed tendency to initiate joint attention bids. To further assess the role of the frontal cortex, resting EEG coherence and its relation to joint attention skills in typically developing infants was examined (Mundy, Card, & Fox, 2000). EEG coherence is a measure of phase synchrony between spatially separated EEG generators, which provides an index of aspects of neural network integration (Thatcher, Krause, & Hrybyk, 1986). EEG coherence measures of left frontal cortical activity was found to be associated with the infants’ tendency to initiate joint attention at 14 and 18 months. Furthermore, in a follow up study, it was shown that behavioral measures of joint attention and EEG coherence at 14 months were both related to language development at 24 months (Mundy, Fox, & Card, 2003).

In summary, ERP and NIRS data suggest that, as earlier as 5 months, infants are sensitive to triadic social interactions. This early sensitivity to joint attention appears to depend on left prefrontal brain areas. This early emergence of joint attention skills is also supported by behavioural data showing that already by the age of 3 months, infants discriminate between dyadic and triadic interactions (Striano & Stahl, 2005). Despite the early evidence for joint attention, it is important to keep in mind that it
develops continuously throughout the first decade of life, and early indicators of deficits in joint attention are central to most developmental disorders.

Action observation

Human actions are an exceedingly complex set of visual stimuli providing dynamic and continuous information about the behaviour of other humans. The capacity to parse ongoing actions into meaningful segments is critical for the interpretation of others’ behaviour. There is evidence to suggest that in adults and infants, this parsing of action sequences is partly based upon understanding the goal of an action (Blakemore & Decety, 2001; Baldwin, Baird, Saylor, & Clark, 2001). For example, when 8-month-old infants were presented with complete and incomplete goal-directed actions they looked longer at the incomplete than at the complete action (Reid, Csibra, Belsky, & Johnson, 2007). It is possible that the infants detected a mismatch between anticipated and perceived actions, which resulted in increased looking time in the case where an action is terminated before a goal is achieved. This detection might be based on a process called forward-mapping, that involves the continuous prediction of possible motion trajectories and future actions based on their own motor representations (see, e.g., Falck-Yttr, Gredebäck, & von Hofsten, 2006).

Researchers have also asked the question of whether infants come to understand other people’s actions through a mirror neuron system (Rizzolati & Craighero, 2004) that maps an observed action onto infants’ own motor representation of that action. According to the mirror neuron system view, infants are not expected to predict others’ action goals before they can perform the action themselves. In a behavioral study (Falck-Ytter et al., 2006), 12-month-olds but not 6-month-olds were found to
show proactive (anticipatory) goal-directed eye movements during observation of an action (putting objects into a box). Because it is known that infants do not master this kind of motor task until 7 to 9 months of age (Bruner, 1973), this finding was taken as evidence for the mirror neuron system view of action understanding. Furthermore, based on the finding that proactive eye movements were only found when a human agent produced the action but not when the objects were self-propelled (Falck-Ytter et al., 2006), it was argued that a human agent is required to activate the mirror neuron system. These findings are also interesting in light of evidence showing that good motor skills in 8-month-old infants correlate with their sensitivity to discriminate biologically possible from impossible arm movements (Reid, Belsky, & Johnson, 2005). Despite the value of these interesting behavioural findings, a shortcoming is that they provide only indirect evidence for a neural mechanistic explanation.

A candidate neural signature that has been shown to be useful for the study of action perception in adults is the mu wave (oscillatory bursts at 9 - 11 Hz), which can be measured with EEG. This wave activity appears to be associated with the motor cortex, and is diminished with movement or an intent to move, or when others are observed performing actions (Oberman et al., 2005). Therefore, EEG oscillations in the mu wave range recorded over sensorimotor cortex are thought to reflect mirror neuron activity and have been associated with enabling an adult observer to understand an action through motor simulation.

Southgate and colleagues (2009) investigated 9-month-olds mu wave activity over the sensorimotor cortex during elicited reaching for objects. Critically, they also examined whether mu activity was modulated when observing a grasping action performed by
someone else. The results obtained in this study revealed that, like adults, 9-month-old infants display a reduction in mu activity during performing and observing a grasping action. Another interesting finding in this study was that motor activation (mu suppression) was measured before the actual onset of the observed action. Infants must have learned to anticipate the occurrence of the action because they were presented with repeated trials and no mu suppression was evident during the first three trials. This finding of predictive motor activation during action observation supports accounts according to which the mirror neuron system plays an important role in action prediction (Csibra, 2007).

In a follow-up study, 9-month-old infants watched an action (a hand grasping behind an occluder) that could only be interpreted as goal-directed if they are able to predict a hidden outcome (Southgate et al., 2010). As in the previous study, motor activity was measured as indexed by mu activity over sensorimotor cortex. Motor activity during this goal prediction condition was compared to three control conditions which consisted of (1) a turned hand, unable to reach, going behind an occluder, (2) an open grasping hand being placed on the table in front of an occluder, and (3) a turned hand, unable to reach, being placed on the table in front of an occluder. Only when infants watched the grasping hand going behind the occluder mu activity was suppressed, whereas no such suppression was observed during any of the control conditions. This finding provides further evidence for 9-month-olds infants’ ability to predict the goal of an action, and strengthens the notion that the motor system plays a critical role in action understanding. In addition, it shows that already by the age of 9 months motor activity is influenced by top-down processes such goal prediction rather than being simply being driven by observing any kind of action.
However, in both studies (Southgate et al. 2009, in press) the grasping actions presented to the infants in the action observation conditions were in their action repertoire. Thus, in another study (van Elk et al., 2008), the role of motor experience with an action was investigated with 14- to 16-month-old infants. As predicted on the basis of infants’ limited motor experience with walking at this age, infants exhibited stronger mu suppression during the observation of crawling than during the observation of walking. Furthermore, the size of this suppression effect was strongly correlated with the infants’ own crawling experience such that infants who had longer crawling experience showed a stronger mu suppression. These findings provide some first evidence that motor activity during action observation in infants depends on motor experience with an action.

All the studies concerning action understanding presented up to here relied on EEG scalp recordings placed over sensorimotor cortex. However, these scalp recordings cannot be localized to motor cortex activation with certainty during these tasks. Therefore, Shimada and Hiraki (2006) used NIRS to examine whether motor cortex is activated during action execution and action observation. They found that 6- to 7-month-old infants and adults activated motor cortex during the execution and observation of an action. Interestingly, at both ages, the activation of the motor system during action observation was only evoked when the action was presented live, but not when it was presented on video (see Shimada & Hiraki, 2006 for a discussion). However, the mu suppression effects reported using EEG were obtained under live (Southgate et al., 2009, in press) and videos conditions (van Elk et al., 2008) alike. It therefore seems critical to co-register EEG and NIRS in infants in order to clarify this
issue. In any case, Shimada and Hiraki’s (2006) findings further support the notion that there is an intricate link between observing and executing an action in the motor system.

In summary, the findings reviewed show that at least by the age of 9 months the brain processes that underlie motor cognition seem to emerge. There is also some initial evidence that experience with a motor skill influences motor cortex activation during action observation, suggesting that with development, as new motor skills and action patterns are integrated into the developing child’s repertoire, a better perceptual understanding of these actions as performed by others may be acquired.

This review of the early development of the social brain has revealed that newborns enter the world with biases that help them to direct increased processing resources to their social world. Newborns show strong preferences for faces, eye contact and biological motion. These biases, which may be based on subcortical processes, pave the way for the development and gradual specialization of cortical processes that help infants to interact with, and learn about and from, social agents.

Perhaps the most surprising insight from this literature is that some of the brain regions implicated in the adult social brain network are already sensitive to social interaction and cognition during the first year of life. Faces specifically activate the right fusiform gyrus of 2-month-olds, eye contact cues activate the posterior STS (pSTS) and PFC in 4-month-olds, watching biological motion results in functional activation in pSTS in 5-month-olds, joint triadic interaction appears to be processed in regions in the left PFC in 5-month-olds, and finally, observing and executing actions
result in specific brain activation in the motor system in 6- to 7-month-olds. However, from these early activation patterns there is a still a long way to go to reach the highly specialized and specific patterns of responses observed in adults.

**Social brain development in childhood and adolescence**

In the first half of this chapter, we reviewed evidence for the emerging social brain network in early infancy. In the rest of the chapter, we focus on social brain development in adolescence. Most researchers define adolescence as starting with the hormonal and physical changes of puberty. The end of adolescence is harder to define and there are significant cultural variations. However, the end of the teenage years represents a working consensus in Western countries. Adolescence is characterised by psychological changes in terms of identity, self-consciousness and relationships with others. Compared with children, adolescents are more sociable, form more complex and hierarchical peer relationships and are more sensitive to acceptance and rejection by peers (Steinberg & Morris, 2001). Although the factors underlying these social changes are likely to be multi-faceted, one possible cause is development of the social brain. In this chapter, we describe research on the development of face processing, theory of mind and social rejection during adolescence.

**Face processing**

In view of the early face-preferences reviewed in the earlier sections of this chapter, it has therefore been a surprising discovery that both the behavioural and neural bases of face processing abilities continue to develop throughout the first two decades of life. Whether this continuous development is due to the fact that the information that is extracted from faces becomes increasingly complex with age, during adolescence
for example, new face aspects, such as attractiveness, social status or trustworthiness become increasingly important (Scherf, et al. in press), or whether this is simply the result of protracted training with basic face processing strategies together with underlying brain development (see also below) still remains to be determined. It has therefore been suggested that adolescent face processing holds important insights for our understanding of the emerging bases for cognitive and neural face processing from childhood through adulthood (Scherf et al. in press).

An early study (Carey et al. 1980) showed improvement in facial identity recognition across the first decade of life, followed by a brief dip in performance at age 12. In a more recent study by Mondloch and colleagues (Mondloch et al. 2003), 6, 8 and 10-year-old children and adults had to compare faces on the basis of identity (with facial expression and head orientation varying), facial expression, gaze direction and sound being spoken. Results showed that, in comparison to adults, the 6-year-olds made more errors on every task, and the 8-year-olds made more errors on three of the five tasks, namely when matching the direction of gaze and on the two identity tasks. The 10-year-olds made more errors than did adults on the identity task in which head orientation varied. This suggests that basic face processing abilities, here the ability to recognize identity in a context-invariant manner, continue to develop until at least the end of the first decade of life. Last, it would have been interesting to assess how a sample of adolescents perform on the tasks used by Mondloch and colleagues.

Another study investigated the developmental trajectories of emotional expression processing in children (7-13 years), adolescents (14-18 years) and adults (Thomas et al. 2007) and found emotion processing develops continuously beyond early
childhood, with specific expressions following distinct trajectories. More specifically, adults were more accurate at identifying the emotion shown than were children and adolescents. However, whereas recognition accuracy for fear showed a linear improvement across the three age groups, anger showed a quadratic trend, with sharp improvement between adolescence and adulthood. This suggests that adolescence is characterized by continuing improvement in facial emotion recognition, but that the shape of the developmental trajectory may differ between emotions.

With the recent advent of paediatric neuroimaging methods (see Chapter 2), new vistas have been opened to study the implementation of cognitive functions in the developing brain (Blakemore et al. 2011). With regards to face processing abilities, recent developmental neuroimaging studies have shown that the protracted development at the behavioural level is mirrored at the brain level by prolonged cortical specialisation within the regions of the face network (Cohen Kadosh & Johnson, 2007). In one fMRI study, children, adolescents and adults passively viewed photographic images of faces vs. objects, places or abstract patterns (Golarai, et al., 2007). Results showed an age-related increase in the activation within right fusiform cortex, with adults showing a significantly larger activation than child groups and the adolescent group exhibiting an intermediate pattern. In addition, the expansion of the fusiform face area (FFA), into surrounding cortex was correlated with a behavioural improvement in recognition memory for facial identity. In a different study, Scherf and colleagues (Scherf, et al. 2007) showed children (5-8 years), adolescents (11-14 years) and adults short movie clips of faces, places and objects. They observed an age-related increase in face-selective FFA activation between childhood and adolescence, as well as an increase in face-selective activation in the STS.
More recent evidence from two developmental fMRI studies contrasts sharply with the studies reviewed above in that they did not find developmental differences in face processing in children and adults (Cantlon et al. 2011; Pelphrey et al. 2009). In the first study, Pelphrey and colleagues (Pelphrey, et al., 2009) compared neural responses to faces, flowers, objects and bodies in the core face areas in children (7-11 years) and adults. They found no developmental changes in face-selectivity in the FFA from mid-childhood to adulthood when contrasting face-specific responses with those to flower stimuli, suggesting that face processing is adult-like from mid-childhood. It is less clear, however, whether similar results would have been obtained in this study upon contrasting face responses with neural responses to the other stimulus categories (i.e., objects, bodies), a question that is particularly relevant as both categories are preferentially processed in adjacent cortical areas in the mature brain.

In the second study, Cantlon et al. (2011) observed a robust FFA response in children as young as 4 years for faces in comparison to other categories, such as shoes, letters, numbers or scrambled images. A particularly interesting finding with regard to the question of cortical specialization was the observation that responses for the non-preferred stimulus categories (e.g., shoes in the FFA) decreased with age. This led the authors to suggest that cortical specialisation might reflect category-selective ‘pruning’ in a given brain region. Moreover, this findings speaks to current theoretical frameworks of cortical specialization, such as the Interactive Specialisation approach to human brain development (Johnson, 2011), which predict that view that postnatal functional brain development relies less on the slow maturation of particular core areas, but rather on significant specialization and fine-tuning of these areas (Johnson,
Grossmann, & Cohen Kadosh, 2009), both as a result of environmental experience and brain development. In addition, it has been suggested that this specialisation process may reflect a continuous reorganization process during which systematic connections between cortical areas are strengthened and core areas become increasingly specialised (Cohen Kadosh, 2011).

Last, a recent developmental fMRI study used dynamic causal modelling analysis (Friston, et al. 2003) to examine task-dependent interactions among cortical face processing regions in three face processing tasks (Cohen Kadosh et al. 2011). Dynamic causal modelling (DCM) approaches can be used to assess not only functional connectivity patterns (correlations in activation between different brain regions), but also to determine how experimental input influences these connectivity patterns (effective connectivity) (Friston et al., 2003). This allows one to test the influence of top-down modulation via different cognitive processes. For example, DCM assesses experimental input in two ways: the first step tests the direct influence on specific anatomical nodes in the network, an influence which could be compared to direct, stimulus driven sensory inputs. The second input is largely stimulus-independent and modulates the coupling between nodes; comparable to the different attentional states induced by a task instruction and when participants use a different cognitive strategy for each task. A better understanding of the influence of top-down cognitive task strategies on brain activation is particularly important for developmental neuroimaging studies, which assess how developmental changes in cognitive abilities are reflected in differential brain activation (Cohen Kadosh, 2011). In the study by Cohen Kadosh and colleagues, this DCM analysis enabled investigation of age group differences (in children (7-8 years), pre-adolescents (10-11 years), and adults) and the
impact of differing task demands (matching based on identity, emotion or gaze) on effective connectivity between regions (Cohen Kadosh et al. 2011) (Figure 3). They found that the same basic cortical network, comprising FFA, STS and inferior occipital gyrus was present in all age groups. However, there was an age-related increase in the extent of top-down cognitive strategy modulation of network connections for the three tasks, with only adults showing task-specific strengthening of specific network paths. This finding was interpreted as a cumulative effect of exposure and training, such that the cortical network for face processing becomes increasingly fine-tuned with age.

In sum, recent evidence has suggested that the observed developmental trajectory for face processing abilities is also mirrored by protracted development at the brain level (Cohen Kadosh & Johnson, 2007). It remains to be determined whether both behavioural and neural face processing continues to develop during adolescence, as some studies suggest (Carey, et al., 1980; Scherf, et al., in press), or whether the observed findings of lower face processing abilities during this developmental period reflect a general shift in social information processing (Scherf, et al., in press).

**Theory of mind development**

The ability to attribute mental states to other people is known as theory of mind or mentalising. An understanding of others’ mental states plays a critical role in social interaction because it enables us to work out what other people want and what they are about to do next, and to modify our own behaviour accordingly. There is a rich literature on the development of social cognition in infancy and childhood, pointing to step-wise changes in social cognitive abilities during the first five years of life. While
certain aspects of theory of mind are present in infancy (Baillargeon et al. 2010), it is not until around the age of four years that children begin explicitly to understand that someone else can hold a belief that differs from one's own, and which can be false (Barresi & Moore, 1996).

There has been surprisingly little empirical research on social cognitive development beyond childhood. Only recently have studies focused on development of the social brain beyond early childhood, and these support evidence from social psychology that adolescence represents a period of significant social development. Recently, a number of fMRI studies have investigated the development of the functional brain correlates of mentalising during adolescence. These studies have used a wide variety of mentalising tasks – involving the spontaneous attribution of mental states to animated shapes, reflecting on one's intentions to carry out certain actions, thinking about the preferences and dispositions of oneself or a fictitious story character, and judging the sincerity or sarcasm of another person's communicative intentions (see Blakemore, 2008). Despite the variety of mentalising tasks used, these studies of mental state attribution have consistently shown that dorsal medial prefrontal cortex (mPFC) activity during mentalising tasks decreases between adolescence and adulthood (Figure 4). Each of these studies compared brain activity in young adolescents and adults while they were performing a task that involved thinking about mental states (see Figure 4 for details of studies). In each of these studies, mPFC activity was greater in the adolescent group than in the adult group during the mentalising task compared to the control task. In addition, there is evidence for differential functional connectivity between mPFC and other parts of the mentalising network across age (Burnett & Blakemore, 2009).
To summarise, a number of developmental neuroimaging studies of social cognition have been carried out by different research groups around the world, and there is striking consistency with respect to the direction of change in mPFC activity. It is not yet understood why mPFC activity decreases between adolescence and adulthood during mentalising tasks, but two non-mutually exclusive explanations have been put forward (see Blakemore, 2008, for details). One possibility is that the cognitive strategy for mentalising changes between adolescence and adulthood. A second possibility is that the functional change with age is due to neuroanatomical changes that occur during this period. Decreases in activity are frequently interpreted as being due to developmental reductions in grey matter volume, presumably related to synaptic pruning. However, there is currently no direct way to test the relationship between number of synapses, synaptic activity and neural activity as measured by fMRI in humans (see Blakemore, 2008, for discussion). If the neural substrates for social cognition change during adolescence, what are the consequences for social cognitive behaviour?

**Online mentalising usage is still developing in mid-adolescence**

Most developmental studies of social cognition focus on early childhood, possibly because children perform adequately in even quite complex mentalising tasks at around age four. This can be attributed to a lack of suitable paradigms: generally, in order to create a mentalising task that does not elicit ceiling performance in children aged five and older, the linguistic and executive demands of the task must be increased. This renders any age-associated improvement in performance difficult to attribute solely to improved mentalising ability. However, the protracted structural
and functional development in adolescence and early adulthood of the brain regions involved in theory of mind might be expected to affect mental state understanding. In addition, evidence from social psychology studies shows substantial changes in social competence and social behaviour during adolescence, and this is hypothesised to rely on a more sophisticated manner of thinking about and relating to other people – including understanding their mental states (Steinberg, 2005).

Recently, Dumontheil, Blakemore and colleagues adapted a task that requires the online use of theory of mind information when making decisions in a communication game, and which produces large numbers of errors even in adults (Keysar et al. 2003). In our computerised version of the task, participants view a set of shelves containing objects, which they are instructed to move by a “Director,” who can see some but not all of the objects (Dumontheil et al. 2010; Figure 5). Correct interpretation of critical instructions requires participants to use the director’s perspective and only move objects that the director can see (the director condition). We tested participants aged between 7 and 27 years and found that, while performance in the director and a control condition followed the same trajectory (improved accuracy) from mid-childhood until mid-adolescence, the mid-adolescent group made more errors than the adults in the director condition only. These results suggest that the ability to take another person’s perspective to direct appropriate behaviour is still undergoing development at this relatively late stage.

Social evaluation: acceptance and rejection

Social psychology studies have shown that adolescents, and by some accounts particularly female adolescents, are more sensitive to being excluded from a social
interaction by peers, relative to adults or younger children (O’Brien & Bierman, 1988; Kloep, 1999). In cases where risky behaviour is a group norm, this effect could contribute to the impact of peer influence on risky behaviour. A recent study (Sebastian et al. 2010a) investigated social rejection experimentally, using a computerised ball-passing paradigm known as Cyberball (Williams et al., 2000). In Cyberball, participants are told that they are playing a ball-passing game over the internet with two other players, represented by cartoon drawings. In reality, the players are pre-programmed computer algorithms, which systematically include (by passing the ball to), or exclude participants. In this study, female adolescents (young adolescents: 11-14 years; mid-adolescents: 14-16 years) showed significantly reduced self-reported positive mood following episodes of exclusion (social rejection) than did female adults (22-47 years). Additionally, levels of anxiety were disproportionately increased following social rejection in younger adolescents (11-13 years) relative to adults, while anxiety was sustainedly high in older adolescents (14-15 years). Thus, female adolescents show heightened sensitivity to social rejection in an experimental context.

Neuroimaging studies are beginning to explore the neural basis of this effect. One study used the Cyberball paradigm, combined with fMRI in a group of adolescents (12-13 years) (Masten et al., 2009). The results showed patterns of brain activity that were similar to those in a previous study in adults (Eisenberger et al. 2003): positive correlations were found between self-reported distress, and activity within visceral pain and negative affect-related regions (e.g. insula) during social exclusion vs. inclusion; and negative correlations were found between self-reported distress and
activity in regions associated with emotion regulation, including ventrolateral prefrontal cortex (VLPFC).

One recent study (Sebastian et al., 2011) directly compared female adolescents (14-16 years) and female adults (23-28 years) during a modified version of the Cyberball task and found that adults activated VLPFC to a greater extent during exclusion than inclusion conditions, while adolescents exhibited the reverse pattern. Since right VLPFC has previously been associated with the regulation of distress during social exclusion (Eisenberger et al., 2003), it is possible that a reduced engagement of this region in adolescents in response to rejection-related stimuli underlies the increased affective response seen in adolescents in behavioural studies. A similar result was found in an fMRI study exploring neural responses to the automatic processing of rejection-related information (Sebastian et al., 2010b). This study compared female adolescents (N=19, 14-16 years) and adults (23-28 years) on a rejection-themed emotional Stroop task in which participants were asked to indicate the ink colour in which rejection, acceptance and neutral words were written. In adults, rejection-themed words activated the right VLPFC to a greater extent than acceptance or neutral words; while this pattern of responding was not seen in the adolescent group. These studies are consistent with theories suggesting that prefrontal regulatory mechanisms continue to develop between mid-adolescence and adulthood (e.g. Nelson et al., 2005), and this may be one factor underlying observed adolescent hypersensitivity to rejection.

Rejection by peers is an extreme form of peer evaluation. This was the subject of a recent fMRI study that used an internet chat-room paradigm with male and female
participants aged 9-17 years (Guyer et al., 2009). Results showed that in females only, there was an age-related increase in activity during expectation of peer evaluation within brain regions involved in affective processing (nucleus accumbens, hypothalamus, hippocampus and insula), but no differences within the anterior cingulate cortex (ACC) or other social brain regions. The finding of gender differences in the neural response to social evaluation is in line with reports of greater social anxiety in female adolescents than in males, in response to negative social evaluations in everyday life (La Greca & Lopez, 1998). However, the possibility that female adolescents are more sensitive to social rejection than are males has not been tested empirically. Guyer et al. (2009), for example, did not find gender differences in behaviour on their task.

Recently, an fMRI study investigated peer evaluation and rejection across age, in groups of pre-adolescent (8-10 years), adolescent (12-14; 16-17 years) and adult (19-25 years) participants (Gunther Moor et al., 2010). In this experiment, participants supplied photos of their faces in advance and were told that these would be rated by a panel of peers. Then, during fMRI scanning, participants viewed a sequence of photographs of same-age individuals who they were led to believe comprised the panel of peers, and for each photo answered the yes/no question “Do you believe this person liked you?” This was followed by fictitious yes/no feedback response indicating whether the individual depicted in the photo liked the participant or not. Results showed an age-related increase in activity within ventral mPFC, ACC and striatum when participants predicted they would be liked by a peer, while predicted social rejection resulted in increasing activity with age in affect-regulation regions such as orbito-frontal cortex and lateral PFC. An interesting point to note in this study
is the age-related increase in ventral mPFC activity, while mentalising studies show age-related decreases in the more dorsally-situated anterior rostral mPFC (see also Moriguchi et al., 2007). This difference could relate to possible functional subdivisions within mPFC, a large and incompletely functionally-characterised brain area (Gilbert et al. 2010).

**Implications for education**

A recent Royal Society policy report stated that common ground between education and neuroscience ‘suggests a future in which educational practice can be transformed by science, just as medical practice was transformed by science about a century ago’ (Royal Society, 2011). The evidence reviewed above shows that infants enter the world with biases that allow them to quickly develop skills that help them interact with and learn from others. Very early in ontogeny the human brain becomes tuned to processing social information thus paving the way to benefit from others’ knowledge and instruction. This has important implications for education because it demonstrates that the fundamental social capacities, which facilitate and profit from teaching and instruction, are laid down early in development. In fact, it has been proposed that social communication among humans is adapted to facilitate the transmission of generalizable knowledge between individuals. This communication system has been termed ‘natural pedagogy’ and it is thought to enable fast and efficient social learning of cultural knowledge (Csibra & Gergerly, 2009). There is now accumulating evidence that human infants are equipped to benefit from ‘natural pedagogy’. This new understanding of the infant as a competent and prepared social learner is likely to impact our early education practices before entering school. In particular, future research will allow us to further specify the conditions under which
infants learn from others most efficiently and thus help us improve infants’ learning environments.

The evidence reviewed above suggests continuing development across adolescence in the neural correlates of key social cognitive processes including face processing, mentalising, peer influence and the emotional response to social evaluation (acceptance and rejection). These data could have particular relevance for pastoral provision in schools, particularly at secondary level.

There is an increasing realization that schools play a critical role in pupils’ social and emotional development. In the UK, the ‘Social and Emotional Aspects of Learning’ (SEAL) programme (2007) is now implemented in 70% of secondary schools (Humphrey et al., 2010, DFE Research Report). However, this report also found considerable variability in SEAL’s effectiveness in promoting socioemotional skills and mental health among pupils, with few schemes subscribing to evidence-based interventions. Cognitive neuroscience is well placed to provide an evidence base that can inform educational policy on this issue (Viding et al., 2011), via its characterisation of key cognitive and neural processes underlying social and emotional development. For example, managing social relationships is a significant challenge for adolescents. Relational or social forms of bullying are common within school peer groups; for example one recent study (Wang et al., 2009) found that 27.4% of adolescent girls (mean age 14.3 years) reported being excluded or ignored by a group of peers while at school. Being bullied (including relational aggression) is associated with decreased school achievement and psychological wellbeing (Hawker and Boulton, 2000; Boulton et al., 2008); thus, a greater understanding of adolescent responses to phenomena would be helpful.
such as social rejection (such as that provided by the above studies) may contribute to greater understanding of the factors contributing to schooling success and failure (Blakemore, 2010). The next major challenge for educational neuroscience is to work out how the potential for cognitive neuroscience evidence to influence school-based interventions may be best realized. This will likely require the training of ‘brokers’ between education and neuroscience, who can build bridges between these two currently disparate fields (Viding et al., 2011).

If early childhood is seen as a major opportunity – or a “sensitive period” - for teaching, so too should the teenage years. Sensitive periods can be thought of as periods of development in which the brain is particularly susceptible to certain environmental stimuli and particularly efficient at processing and assimilating new information – at learning. It is possible that certain skills might be particularly amenable to learning during adolescence, while for other skills it might be too late- or even too early. Understanding the brain mechanisms that underlie learning and memory, and the effects of genetics, the environment, emotion and age on learning could transform educational strategies and enable us to design programs that optimise learning for people of all ages and of all needs. Neuroscience can now offer some understanding of how the brain learns new information and processes this information throughout life (Blakemore & Frith, 2005). Understanding the brain basis of social functioning and social development is crucial to the fostering of social competence inside and outside the classroom. Social functioning plays a role in shaping learning and academic performance (and vice versa), and understanding the neural basis of social behaviour can contribute to understanding the origins and process of schooling success and failure. The finding that changes in brain structure
continue into adolescence (and beyond) has challenged accepted views, and has
given rise to a recent spate of investigations into the way cognition (including social
cognition) might change as a consequence. Research suggests that adolescence is a
key time for the development of regions of the brain involved in social cognition and
self-awareness. This is likely to be due to the interplay between a number of factors,
including changes in the social environment and in puberty hormones, as well as
structural and functional brain development and improvements in social cognition.

Adolescence is a time of opportunity for learning new skills and forging an adult
identity. However, it is also a time of vulnerability, as adolescents begin to face adult
challenges whilst still developing physically, socially and cognitively (Steinberg, 2005).
The idea that teenagers should still go to school and be educated is relatively new. And
yet, the research on brain development suggests that education during the teenage
years is vital, with the brain needing to be moulded and shaped during this period of
relative plasticity. Perhaps the aims of education for adolescents might change based
on these recent neuroscientific findings to include abilities that are controlled by the
parts of the brain that undergo most change during adolescence. These abilities
include cognitive control, multi-tasking and planning – but also self-awareness and
social cognitive skills such as extracting social information from faces, regulating
emotional responses during peer interactions, perspective taking and the
understanding of other people's minds.
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References


symposium on cognition: Visual perception and cognition in infancy.


Figures

Figure 1

This figure shows 4-month-olds’ hemodynamic responses (oxygenated hemoglobin) to mutual gaze (black) and averted gaze (white) as measured with fNIRS from the right prefrontal and right temporal cortical regions (marked by arrows in the bottom panel). This figure was adapted from Grossmann et al. (2008).
Figure 2

This figure shows 5-month-olds’ hemodynamic responses (oxygenated hemoglobin) to joint attention (black), no referent (grey), no eye contact (white) conditions as measured with fNIRS from a left dorsal prefrontal cortical region (marked by an arrow in the right panel). This figure was adapted from Grossmann & Johnson (2010).
Figure 3

Developmental changes in cortical response patterns in the core face network in children aged 7-11 years and adults. While the overall network configuration was confirmed for all three age groups, a continuous increase in functional response was observed in the two child groups, along with changing patterns of effective connectivity in the network. Most notably, the two child groups did not exhibit any task-dependent changes in network connectivity, a finding which has been attributed to lower levels of processing proficiency. A) Percent signal change in brain activation in three core face network regions as a function of age and task (Identity task = red; Expression task = blue, Gaze task = green). B) Dynamic causal modelling analysis of the developmental changes in the core face network in three age groups. Solid arrows indicate significant changes in effective connectivity between two network regions, dotted arrows indicate nonsignificant effects. Black arrows indicate the intrinsic
connection between the areas of interest. Colored arrows indicate modulatory effects of each task on the connection between the areas. Abbreviations: IOG= inferior occipital gyrus; FG= Fusiform Gyrus; STS= superior temporal sulcus. Adapted from Cohen Kadosh et al., 2011.
Figure 4

A section of the dorsal mPFC that is activated in studies of mentalising: Montreal Neurological Institute (MNI) 'y' coordinates range from 30 to 60, and 'z' coordinates range from 0 to 40. Dots indicate voxels of decreased activity during seven mentalising tasks between late childhood and adulthood (see refs 10, 16 for references). The mentalising tasks ranged from understanding irony, which requires separating the literal from the intended meaning of a comment, thinking about one's own intentions, thinking about whether character traits describe oneself or another familiar other, watching animations in which characters appear to have intentions and emotions and thinking about social emotions such as guilt and embarrassment [9].
Figure 5

(a-b) Images used to explain the Director condition: participants were shown an example of their view (a) and the corresponding director’s view (b) for a typical stimulus with four objects in occluded slots that the director cannot see (e.g. the apple). (c-d) Example of an Experimental (c) and a Control trial (d) in the Director condition. The participant hears the verbal instruction: “Move the small ball left” from the director. In the Experimental trial (c), if the participant ignored the director’s perspective, she would choose to move the distractor ball (golf ball), which is the smallest ball in the shelves but which cannot be seen by the director, instead of the larger ball (tennis ball) shared by both the participant’s and the instructor’s perspective (target). In the Control trial (d), an irrelevant object (plane) replaces the distractor item.