Social cognition and abstract thought in adolescence: The role of structural and functional development in rostral prefrontal cortex

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Abstract

Background. The rostral prefrontal cortex (RPFC) has increased in size and undergone changes in terms of its cellular organisation during primate evolution. In parallel emerged the ability to detach oneself from the immediate environment and process abstract thoughts and solve problems, as well as the ability to understand other individuals’ thoughts and intentions. The RPFC is thought to play an important role in supporting these abilities: lateral RPFC is involved in processing and focusing on abstract thoughts and medial RPFC is involved in social cognition. Adolescence is a time characterised by change – hormonally, physically, psychologically and socially. Yet until fairly recently this period of life was neglected by cognitive neuroscience. In the past decade, large scale structural MRI studies have demonstrated development during adolescence of white and grey matter brain structure, with more protracted changes in the RPFC than in most other regions. Several fMRI studies have found that activity in the lateral and medial parts of RPFC shows changes between adolescence and adulthood during tasks of abstract thought and social cognition, respectively. Performance on both types of task also continues to improve until late adolescence. These findings highlight how adolescence, and not only childhood, is thus a time of continued maturation of brain and behaviour, when education and the environment can have an impact on cognitive development.

Rostral prefrontal cortex in humans

Rostral prefrontal cortex (RPFC), which corresponds approximately to Brodmann area 10 (BA10, Brodmann 1908, 1909), is a large brain region in humans and is thought to be subdivided into separate subregions distinct in terms of cellular organization and function (Christoff & Gabrieli, 2000; Gilbert et al., 2006). Two quite different types of cognitive ability have been associated with the RPFC. The lateral parts of RPFC (rostrolateral prefrontal cortex, RLPFC) appear to support the ability to detach oneself from the environment and to elaborate, evaluate and maintain abstract rules and information, and thus it is involved in reasoning, problem-solving.
solving, and more generally abstract thinking (Amati & Shallice, 2006; Christoff & Gabrieli, 2000; Christoff et al., 2009; Gilbert et al., 2007; Koechlin et al., 2003; Ramnani & Owen, 2004). These types of processes have been included in the general “working memory” category in meta-analyses of neuroimaging studies (Cabeza & Nyberg, 2000; Gilbert et al., 2006) (see Figure 1). The medial aspect of RPFC, or medial prefrontal cortex (MPFC), is implicated in social cognition, that is, the understanding of other people’s minds (see Figure 1).

In the last decade, large scale magnetic resonance (MRI) studies have shown that the RPFC is one of the last brain regions to reach maturity in humans (see Dumontheil et al., 2008, for review). This region is also particularly interesting in terms of its cellular organisation and connection with other regions. RPFC is the only prefrontal region that is predominantly interconnected with supramodal cortex in the PFC (Andersen et al., 1985; Petrides & Pandya, 1999), anterior temporal cortex (Moran et al., 1987; Amaral & Price, 1984) and cingulate cortex (Andersen et al., 1985; Arikuni et al., 1994; Bachevalier et al., 1997; Morecraft & Van Hoesen, 1993). In addition, its projections to these other regions are broadly reciprocal (Passingham et al., 2002; see Ramnani & Owen, 2004, for review). RPFC has a low cell density, which may indicate that this region in humans has more space available for connections both within this region and with other brain regions (Semendeferi et al., 2001). RPFC also has a particularly high number of dendritic spines per cell, an indicator of the number of synaptic connections, which suggests that the computational properties of RPFC are more likely to involve the integration of inputs than those of comparable areas (Ramnani & Owen, 2004).

This paper will focus on: how social cognition and the ability to attend to and manipulate abstract thoughts develop during adolescence; how the structural and functional development of the RPFC may underlie the behavioural changes observed during adolescence; and the potential implications of these findings for education policy and practice.

![Figure 1. Schematic representation of the functional specialisation of rostral prefrontal cortex, shown on a horizontal slice (adapted from Gilbert et al., 2006). Two axes of specialisation have been observed: on the y-axis, mentalising tasks recruit more posterior RPFC than do multitasking tasks (which include task switching and dual tasks); on the x-axis, mentalising activates the medial part of RPFC while episodic and working memory tasks, which include problem solving, abstract thinking and relational reasoning tasks (see Cabeza & Nyberg, 2000; Gilbert et al., 2006) activate lateral RPFC. Multitasking does not exhibit specificity on the x-axis. No hemispheric specificity has been consistently observed.](image-url)
Social cognition in development

Humans are an exquisitely social species. We are constantly reading each others’ 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. This is known as theory of mind or mentalising (Frith & Frith, 2007). Developmental psychology research on theory of mind has demonstrated that the ability to understand others’ mental states develops over the first four or five years of life (e.g., Happé et al., 1995). 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 to explicitly understand that someone else can hold a belief that differs from one’s own, and which can be false (Barresi & Moore, 1996). 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 (Frith & Frith, 2007).

The importance of social interaction in learning

There is evidence that social interaction is special and plays a particular role in learning. Kuhl and colleagues (2003) studied American babies who had grown up hearing only English and thus were not able to distinguish between certain Chinese Mandarin sounds. The authors trained three groups of nine-month-old American babies: one group interacted with a real native Chinese speaker, who played with and read to them; a second group saw movies of the same Chinese speaker; the third group heard the same Chinese speaker through headphones. The content and the time of exposure were identical in all three groups. The group that had been exposed to a real live Chinese person significantly improved their ability to distinguish between the two sounds, performing at around the same level as native Chinese babies. In striking contrast, babies who had been exposed to the same amount of Chinese but in the form of video or sound recordings showed no learning and their post-training performance was the same as the American babies who had received no exposure.

These results show that social interaction is a critical and constraining factor for learning. There appears to be something special about social interaction with a real live person that is not present from watching videos or hearing sound recordings of the same person. What is special about social interaction with a real person is not yet understood. One possibility is that social interaction increases infants’ motivation through enhanced attention and arousal. Social interaction also directs the adult trainer to focus on the learner’s individual needs and tailors the training content for the learner (see Kuhl, 2007, for review). In addition, by nine months, infants start to understand that pointing to, or looking in the direction of, an object indicates that this object is being referred to. This is one of the first building blocks of theory of mind (see Frith & Frith, 2007, for review), and this understanding is thought to be linked to the development of language, in particular the acquisition of new vocabulary (see Akhtar & Gerstbacher 2007 for discussion).

The social brain

Over the past 15 years, a large number of independent studies have shown remarkable consistency in identifying the brain regions that are involved in theory of mind or mentalising. These studies have employed a wide range of stimuli including stories, sentences, words, cartoons and animations, each designed to elicit the attribution of mental states (see Amodio & Frith, 2006, for review). In each case, the mentalising task resulted in the activation of a network of regions including the posterior superior temporal sulcus (pSTS) at the temporo-parietal junction (TPJ),
the temporal poles and the dorsal MPFC (see Burnett & Blakemore, 2009b). The agreement between neuroimaging studies in this area is remarkable and the consistent localisation of activity within a network of regions including the pSTS/TPJ and MPFC, as well as the temporal poles, suggests that these regions are key to the process of mentalising.

**Development of mentalising during adolescence**

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 (Frith & Frith, 2007). However, 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. Most researchers in the field use the onset of puberty as the starting point for adolescence. 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 (Steinberg, 2010). 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 underlying factors of these social changes are most likely to be multi-faceted, one possible cause is development of the social brain.

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 (Happé et al., 1995). On the one hand, this could be attributed to a lack of suitable paradigms: 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 may need to be increased. However, such increases in task complexity render any age-associated improvement in performance difficult to attribute solely to improved mentalising ability. On the other hand, the good performance of 4–5 year-olds could be attributed to qualitative differences in 2nd person perspective abilities, with basic abilities emerging very early, and more complex abilities, potentially associated with executive functioning, gradually improving during childhood and adolescence. The protracted structural (Giedd & Rapoport, 2010; Shaw et al., 2008) and functional (Blakemore, 2008) development of the brain regions involved in theory of mind in adolescence and early adulthood might indeed 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 (Steinberg, 2010), and this is hypothesised to rely on a more sophisticated manner of thinking about and relating to other people – including understanding their mental states.

Recently, we 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., 2010a). Correct interpretation of the instructions requires participants to use the director’s perspective and only move objects that the director can see (the director condition) (see Figure 2a).

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 (see Figure 2b). 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.
A number of fMRI studies have investigated the development during adolescence of the functional brain correlates of mentalising (see Blakemore, 2008 for review). 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. Despite the variety of mentalising tasks used, these studies of mental state attribution have consistently shown that MPFC activity during mentalising tasks decreases between adolescence and adulthood. These studies compared brain activity in young adolescents and adults while they were performing a task that involved thinking about mental states. 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 (see Figure 2c and Blakemore, 2008). The mentalising tasks ranged from understanding irony, which requires separating the literal from the intended meaning of a comment (Wang et al., 2006), thinking about one’s own intentions (Blakemore et al., 2007), thinking about whether character traits describe oneself or another familiar other (Pfeifer et al., 2007; 2009), watching animations in which characters appear to have intentions and emotions (Moriguchi et al., 2007) and thinking about social emotions such as guilt and embarrassment (Burnett et al., 2009). In addition, there is evidence for differential functional connectivity between MPFC and other parts of the mentalising network across age (Burnett & Blakemore, 2009a).

To summarise, a number of developmental neuroimaging studies of social cognition show 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. For example, adults may rely more on previous experiences to interpret social situations than adolescents, who instead might base their judgement on novel computations performed in the MPFC. This possibility may be related to the skill learning hypothesis (Johnson, 2011), whereby one region first supports a certain function, but another brain region may take over later in development, and according to which the PFC may be particularly involved during the learning of new abilities. 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, and Questions for future research section below).

Development of abstract thinking

Abstract thinking can be considered as the manipulation of self-generated thoughts, or thoughts that are not directly connected to the environment. RLPFC is thought to be specifically involved in the elaboration, evaluation and maintenance of abstract rules and information (Amati & Shallice, 2007; Christoff & Gabrieli, 2000; Christoff et al., 2009; Koechlin et al., 2003; Ramnani & Owen, 2004). The ability to resist distraction from one’s environment is critical for abstract thinking. Recent work suggests that RLPFC also supports the ability to flexibly control whether one attends to the environment or to self-generated thoughts (Burgess et al., 2007). Two experimental paradigms (the Shapes task and the Alphabet task) were used to assess the development of abstract thinking, and the selection of abstract thoughts vs. environmentally-derived information, during adolescence. In the following section, we report the results of a large behavioural study of these tasks and then the results of neuroimaging studies.

Relational reasoning development during adolescence

The elaboration and manipulation of abstract rules has been investigated using tasks that require relational reasoning. The relational reasoning demands of a problem can be defined
in terms of the number of dimensions, or sources of variation, that need to be considered simultaneously to reach a correct solution. Children under 5 years can solve 0- and 1-relational problems, but fail to solve 2-relational problems (Halford et al., 1998). Early improvements in relational reasoning may reflect a shift from a focus on object similarity to relational similarity (Rattermann & Gentner, 1998). Further improvements during childhood and adolescence may relate to increased relational knowledge or increased working memory capacity (Crone et al., 2009; Sternberg & Rifkin, 1979: see Richland et al., 2006, for discussion).

We recently employed the Shapes task, a relational reasoning task (Christoff et al., 2003; Bunge et al., 2009), which reliably activates RLPFC at the single subject level in adults (Smith et al., 2007), to investigate relational reasoning development during adolescence in a large sample of healthy participants (Dumontheil et al., 2010c). The Shapes task required participants to assess whether two pairs of items, which could vary in shape and/or texture, differed or changed along the same dimension. The pairs of items could both show texture differences or both show shape differences, in which case participants were asked to respond yes – i.e., the pairs change along the same dimension (match). Alternatively, one pair of items differed in texture while the other pair differed in shape, in which case participants were asked to respond no – i.e., the pairs change along different dimensions (no-match) (see Figure 3a). One hundred and seventy-nine female participants aged 7 to 27 years old participated in the study. The results show a non-linear pattern of improvement in accuracy in the Shapes task across age. After an early improvement in accuracy, with 9–11 year olds performing at adult levels, performance dips in the 11–14 year olds and gradually improves again to adult levels throughout late adolescence (see Figure 3b).

**Development of the flexible selection of self-generated thoughts**

An important aspect of the manipulation of abstract thought resides in the ability to modulate the balance between cognition that is provoked by perceptual experience (stimulus-oriented, SO) and that which occurs in the absence of sensory input (self-generated, or stimulus-independent, SI) (Burgess et al., 2007). In the same large sample of participants described above, we used a single task (“Alphabet” task) that could be performed on the basis of either SO or SI information, without high working memory requirements (Gilbert et al., 2005, 2007, 2008). Participants were asked to classify letters of the alphabet according to whether the upper case letter contained a curve or not. In SO blocks consecutive letters of the alphabet were presented on the screen, while in SI blocks either no letter (No-distractor condition) or distracting non-consecutive letters (Distractor condition) were presented on the screen. In SI blocks the participant were asked to continue going through the alphabet sequence in their head and continue responding (see Figure 4a). Different patterns of development were observed for the different aspects of this task. Resistance to visual distractors exhibited small improvements with age, both in accuracy and speed of responding, while the manipulation of SI thoughts and switching between SI and SO thoughts showed steeper speed of responding improvements extending into late adolescence (see Figure 4b).

Thus, behavioural changes in performance, in terms of either accuracy or reaction times, were observed in both the Shapes and Alphabet tasks, but the developmental trajectories were task- and condition-specific. In a second set of studies, using the same tasks, we collected functional and structural MRI data to investigate the developmental changes in brain function associated with abstract thought during adolescence, and how these changes in brain function relate to developmental changes in brain structure.
There is evidence that the developmental time course of changes in RLPFC structure can have an impact on cognitive performance. Indeed, in a large MRI study of development, Shaw and colleagues (2006) stratified their participants on the basis of Weschler intelligence scales, which give a standardized intelligence quotient (IQ) based on subtests assessing verbal and non-verbal knowledge and reasoning. Shaw et al. (2006) demonstrated that, in the absence of large differences in brain structure in childhood or in adulthood, different developmental trajectories of grey matter structure in groups of average and superior intelligence led to striking differences in cortical thickness in the superior frontal cortex and RLPFC specifically during adolescence.
In the past decade, functional MRI studies of lateral PFC development have observed a less consistent pattern of change during adolescence than the MPFC studies, with reports of both increases and decreases of task-related activations (see Luna et al., 2010 for review). As in the MPFC literature, decreases are frequently interpreted as being due to developmental reductions in grey matter volume, presumably related to synaptic pruning. Increases are thought to relate
to improved and more localized task-specific processing, potentially facilitated by faster long-range connections due to increased axonal myelination and size (Luna et al., 2010). Understanding the link between structural and functional changes is critical in understanding the mechanisms of neurocognitive development, yet very few studies have directly compared structural and functional data within the same individuals (Olesen et al., 2003; Lu et al., 2009). We attempted to address this issue of the relationship between brain structure and function, with the RLPFC as a particular region of interest, and tested variants of the two paradigms described above using fMRI, comparing participants aged 11–18 years with adults. One previous study had provided evidence of changes in RLPFC activation between childhood (age 8–12 years) and adulthood using a relational reasoning Raven’s matrices task (Crone et al., 2009).

fMRI and MRI data were collected in a group of 37 participants aged 11 to 30 years old (Dumontheil et al., 2010b, 2010c). Analysis of the Shapes task revealed that, although a consistent set of RLPFC and parietal cortex regions were activated across age groups, the fMRI results revealed a complex picture of linear and non-linear changes with age. In the posterior left RLPFC, there was an increase in activity between early and mid-adolescence, followed by a decrease in activity between mid-adolescence and adulthood (see Figure 3c). In terms of structure, grey matter volumes in this region significantly decreased between age 14–18 and adulthood, while no changes in white matter volumes were observed. Importantly, when combining functional and structural (as well as behavioural) data, we observed that the differences in performance and brain structure between the age groups accounted for most of these functional developmental changes in RLPFC activity.

Analysis of the Alphabet task revealed a different pattern of developmental changes in the RLPFC. The right superior RLPFC exhibited a decrease in activity with age when participants switched between SO and SI thoughts (Figure 4c). Here again analyses of brain structure showed that grey matter volumes in this region decreased with age. However, in this case, the functional changes observed during adolescence were not purely consequences of structural maturation or performance changes with age. These results thus offer a complex picture of the relationship between structural and functional brain maturation and developmental changes in behaviour and show that changes observed, and their interplay, will be dependent on the particular paradigm used.

Questions for future research

Our neuroimaging findings combining structural and functional MRI data suggest that it is unlikely that functional changes reflect a single developmental process, but rather a multitude of processes such as local changes in grey and white matter structure, the maturation of complex balancing brain networks (e.g., the subcortical emotional processing and top-down prefrontal regulation systems (Hare et al., 2008)) as well as the establishment of functional synchronization across networks of brain regions (Uhlhaas et al., 2009) and changes in the cognitive strategy applied to perform the tasks. Our results reinforce the importance of combining a variety of measures when studying cognitive development; however, further work will be needed to better identify the contribution of these different maturational processes to functional changes in the PFC.

In the Shapes task, both behavioural and fMRI data showed non-linear patterns of changes with age. Non-linear developmental changes have been reported previously during adolescence, in a variety of cognitive tasks including face processing and match-to-sample tasks (e.g., Carey et al., 1980; Diamond et al., 1983; McGivern et al., 2002). Typically, a dip in performance is observed around the start of puberty (age 11–12 years old) and its timing can differ
between genders (McGivern et al., 2002). This coincides with the “educational dip” that is often observed in terms of educational attainment (West et al., 2010; Whitby et al., 2006) Further work will be needed to better understand how dips in performance during adolescence relate to puberty and biological factors such as brain structure and neurotransmitter systems, or social and environmental factors such as motivation and a move to a new school (West et al., 2010; Whitby et al., 2006).

**Future possibilities for education policy and practice**

There are many questions that remain to be investigated in this new and rapidly expanding field. The study of neural development during adolescence is likely to have important implications for society in relation to education and the legal treatment of teenagers, as well as a variety of mental illnesses that often have their onset in adolescence.

Knowledge of how the brain develops and learns has the potential to have a profound impact on education in the future. 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 (see Blakemore & Frith, 2005; Royal Society Brain Waves Report, 2011).

As described above, social interaction with a real live person is critical for at least some types of early learning (Kuhl et al., 2003), suggesting that, while not necessarily harmful, DVDs and CDs aimed at teaching babies and young children may not be associated with optimal learning. More importantly, the time spent watching DVDs is time that could otherwise be spent in social interaction with a real person, and denying the developing brain of this might have negative consequences. We need to ask whether online social networking, which is particularly popular with teenagers, is the same as real live interaction, or whether it might be denying the developing teenage brain important real life interactions? There is as yet no research on this important question. There is a growing industry for the development of robot nannies, robot carers and robot companions for the elderly in ageing societies such as Japan. But are robot companions the same as real friends? Does social interaction with robots determine happiness in the same way as social relationships with people (Argyle, 2001)? Can distance learning via a computer ever compare with learning from a real human teacher? These are open questions, ripe for research.

Understanding the brain basis of social functioning and social development may improve the fostering of social competence inside and outside the classroom, in support of previous social psychological research in this domain (e.g., Durlak et al. in press). Social functioning plays a role in shaping learning and academic performance (and vice versa), and understanding the neural basis of social behaviour may 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, as well as in problem solving and abstract thinking. 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 and reasoning abilities.

If early childhood is seen as a major opportunity – or a “sensitive period” – for teaching, so too should the teenage years. During both periods, significant brain reorganisation is taking place. The idea that teenagers should still go to school and be educated is relatively new. And yet
the brain is still developing during this period, is adaptable, and can be moulded and shaped. Perhaps the aims of education for adolescents might usefully include a focus on abilities that are controlled by the parts of the brain that undergo most change during adolescence, including those described in this review: social cognition and the understanding and awareness of the potentially different perspective of others, abstract thinking and reasoning, and the ability to focus on one's own thoughts in spite of environmental distraction. Finally, it might be fruitful to include in the curriculum some teaching on the changes occurring in the brain during adolescence. Adolescents might be interested in, and could benefit from, learning about the changes that are going on in their own brains.

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References
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