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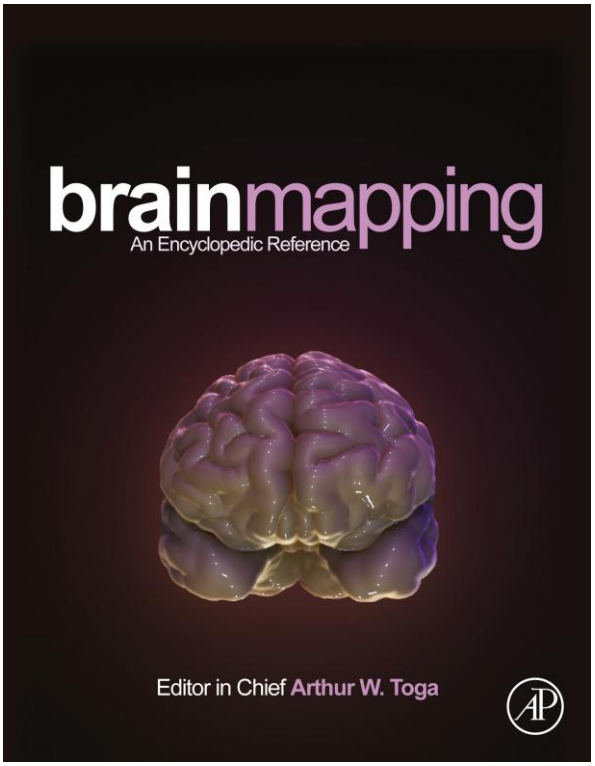

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The Social Brain in Childhood and Adolescence

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Glossary

Functional magnetic resonance imaging (FMRI)/ neuroimaging fMRI, a noninvasive neuroimaging technique that assesses local changes in blood flow that occur in response to the metabolic demands of synaptic activity (i.e., blood oxygenation level-dependent or 'BOLD' response) during a cognitive task.

Social brain A network of regions underpinning the processing of social cues.

Theory of mind The ability to understand the contents of another's mind in terms of thoughts, beliefs, and feelings and to use this knowledge to predict behavior.

Human beings are an extensively social species, and much of our time is spent in social interactions. We use facial expressions to communicate our emotional states and attentional focus, and we infer thoughts and intentions from a person's gestures and actions. The cognitive process by which we understand and use these cues generated by conspecifics or ourselves has been termed social cognition. In the brain, these social–cognitive abilities are supported by a network of regions termed the 'social brain network.' This comprises brain regions such as the fusiform gyrus (FG), the amygdala, the superior temporal sulcus (STS) and temporoparietal junction (TPJ), and the prefrontal cortex (Blakemore, 2008; Burnett, Sebastian, Cohen Kadosh, & Blakemore, 2011; Frith & Frith, 2007) (**Figure 1**).

Developmental changes in social-cognitive abilities are only part of a general program of development, in that they go along with substantial social, cognitive, hormonal, and physiological maturation during childhood and adolescence (Blakemore, 2008; Burnett et al., 2011). Together, these different factors facilitate impressive developmental changes, which enable the individual , for example, to think more rationally, to interact successfully with peers and to acquire adequate emotional coping strategies. At the brain level a variety of developmental factors drive these changes, such as physical growth and hormonal changes. These are accompanied by impressive cognitive development, which enables the individual, for example, to think more rationally and to acquire adequate emotional coping strategies. At the brain level, this development is reflected in both gray matter changes, such as axonal sprouting, synaptic pruning, and synaptogenesis, and white matter changes due to ongoing myelination and fiber organization (Giedd et al., 1999; Harris, Reynell, & Attwell, 2011; Lebel & Beaulieu, 2011; Petanjek et al., 2011; Tamnes et al., 2013). These changes affect not only the underlying brain structure but also the functional responsiveness and processing abilities of the developing brain. It remains to be determined whether age-dependent differences in functional activity mainly reflect a lack of specialization of still developing neuronal networks or whether they are the results of different cognitive strategies being used at each developmental stage (see Blakemore et al., 2008; Cohen Kadosh, Johnson, Dick, Cohen Kadosh, & Blakemore, 2013). While prolonged trajectories do carry a certain risk of developing maladaptive cognitive strategies and/or brain networks, they also provide a window of opportunity by providing the individual with flexibility in changing the social environments (Thompson-Schill, Ramscar, & Chrysikou, 2009).

Recent methodological advances have provided us with increasingly sophisticated techniques to pinpoint these changes in the brain *in vivo* (Dick, Lloyd-Fox, Blasi, Elwell, & Mills, 2013). Specifically, functional magnetic resonance imaging (fMRI), a noninvasive neuroimaging technique, has played an important role in revealing how the functional brain correlates social–cognitive processes change during development. In most fMRI studies, participants are asked to perform (social) cognitive tasks while changes in neural activity are being recorded. The changes are assessed by looking at local changes in blood flow, which occur in response to the metabolic demands of synaptic activity (i.e., blood oxygenation level-dependent or 'BOLD' response) (Attwell & Iadecola, 2002; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). The rationale behind this approach is that brain regions that are involved in a specific task will be more active in comparison to other nonsupportive brain regions and hence exhibit higher levels of blood flow.

In this article, we will illustrate the developmental changes in the social brain based on examples of two specific social–cognitive skills: (1) face-processing abilities, a basic social–cognitive skill, and (2) the ability to attribute and evaluate other's mental states (also termed 'theory of mind (ToM)'), a highly complex social ability. We will end by highlighting how a better understanding of the developmental changes in social–cognitive skills during childhood and adolescence could also provide an important breakthrough for applied research addressing the social deficits in many developmental disorders (e.g., autism spectrum disorder and social anxiety). If we were able to determine sensitive and critical periods of change, we could use this knowledge to develop interventions to boost resilience and help avert maladaptive outcomes in social–cognitive functioning (Cohen Kadosh, Linden, & Lau, 2013; Haller, Cohen Kadosh, & Lau, 2014; Haller, Cohen Kadosh, Scerif, & Lau, in preparation).

Face Processing

The neural circuitry underlying face processing is one of the best-studied neural responses of the brain. This makes it an

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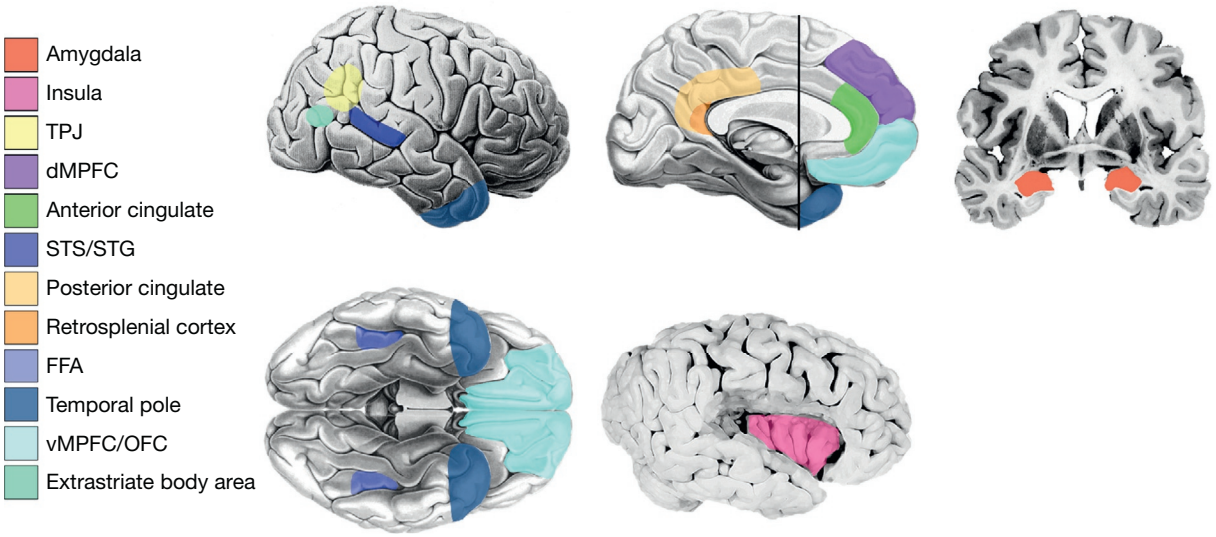

Figure 1 Network of brain regions supporting social cognition. Abbreviations: dMPFC = dorso-medial prefrontal cortex; FFA= fusiform face area; STS/STG = superior temporal sulcus/gyrus; TPJ = temporo-parietal junction; vMPFC/OFC = ventro-medial prefrontal cortex/ orbitofrontal cortex. Reprinted with permission from Kennedy & Adolphs, 2012.

ideal model for investigating the mechanisms of cortical specialization of social–cognitive functions during development. Human faces are highly salient stimuli, which carry much information for the viewer. To extract this information, mature face processors rely on specialized processing strategies (Maurer, Le Grand, & Mondloch, 2002), which reflect a high level of expertise (Gauthier & Nelson, 2001). We devote preferential attention to faces almost from birth (Farroni et al., 2005; Johnson, Dziurawiec, Ellis, & Morton, 1991). Nonetheless, it has been shown that children require 10 years or more of practice to process faces with adultlike proficiency (Cohen Kadosh, 2011; Durand, Gallay, Seigneuric, Robichon, & Baudouin, 2007; Karayanidis, Kelly, Chapman, Mayes, & Johnston, 2009; Mondloch, Geldart, Maurer, & Le Grand, 2003; Mondloch, Le Grand, & Maurer, 2002). One advantage of this extended acquisition window could be that it allows the individual to respond flexibly to different information processing demands during development. That is, whereas infants and young children may focus on learning to identify a particular emotional expression and to read intent from eye gaze direction, older children or adolescents will have to become proficient at processing more complex social face aspects, such as attractiveness or mating potential (Scherf, Behrmann, & Dahl, 2012).

The protracted acquisition of face-processing abilities is mirrored by slowly emerging specialized face networks in the brain (Cohen Kadosh & Johnson, 2007; Kanwisher, 2010). Neural face processing relies on a core network of brain regions, including the inferior occipital gyrus (IOG), the FG, and the STS (Cohen Kadosh, Henson, Cohen Kadosh, Johnson, & Dick, 2010; Haxby, Hoffman, & Gobbini, 2000). Children show face-preferential activation in these core network regions from an early age (Cantlon, Pinel, Dehaene, & Pelphrey, 2011; Cohen Kadosh, Johnson, Dick, Cohen Kadosh, & Blakemore, 2012). Communication within this network (as assessed with effective connectivity measures) is less strong in comparison with adults (Cohen Kadosh, Cohen Kadosh, Dick, & Johnson, 2011).

Other work has provided evidence of ongoing specialization within the core face network for both basic-level and individual-level face-processing responses (Cohen Kadosh, Johnson, Henson, Dick, & Blakemore, 2013; Cohen Kadosh et al., 2012; Golarai et al., 2007; Scherf et al., 2012). These two processing levels refer to either faces being differentiated from other object categories, such as houses (basic-level face processing), or faces being differentiated from each other on the basis of specific face aspects, such as identity (individual-level processing). Golarai et al. (2007) assessed basic-level face-processing responses in children, adolescents, and adults using photographic images of faces, objects, places, or abstract patterns. They found significant signal differences between the groups. While adults showed more extensive activation than children in the right FG, adolescents exhibited an intermediate pattern. In addition, the age-related expansion of the fusiform face area (FFA) into the surrounding cortex correlated with improving face recognition memory. In a different study, Scherf, Luna, Avidan, and Behrmann (2011) found evidence for basic-level and individual-level face processing in the bilateral FFA in adults, while adolescents (11–14 years) showed categorical processing bilaterally and individual-level processing only in the left FFA. A group of children (6–10 years) exhibited neither categorical nor individual-level processing in either the left or right FFA. These findings lead the authors to suggest that face processing shifts from categorical to individual-level face processing, as well as from a bilateral to more specialized right-lateral processing with development. Cohen Kadosh and colleagues (2012) reported age-dependent increase in individual-level face-processing patterns in the right IOG (Cohen Kadosh et al., 2010). The authors found differential activation patterns in children (7–11 years) and adults, but not in adolescents (12–17 years). This seemed to suggest a shift from a simplistic cognitive strategy in childhood to a more

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complex and strategic use in adults. Interestingly, adolescents did not exhibit systematic, strategy-dependent response patterns, a finding that was interpreted to reflect the heterogeneity of processing strategies in this transitional stage.

Along with the observed age-dependent increase in face selectivity within the core face network regions, a decrease in face responsivity in regions outside the network has been documented (Johnson, Grossmann, & Cohen Kadosh, 2009). Several studies have reported activation in the bilateral inferior frontal gyrus (IFG) in children, but not in adults (Gathers, Bhatt, Corbly, Farley, & Joseph, 2004; Passarotti, Smith, DeLano, & Huang, 2007; Passarotti et al., 2003; Scherf, Behrmann, Humphreys, & Luna, 2007), suggesting that this region supports the initial acquisition of face-processing abilities. This interpretation is strengthened by the results from a recent study, which showed that increased cortical excitability levels (i.e., increased glutamate levels) in the IFG correlated with face-processing performance in 7-year-old children, but not in adults (Cohen Kadosh, Krause, King, Near, & Cohen Kadosh, under review).

In summary, recent evidence has suggested that the protracted developmental trajectory for face-processing abilities is also mirrored by extended development at the brain level (Cohen Kadosh & Johnson, 2007). It remains to be determined whether the behavioral and neural development in face processing is domain-specific as some studies suggest (Carey, et al., 1980; Scherf, et al., 2011) 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., 2011).

Theory of Mind

The ability to attribute mental states such as intentions, beliefs, and feelings and to understand their consequences for emotional experiences, cognition, and behavior has been termed theory of mind (ToM; Wimmer & Perner, 1983). To date, a substantial number of fMRI studies have accumulated, detailing in a surprisingly consistent manner the 'social brain' subserving this capacity in adults. These studies have attested to a network of regions including, but not limited to, the (dorsal and ventral) medial prefrontal cortex (MPFC), (posterior) STS, TPJ, and temporal poles (e.g., Frith & Frith, 2003, 2006; Gallagher & Frith, 2003; Saxe & Kanwisher, 2003; Van Overwalle, 2009).

Given the complexity of this skill, it is perhaps not surprising that a large body of research has shown that ToM develops throughout childhood and adolescence (Blakemore, 2008; Cohen Kadosh, 2011; Cohen Kadosh & Johnson, 2007; Dumontheil, Hassan, Gilbert, & Blakemore, 2010; Mondloch et al., 2002). While behavioral work has mainly focused on young children and the initial acquisition of ToM with only few studies demonstrating behavioral changes in adolescence (Dumontheil, Apperly & Blakemore, 2010; Vetter, Leipold, Kliegel, Phillips, & Altgassen, 2012), imaging research has assessed these abilities mostly in older, adolescent samples.

Studies of the neural correlates of ToM have consistently found developmental differences between children or adolescents and adults particularly with regard to recruitment of the frontal and temporal 'social brain' areas. With one of the youngest samples, an fMRI study by Saxe, Whitfield-Gabrieli, and Pelphrey (2009) presented children between the ages of 6 and 11 with ToM illustrations that contained both physical and mental attributes and descriptions of the protagonists. Whereas the TPJ was activated by both mental and physical stories in younger children, it responded selectively to descriptions of mental states in older children. This could indicate specialization of this social brain region with age.

There is now a corpus of data suggesting that the neural underpinnings of ToM continue to develop beyond childhood and throughout adolescence. Employing a task that required participants to decide whether a verbal message was ironic or sincere, Wang, Lee, Sigman, and Dapretto (2006) found that, in young adolescents between 9 and 14 years of age, the MPFC and left IFG were more active than in adults (aged 23–33). The authors also reported a negative correlation between age and activity in the MPFC attesting to protracted developmental trends. Another study by Blakemore, den Ouden, Choudhury, and Frith (2007) investigated the neural correlates of thinking about one's own intentions in adolescents (aged 12–18) and adults (aged 22–38). The authors employed scenarios about intentional and physical causality, respectively. While both groups showed an activation of the 'social brain network' in response to intentional causality as compared with the physical causality, adolescents exhibited greater activation in the dorsal MPFC than adults in response to intentionality. The opposite was true for a region in the right STS, which was found to be more active in response to intentional causality in adults than in adolescents. The authors proposed that the relative roles of the different neural circuits underlying ToM change with age, with activity moving from anterior midline (e.g., the dorsal medial PFC) regions to posterior temporal (e.g., the STS) regions. More recent studies have often employed multiple adolescent groups to track changes in the development of functional neural architecture across adolescence more closely. Two studies using different paradigms that tap into other-related thoughts in terms of fairness and attribution of mental states to facial cues, respectively (Gunther Moor et al., 2011; Van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2011), have shown decreasing MPFC activity across adolescence. Van den Bos et al. (2011) additionally reported a gradual age-associated increase in TPJ activation across adolescent age groups. Interestingly, Gunther Moor et al. (2011) reported increased ventral, rather than dorsal, MPFC activation in adolescent age groups in comparison to adults. This difference in localization within MPFC areas may be due to the affective nature of the face-processing task. The 'Reading the Mind in the Eyes' test requires participants to attribute emotional states to expressive eye regions. Further support for this interpretation comes from a recent study by Sebastian et al. (2012) that directly compared cognitive to affective ToM using cartoon vignettes in adolescents aged between 11 and 16 and adults aged between 24 and 40. While both types of cartoon stories activated the social brain network, thinking about affective vignettes was associated with increased ventral MPFC activity in comparison with the cognitive vignettes across groups but more so in adolescents as compared with adults.

All in all, fMRI studies of social cognition attest to functional developmental trends in frontal and potentially posterior regions, specifically with a decrease in MPFC regions from adolescence to adulthood (note an exception; Moriguchi, Ohnishi,

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Mori, Matsuda, & Komaki, 2007). However, in the absence of more systematic longitudinal investigations it is difficult to map trajectories with certainty. Adolescent functional brain development is complex and it is likely that not all age-associated changes are linear but some may also be quadratic. Recent research has started to tackle the issue of assessing brain development not only in relation to chronological age but also in relation to other significant developmental processes during this period, most notably puberty and associated hormonal changes (e.g., Goddings et al., 2014). We are also only beginning to understand how functional changes are associated with developing social–cognitive processes and how these link to complex (linear and quadratic region-specific) structural maturations in the brain (Mills et al., 2014). The central task for developmental neuroimaging research in the next decade will be to disentangle the complex interactions between genetic, physiological (specifically hormonal), and environmental changes that influence the developing social brain in the transition from childhood to adolescence and early adulthood. It is already becoming clear that a comprehensive understanding of the changing behavioral and neural bases of social–cognitive abilities would be invaluable to more applied, translational research approaches into pediatric mental health, specifically for anxiety disorders or autism spectrum conditions. This knowledge will allow us to develop models for translation into effective intervention approaches, targeting specific periods of cognitive and or neural plasticity during this developmental period (Cohen Kadosh, Linden, et al. 2013).

Conclusions

Social–cognitive skills refer to our ability to interpret social cues in our interactions with others. Based on the example of basic (face processing) and complex (ToM) social–cognitive skills, we have shown that the social brain develops continuously during childhood and adolescence. While such a prolonged developmental trajectory may seem a risk factor, it could actually represent a developmental advantage that allows the individual to respond flexibly to changing social environmental demands and expectations. Future work is now needed to understand how we can harness these prolonged periods of cognitive and neural plasticity for targeted translational approaches and help enhance and adjust social–cognitive functioning during a critical developmental period.

See also: **INTRODUCTION TO ACQUISITION METHODS**: Functional MRI Dynamics; Obtaining Quantitative Information from fMRI; Temporal Resolution and Spatial Resolution of fMRI; **INTRODUCTION TO ANATOMY AND PHYSIOLOGY**: Lateral and Dorsomedial Prefrontal Cortex and the Control of Cognition; **INTRODUCTION TO CLINICAL BRAIN MAPPING**: Developmental Brain Atlases; Limbic to Motor Interactions during Social Perception; **INTRODUCTION TO SOCIAL COGNITIVE NEUROSCIENCE**: Mentalizing and Psychopathology in Schizophrenia, Depression, and Social Anxiety; Mentalizing; Neural Correlates of Social Cognition Deficits in Autism Spectrum Disorders; Social Knowledge; The Neural Correlates of Social Cognition and Social Interaction; **INTRODUCTION TO SYSTEMS**: Face Perception.

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