

Social and Nonsocial Functions of Rostral Prefrontal Cortex: Implications for Education

Sam J. Gilbert¹ and Paul W. Burgess¹

ABSTRACT—In this article, we discuss the role of rostral prefrontal cortex (approximating Brodmann Area 10) in two domains relevant to education: executive function (particularly prospective memory, our ability to realize delayed intentions) and social cognition (particularly our ability to reflect on our own mental states and the mental states of others). We review evidence from neuropsychology and neuroimaging suggesting the involvement of rostral prefrontal cortex in these domains and discuss an overarching framework that seeks to characterize these functions in terms of attentional selection between perceptual and self-generated information. In addition, we present neuroimaging evidence in adults suggesting considerable functional specialization within this region. We conclude by discussing implications of these results for education and suggest directions for further research.

As the functions of specific regions of the human brain are increasingly well understood, research within cognitive neuroscience may be expected to deliver new insights relevant to education. Of course, one way in which such research may be informative is by elucidating the ways in which functions supported by particular brain regions develop through childhood. In addition, knowledge of the neural underpinnings of particular cognitive processes may inform theories of the ways in which such cognitive processes interrelate. This in turn may have important consequences for our understanding of the ways in which learning and development within one domain may generalize to another. In this article, we consider research into the functions of one particular brain region: the rostral prefrontal cortex (also referred to as anterior

prefrontal cortex, the frontal pole, frontopolar cortex, or Brodmann Area 10). The approximate location of this region in the human brain is illustrated in Figure 1.

There are several reasons to believe that the functions of rostral prefrontal cortex may be particularly relevant to education. First, this is a conspicuously large region in the human brain. Not only in terms of absolute volume but also in terms of size relative to the rest of the brain, the rostral prefrontal cortex has been estimated to be over twice as large in the human brain as is in the chimpanzee brain (Semendeferi, Armstrong, Schleicher, Zilles, & Van Hoesen, 2001). It is probably the single largest cytoarchitectonic region within the human frontal lobes (Christoff et al., 2001). It therefore seems likely that this brain region plays an important role in human cognition. Second, and of particular relevance to education, the rostral prefrontal cortex is one of the regions of the human brain that matures most slowly during development (Dumontheil, Burgess, & Blakemore, 2008). It is one of the last regions of the brain to achieve myelination (Fuster, 1997; Semendeferi et al.,

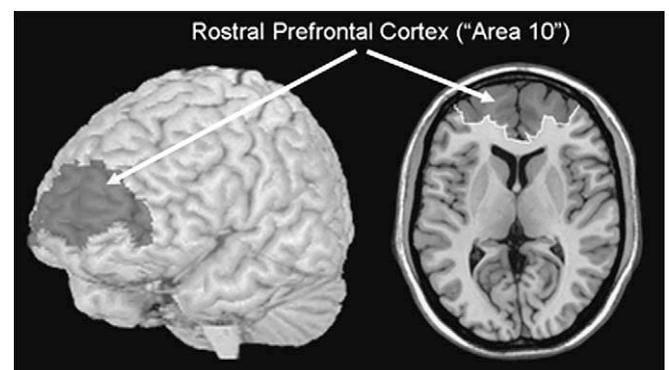


Fig. 1. Approximate location of rostral prefrontal cortex, or Brodmann Area 10, of the human brain, shown in dark gray. The left panel shows the lateral surface and the right panel shows an axial slice of a T1-weighted anatomical MRI image.

¹Institute of Cognitive Neuroscience and Department of Psychology, University College London

Address correspondence to Sam J. Gilbert, Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, UK; e-mail: sam.gilbert@ucl.ac.uk.

2001, p. 37). Moreover, imaging studies reveal both structural (e.g., Sowell, Thompson, Holmes, Jernigan, & Toga, 1999) and functional (e.g., Blakemore, den Ouden, Choudhury, & Frith, 2007) changes in this region through childhood, adolescence, and into adulthood (see Dumontheil et al., 2008, for a review). Understanding the changes that take place in this region may therefore contribute useful insights relevant to education.

The present article is structured as follows. First, we review evidence suggesting an important role of rostral prefrontal cortex in two domains: executive function (EF, processes involved in high-level behavioral organization) and social cognition (in particular, reflecting on our own mental states and those of other people). Second, we describe work from our own laboratory and others suggesting that these functions of rostral prefrontal cortex may be understood in terms of the demands that various situations place on deliberate biasing of the attentional balance between perceptual and self-generated information. Third, we discuss evidence showing that, despite the utility of this general framework for understanding the functions of rostral prefrontal cortex, at a finer scale, there is evidence for considerable functional segregation within this region. We conclude by discussing implications of these findings in terms of generalization of learning and development from one domain to another and in terms of attentional strategies for promoting efficient learning.

FUNCTIONS OF ROSTRAL PREFRONTAL CORTEX

EF

EF is an umbrella term encompassing a wide range of high-level processes for controlling and organizing behavior, such as planning, inhibition, multitasking, monitoring, and so on (Burgess, 1997; Monsell, 1996; Shallice, 1988; Stuss & Knight, 2002). Although the frontal lobes, and particularly the prefrontal cortex, have long been recognized as playing an important role in higher level control (e.g., Luria, 1966; Penfield & Evans, 1935; Shallice, 1982), only recently have neuroimaging and neuropsychological studies begun to delineate distinct regions of prefrontal cortex supporting different aspects of EF. Evidence for such distinctions originated in part from studies of patients with frontal lobe lesions, who experienced behavioral disorganization in everyday life with such severity that they were unable to return to work at their previous level, yet performed well on classical tests of EF. Examples of these classical tests are the Stroop task (Stroop, 1935), requiring participants to inhibit a prepotent response; the Wisconsin Card Sorting Test (Grant & Berg, 1948), requiring participants to switch flexibly from one card-sorting strategy to another; the Tower of London test (Shallice, 1982), requiring participants to plan in advance a sequence of moves to solve a problem; and tests of verbal fluency (Benton, 1968), requiring

participants to generate a large number of items within a certain category (e.g., words beginning with the letter F), while monitoring their output for repeated items.

Shallice and Burgess (1991) designed two new tasks—the “Multiple Errands Test” and “Six Element Test”—that were sensitive to deficits in three patients with frontal lobe lesions, who performed these other tests of EF within normal limits. The Multiple Errands Test is a real-life multitasking test carried out in a shopping center. Participants have to complete a number of tasks while following a set of rules (e.g., no shop can be entered other than to buy something). The Six Element Test also involves multitasking, but in a more constrained setting. Participants are required to switch efficiently among three simple subtasks, each divided into two sections, within 15 min, while following some arbitrary rules (e.g., you cannot do Part A of a subtask followed immediately by Part B of the same subtask). The tasks cannot be completed within 15 min, so participants are required voluntarily to switch from one subtask to another before any subtask is completed.

Subsequent studies have suggested that tests of multitasking, particularly those that are relatively ill constrained or ill structured (i.e., requiring participants to organize their own behavior rather than following specific instructions), are sensitive to lesions within the rostral prefrontal cortex (Burgess, 2000; Burgess, Veitch, Costello, & Shallice, 2000). Thus, specific aspects of EF may depend particularly on rostral prefrontal cortex, rather than other regions of the frontal lobes. Other neuroimaging studies also point to an important role of rostral prefrontal cortex in high-level cognitive control, involving flexible organization of complex behavior (Christoff & Gabrieli, 2000; Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999; Ramnani & Owen, 2004). One characteristic of several tests of EF that appear to be sensitive to lesions in rostral prefrontal cortex (e.g., Six Element Test and Multiple Errands Test, Shallice & Burgess, 1991; Greenwich Test, Burgess et al., 2000) is that they depend upon the ability to encode a delayed intention for future action, and then realize that intention when the appropriate time arrives. This ability has been termed prospective memory (PM; Brandimonte, Einstein, & McDaniel, 1996; Kliegel, McDaniel, & Einstein, 2008).

Everyday examples of PM would include remembering to post a letter when one sees a mailbox or remembering to make a telephone call at a particular time. Not only do neuropsychological studies suggest deficits in PM in participants with lesions to the rostral prefrontal cortex but also neuroimaging studies indicate the involvement of rostral prefrontal cortex in PM (e.g., Burgess, Quayle, & Frith, 2001; Burgess, Scott, & Frith, 2003; Okuda et al., 1998; Simons, Schölvinc, Gilbert, Frith, & Burgess, 2006). In addition, consistent with the slow maturation of rostral prefrontal cortex, developmental studies of PM reveal considerable development of this ability through adolescence and into

adulthood (Dumontheil et al., 2008; Gujardo & Best, 2000; Wang, Kliegel, Yang, & Liu, 2006; Ward, Shum, McKinlay, Baker-Tweney, & Wallace, 2005).

Social Cognition

Recent social-cognitive neuroscience studies have pointed to a role for processes supported by medial prefrontal cortex, especially the most rostral part, in tasks involving reflection on one's own mental states or the mental states of others (Frith & Frith, 2006). The bulk of this evidence has come from neuroimaging studies using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI; and indeed, evidence from neuropsychology has not always been consistent, suggesting the importance of future studies using additional methods; Bird, Castelli, Malik, Frith, & Husain, 2004). Several types of experimental paradigm have converged on the medial rostral prefrontal cortex as a region playing an important role in social cognition. Perhaps the most direct of these are studies where participants are instructed to perform a task that explicitly requires the consideration of another person's mental states for correct performance, for example, where participants are presented with a verbal description or cartoon depicting a protagonist's behavior and are required to explain that behavior in terms of the protagonist's mental states (e.g., Gallagher et al., 2000). Such "off-line" paradigms may be contrasted with "online" paradigms where participants are required to actively predict the ongoing behavior of another person, rather than provide a retrospective account to explain a story. For instance, one online test of mentalizing involved informing participants that they were engaging in a competitive game with an experimenter. This condition was compared with a situation where they were told that they were playing the game against a computer (Gallagher, Jack, Roepstorff, & Frith, 2002). It does not seem that such online paradigms require participants to be actively involved in a social interaction with another person in order to produce activation in medial rostral prefrontal cortex. Even watching a videotaped social interaction between two other people seems sufficient to yield activity in this region (Iacoboni et al., 2004).

Another type of task that has been associated with medial rostral prefrontal activation involves asking participants to make judgments on enduring psychological characteristics (e.g., character traits). Such paradigms have produced medial rostral prefrontal activation, regardless of whether participants are required to judge their own character traits (Johnson et al., 2002), those of other people (Schmitz, Kawahara-Baccus, & Johnson, 2004), or even those of other animals (Mitchell, Banaji, & Macrae, 2005). A further category of task associated with activity in medial rostral prefrontal cortex involves explicitly asking participants to reflect on their own emotional states (Damasio et al., 2000;

Lane, Finnk, Chau, & Dolan, 1997) or those of other people (Ochsner et al., 2004).

Along with the importance of development of social cognition for interpersonal and emotional behavior, the ability to reflect on one's own mental states is an important precursor to metacognitive knowledge conducive to efficient learning. For example, a longitudinal study by Lockl and Schneider (2007) found that children's mentalizing ability at ages 3 and 4 significantly predicted their understanding of their own memory processes (i.e., "metamemory") at age 5, for instance, recognizing that memory performance improves when there are fewer items to memorize, when they can be studied for a longer period of time, and when they are organized into categories rather than presented randomly.

THE "GATEWAY HYPOTHESIS" OF ROSTRAL PREFRONTAL CORTEX FUNCTION

The evidence reviewed above suggests that rostral prefrontal cortex plays a role in at least two domains—PM and mentalizing—that have little obvious commonality. Indeed, a recent meta-analysis of functional imaging studies (Gilbert, Spengler, Simons, Steele, et al., 2006) showed that activity in rostral prefrontal cortex has been reported in many domains even beyond EF and social cognition, such as perceptual processes, episodic memory retrieval, and language (see also Burgess, Simons, Dumontheil, & Gilbert, 2005). One might conclude from this that damage to rostral prefrontal cortex should cause impairment on a correspondingly large variety of tasks. However, this is not the case. Circumscribed lesions to the rostral prefrontal cortex typically leave performance on tests of intellectual, memory, language, motor skills, visual perception, and many problem-solving abilities virtually intact (Burgess, 2000; Burgess, Dumontheil, & Gilbert, 2007; Burgess et al., 2005). But such lesions do seem to cause performance impairments particularly in open-ended, "ill-structured" situations that may require multitasking and PM (Burgess, 2000; Burgess et al., 2005).

One account that seeks to explain the varied evidence from neuroimaging and neuropsychology on the role of rostral prefrontal cortex in such diverse domains has been termed the "gateway hypothesis" (Burgess et al., 2005, 2007). This hypothesis posits a basic distinction between two forms of thought. "Stimulus-oriented" thought refers to cognition that is oriented toward information currently perceived through the senses, or that is to be perceived through the senses, for example, inspecting or looking for an object. "Stimulus-independent" thought refers to cognition that is decoupled from information in the current sensory environment, for example, novel creative thought or imagining an object unrelated to one's current environment. It is well established that brain regions involved in perceiving certain types of

stimulus (e.g., faces) may also participate in thoughts about that type of stimulus in the absence of direct perceptual stimulation (e.g., Farah, 2000; Kosslyn, Thompson, Kim, & Alpert, 1995; O'Craven & Kanwisher, 2000). If we are to avoid confusion over whether we are actually perceiving something, or merely thinking about it, it therefore seems important that we are able to regulate the balance between stimulus-oriented and stimulus-independent thought (Simons, Davis, Gilbert, Frith, & Burgess, 2006).

According to the gateway hypothesis, rostral prefrontal cortex plays a role in this process, influencing the attentional balance between perceptual and self-generated information. For instance, in situations involving PM, participants must bear in mind an internally represented intention to act in a certain way in the future, while also monitoring events in the external environment as part of whatever task is currently being performed. It therefore seems likely that PM will depend critically on the ability to flexibly deploy attention between the external environment and the internal representations, potentially explaining the deficits of patients with rostral prefrontal damage in tasks involving PM. Other tasks may not depend so critically on this ability, hence the relatively preserved performance of patients with damage to rostral prefrontal cortex. However, it is plausible that many tasks, although they do not depend on participants' ability to switch attention between self-generated and perceptual information for adequate performance, may nonetheless provoke such switches of attention during performance, hence the activation seen in rostral prefrontal cortex associated with such tasks. For instance, in many neuroimaging investigations of episodic memory retrieval, participants are presented on each trial with a retrieval cue (e.g., a word or picture) and must make a response determined by a previous study phase (e.g., whether the item is old or new, or contextual details associated with its initial presentation such as its visual position). Such paradigms may on each trial provoke switches of attention between stimulus-oriented processing of retrieval cues and stimulus-independent evaluation of the information retrieved. Social neuroscience studies investigating self-reflection may likewise involve switches of attention between stimulus-oriented processing of cues (e.g., names of character traits) and stimulus-independent evaluation of their self-relevance. Reflecting on mental states (one's own or those of other people) is also likely to involve modulating the attentional balance between internally generated information, such as representations of the thoughts that someone else is having about a situation, versus perceptual features of the situation itself, especially if there are conflicts between the two types of information. The gateway hypothesis is therefore able to provide a framework for unifying results from neuroimaging and neuropsychology on the role of rostral prefrontal cortex in a wide range of domains, encompassing

both social and nonsocial functions. Below, we review some direct tests of this hypothesis.

Direct Neuroimaging Investigations of the Gateway Hypothesis

In the first study to directly test the gateway hypothesis (Gilbert, Frith, & Burgess, 2005), we administered three tasks, each of which could be accomplished either by attention to stimuli that were presented on a visual display (i.e., requiring stimulus-oriented attending) or by performing the same tasks "in one's head" only (i.e., stimulus-independent attending). In Task A, participants either tapped a response button in time with a visually presented clock or ignored the visual display (which now presented distracting information) and continued to tap at the same rate as before. Task B required participants either to navigate around the edge of a visually presented shape or to imagine the same shape and continue navigating as before. In Task C, participants classified letters of the alphabet, which followed a regular sequence, according to whether they were made of straight or curved lines. They either classified visually presented letters or mentally continued the sequence and classified the letters that they generated internally. Thus, all three tasks alternated between phases where participants attended to perceptually available information and phases where they ignored this information and attended to self-generated information instead. The appropriate phase (stimulus oriented or stimulus independent) was cued by the visual appearance of the stimuli. Gilbert et al. (2005) investigated both the sustained neural activity that differed between the two phases and the transient activity at the point of a switch between these two phases, using fMRI. Consistently, across all three tasks, medial rostral prefrontal cortex exhibited sustained activity that differed between the two phases, in all three cases showing greater activity when participants attended to perceptual information. By contrast, right lateral rostral prefrontal cortex (and additionally left lateral rostral prefrontal cortex, at a more liberal statistical threshold) exhibited transient activity when participants switched between these phases, regardless of the direction of the switch (see Figure 2). Thus, this study suggests that rostral prefrontal cortex supports selection between stimulus-oriented and stimulus-independent cognitive processes and indicates separable roles of medial and lateral rostral prefrontal cortex in this selection process. These conclusions were replicated in a follow-up study (Gilbert, Simons, Frith, & Burgess, 2006) that ruled out an interpretation of the earlier findings in terms of task-unrelated processes such as "daydreaming" during stimulus-oriented phases of the tasks. The distinction between medial and lateral rostral prefrontal cortex has now been verified in a meta-analysis of 104 neuroimaging studies reporting activation in rostral prefrontal cortex (Gilbert, Spengler, Simons, Frith, & Burgess, 2006).

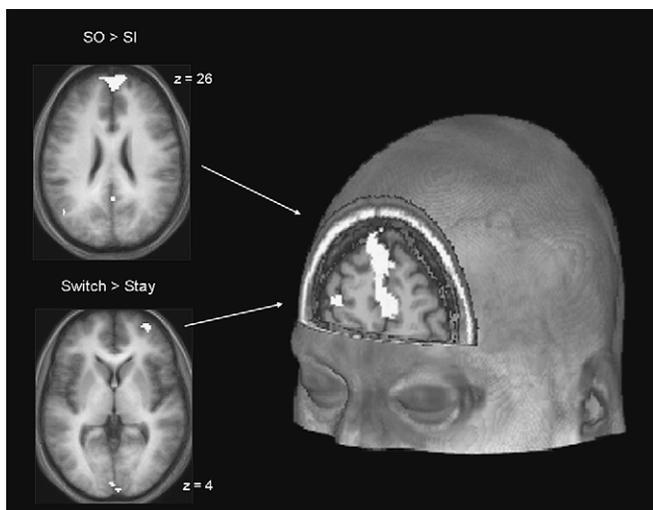


Fig. 2. Brain regions more active during stimulus-oriented (SO) thought than stimulus-independent (SI) thought (upper left-hand panel) and those activated transiently by switches between SO and SI conditions (lower left-hand panel) in the study of Gilbert et al. (2005).

FUNCTIONAL SPECIALIZATION WITHIN ROSTRAL PREFRONTAL CORTEX

The findings from studies directly investigating the gateway hypothesis, and those investigating social cognition, present a paradox. On the one hand, studies investigating the gateway hypothesis demonstrate a role for medial rostral prefrontal cortex in promoting attention toward the external environment, rather than self-generated information. By contrast, studies investigating social cognition suggest that medial rostral prefrontal cortex is engaged by attention toward one's own mental states, rather than perceptually available information. How can these two sets of findings be reconciled?

Gilbert, Spengler, Simons, Steele, et al. (2006) conducted a meta-analysis of functional imaging studies reporting activation within rostral prefrontal cortex. Each study was classified into one of eight different task domains such as episodic memory retrieval, mentalizing (i.e., reflecting on one's own mental states or those of other agents), and multitasking (i.e., performance of more than one task within a block of trials, including PM). Thus, it was possible to investigate whether studies investigating different cognitive domains activated identical regions within rostral prefrontal cortex. Two clear results emerged. First, studies investigating mentalizing were much more likely than studies in other domains to activate medial rather than lateral rostral prefrontal cortex (mentalizing: 88% of activation peaks in medial rostral prefrontal cortex; nonmentalizing: 32%). Second, even within medial rostral prefrontal cortex, studies investigating mentalizing yielded activation peaks that, on average, were significantly

posterior to those from other domains. Thus, one potential resolution of the seemingly contradictory results from studies investigating attention (suggesting a role of medial rostral prefrontal cortex in attention toward perceptual vs. self-generated information) and those investigating social cognition (suggesting a role of medial rostral prefrontal cortex in reflection on one's own mental states, rather than perceptual information) is that different regions of medial rostral prefrontal cortex are involved in these two functions.

In order to investigate this possibility, Gilbert et al. (2007) carried out an experimental investigation that directly compared brain activation related to (a) attention toward perceptual versus self-generated information and (b) thinking about the mental states of another person. Participants performed two of the three tasks investigated by Gilbert et al. (2005), alternating between stimulus-oriented phases where task-relevant information was presented visually, and stimulus-independent phases, where participants were required to perform the same tasks "in their heads." In half of the blocks ("mentalizing blocks"), participants were instructed that they were performing the tasks in collaboration with an experimenter, who controlled the timing of the switches between stimulus-oriented and stimulus-independent phases. In other blocks ("nonmentalizing blocks"), participants were told that these switches were randomly controlled by a computer. In fact, switches were always under computer control, rather than being controlled by the experimenter in mentalizing blocks, but postexperiment debriefing revealed that no participant had suspected this. At the end of each mentalizing block, participants were asked whether the experimenter had been trying to be helpful or unhelpful in his timing of the switches in that block. In the nonmentalizing blocks, participants were simply asked whether the switches were faster or slower than usual. Thus, only in the mentalizing blocks were participants encouraged to think about the experimenter's mental state.

The comparison between stimulus-oriented and stimulus-independent phases and the comparison between mentalizing and nonmentalizing blocks, both yielded activation in medial rostral prefrontal cortex. However, consistent with the earlier meta-analysis, activation related to these two contrasts was in different parts of medial rostral prefrontal cortex, with activity related to mentalizing being significantly posterior and superior to that related to stimulus-oriented versus stimulus-independent attention. Thus, although it may still be accurate to describe rostral prefrontal cortex as a whole as being involved in attentional selection between perceptual and self-generated information, it is clear that there is considerable functional specialization within this region and that different parts may be preferentially involved in social and nonsocial functions (Figure 3).

Functional Specialization at a Finer Scale

The studies reviewed above have approached the question of functional specialization using the relatively crude method of comparing the peak coordinates of activation associated with different cognitive functions after averaging across a group of participants. This approach is useful for examining relatively universal trends for functional specialization across large numbers of participants. However, it may be insensitive to more idiosyncratic functional specialization that may be expressed at a relatively fine-grained level. In order to investigate such fine-grained functional specialization, the data from the study of Gilbert et al. (2007) were examined on participant-by-participant basis. We investigated two separate tasks (spatial/verbal), performed in different scanning sessions, each of which was subjected to the manipulation of two orthogonal factors: (a) stimulus-oriented versus stimulus-independent attention and (b) mentalizing versus nonmentalizing conditions.

Looking at each voxel (i.e., each cube of approximately 3 mm × 3 mm × 3 mm) within medial rostral prefrontal cortex, we examined whether activity related to the two factors above generalized from one task to the other. For instance, if a particular voxel in medial rostral prefrontal cortex responds unusually strongly to the contrast of stimulus-oriented versus stimulus-independent attention in the verbal task, does this predict that the same voxel will respond particularly strongly to the analogous contrast in the spatial task? What about the contrast of mentalizing versus nonmentalizing? These analy-

ses showed that activity related to the stimulus-oriented versus stimulus-independent contrast generalized significantly from one task to the other. Likewise, activity related to the mentalizing versus nonmentalizing contrast also generalized significantly from one task to the other. However, none of the correlations between attentional and mentalizing functions were significantly different from zero. In other words, knowledge of how strongly a particular voxel responded to a particular contrast was significantly predictive of how well that same voxel would respond to the contrast examining the analogous function (attention or mentalizing) in the other task. However, this knowledge did not predict how well that voxel would respond to the other function, even within the same task. These results suggest that, despite being supported by nearby regions of medial rostral prefrontal cortex, attentional and mentalizing functions may in fact depend on separable neural populations.

CONCLUSIONS

The studies reviewed above suggest an important role for rostral prefrontal cortex in two broad domains, both of which have strong links with education: (a) EF, especially PM and multitasking and (b) social cognition, especially reflection on one's own mental states along with the mental states of others (i.e., mentalizing). Behaviorally, development in these two domains has been showed to follow a relatively slow time course, although there has been relatively little research into development of mentalizing after early childhood. Consistent with this behavioral data, functional neuroimaging studies reveal structural and functional change in rostral prefrontal cortex throughout adolescence and into adulthood (see Dumontheil et al., 2008, for a review). In addition, structural imaging studies reveal gender differences in the time course of brain development (Giedd et al., 1999), suggesting that the interrelation between gender differences in learning style and the maturation of specific brain regions may repay further investigation.

The relationship between EF and mentalizing is currently a matter of considerable debate within developmental psychology (e.g., Ozonoff, Pennington, & Rogers, 1991; Perner, Lang, & Kloo, 2002; Sodian & Hülksen, 2005). The functional imaging results discussed above, investigating adults, suggest surprisingly little overlap between regions of rostral prefrontal cortex involved in social and nonsocial functions, despite the proximity of the areas involved in each (Gilbert et al., 2007). One potential consequence of this is that development of one function may not necessarily generalize to the other. However, the possibility of course exists that the functional specialization observed in adulthood emerges relatively late in development, and that these two domains are tied together more closely in childhood than in adulthood.

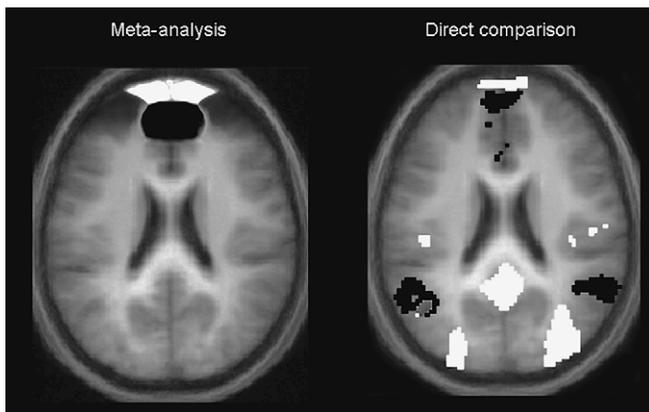


Fig. 3. Functional specialization within medial rostral prefrontal cortex. Left panel: regions associated with mentalizing (black) and multiple-task coordination, including prospective memory (white) in a meta-analysis of functional neuroimaging studies reporting activity in rostral prefrontal cortex (Gilbert, Spengler, Simons, Steele, et al., 2006). Right panel: regions associated with mentalizing (black) and stimulus-oriented versus stimulus-independent attention (white) in a study directly comparing these two functions (Gilbert et al., 2007). The results from these methodologies are remarkably consistent, suggesting that relatively caudal parts of medial rostral prefrontal cortex support mentalizing.

Consistent with this view, longitudinal studies (e.g., Lockl & Schneider, 2007) indicate a relationship between development in these two domains, and training studies (e.g., Kloo & Perner, 2003) suggest that training interventions in one domain can generalize to the other. These results suggest the utility of further research into the possibility that maximum transfer between social and nonsocial skills will occur relatively early in development. In addition, it will be important to study the emergence of functional specialization at different points of development. Such investigations may suggest a time frame for “critical periods” where particular educational interventions would be particularly effective or ineffective.

The general framework of the gateway hypothesis (Burgess et al., 2005, 2007) suggests an overarching function of rostral prefrontal cortex, across many domains, of attentional selection between perceptual and self-generated information (see also Gilbert, Spengler, Simons, Frith, et al., 2006, for further evidence suggesting consistent functions of rostral prefrontal cortex across many domains). The relationship between this attentional function and learning has not yet been systematically explored. However, it has long been recognized that focusing attention on “shallow” perceptual features of a stimulus yields less efficient learning than integration of information with internal representations (e.g., Craik & Tulving, 1975), suggesting that development of a system for orienting attention between stimulus-oriented and stimulus-independent information may play an important role in promoting efficient learning strategies. An interesting topic for future research will be the role of switches between attending to perceptual and self-generated information in order to learn from one’s environment. Of course, the role of such attentional switches in learning may be different at various points of development, suggesting the utility of a developmental approach to this question.

Finally, an important area for further study will be the involvement of rostral prefrontal cortex in developmental disorders. Two disorders of particular relevance to learning and education are attention deficit hyperactivity disorder (ADHD) and autism spectrum disorders (ASD). Functional change in rostral prefrontal cortex has been reported in both ADHD (e.g., Schulz et al., 2004) and ASD (e.g., Castelli, Frith, Happé, & Frith, 2002), suggesting that abnormalities in the region may play a role in a wide range of developmental disorders. Recent studies have begun to investigate the role of abnormalities of rostral prefrontal cortex in developmental disorders on a task-by-task basis (Gilbert, Bird, Brindley, Frith, & Burgess, 2008). Understanding the relationship between such abnormalities in rostral prefrontal cortex and behavioral differences associated with ADHD and ASD may contribute to our understanding of learning both in these developmental disorders and in typical development.

REFERENCES

- Benton, A. L. (1968). Differential behavioural effects in frontal lobe disease. *Neuropsychologia*, 6, 53–60.
- Bird, C. M., Castelli, F., Malik, O., Frith, U., & Husain, M. (2004). The impact of extensive medial frontal lobe damage on “theory of mind” and cognition. *Brain*, 127, 914–928.
- Blakemore, S.-J., den Ouden, H., Choudhury, S., & Frith, C. D. (2007). Adolescent development of the neural circuitry for thinking about intentions. *Social Cognitive and Affective Neuroscience*, 2, 130–139.
- Brandimonte, G., Einstein, G., & McDaniel, M. (1996). *Prospective memory: Theory and applications*. Hillsdale, NJ: Erlbaum.
- Burgess, P. W. (1997). Theory and methodology in executive function research. In P. Rabbitt (Ed.), *Methodology of frontal and executive function* (pp. 81–111). Hove, UK: Psychology Press.
- Burgess, P. W. (2000). Strategy application disorder: The role of the frontal lobes in human multitasking. *Psychological Research*, 63, 279–288.
- Burgess, P. W., Dumontheil, I., & Gilbert, S. J. (2007). The gateway hypothesis of rostral prefrontal cortex (area 10) function. *Trends in Cognitive Sciences*, 11, 290–298.
- Burgess, P. W., Scott, S. K., & Frith, C. D. (2003). The role of the rostral frontal cortex (area 10) in prospective memory: A lateral versus medial dissociation. *Neuropsychologia*, 41, 906–918.
- Burgess, P. W., Simons, J. S., Dumontheil, I., & Gilbert, S. J. (2005). The gateway hypothesis of rostral PFC function. In J. Duncan, L. Phillips, & P. McLeod (Eds.), *Measuring the mind: Speed control and age* (pp. 215–246). Oxford, UK: Oxford University Press.
- Burgess, P. W., Quayle, A., & Frith, C. D. (2001). Brain regions involved in prospective memory as determined by positron emission tomography. *Neuropsychologia*, 39, 545–555.
- Burgess, P. W., Veitch, E., Costello, A., & Shallice, T. (2000). The cognitive and neuroanatomical correlates of multitasking. *Neuropsychologia*, 38, 848–863.
- Castelli, F., Frith, C., Happé, F., & Frith, U. (2002). Autism, Asperger syndrome and brain mechanisms for the attribution of mental states to animated shapes. *Brain*, 125, 1839–1849.
- Christoff, K., & Gabrieli, J. D. E. (2000). The frontopolar cortex and human cognition: Evidence for a rostrocaudal hierarchical organization within the human prefrontal cortex. *Psychobiology*, 28, 168–186.
- Christoff, K., Prabhakaran, V., Dorfman, J., Zhao, Z., Kroger, J. K., Holyoak, K. J., et al. (2001). Rostrolateral prefrontal cortex involvement in relational integration during reasoning. *Neuroimage*, 14, 1136–1149.
- Craik, F. I. M., & Tulving, E. (1975). Depth of processing and the retention of words in episodic memory. *Journal of Experimental Psychology: General*, 104, 268–294.
- Damasio, A. R., Grabowski, T. J., Bechara, A., Damasio, H., Ponto, L. L. B., Parvizi, J., et al. (2000). Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nature Neuroscience*, 3, 1049–1056.
- Dumontheil, I., Burgess, P. W., & Blakemore, S.-J. (2008). Development of rostral prefrontal cortex and cognitive and behavioural disorders. *Developmental Medicine and Child Neurology*, 50, 168–181.
- Farah, M. J. (2000). The neural bases of mental imagery. In M. S. Gazzaniga (Ed.), *The new cognitive sciences* (pp. 965–974). Cambridge, MA: MIT Press.

- Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron*, 18, 531–534.
- Fuster, J. M. (1997). *The prefrontal cortex: Anatomy, physiology, and neuropsychology of the frontal lobe*. Philadelphia: Lippincott-Raven.
- Gallagher, H. L., Happe, F., Brunswick, N., Fletcher, P. C., Frith, U., & Frith, C. D. (2000). Reading the mind in cartoons and stories: An fMRI study of 'theory of mind' in verbal and nonverbal tasks. *Neuropsychologia*, 38, 11–21.
- Gallagher, H. L., Jack, A. I., Roepstorff, A., & Frith, C. D. (2002). Imaging the intentional stance in a competitive game. *Neuroimage*, 16, 814–821.
- Giedd, J. N., Blumenthal, J., Jeffries, N. O., Castellanos, F. X., Liu, H., Zijdenbos, A., et al. (1999). Brain development during childhood and adolescence: A longitudinal MRI study. *Nature Neuroscience*, 2, 861–863.
- Gilbert, S. J., Bird, G., Brindley, R., Frith, C. D., & Burgess, P. W. (2008). Atypical recruitment of medial prefrontal cortex in autism spectrum disorders: An fMRI study of two executive function tasks. *Neuropsychologia*, 46, 2281–2291.
- Gilbert, S. J., Frith, C. D., & Burgess, P. W. (2005). Involvement of rostral prefrontal cortex in selection between stimulus-oriented and stimulus-independent thought. *European Journal of Neuroscience*, 21, 1423–1431.
- Gilbert, S. J., Simons, J. S., Frith, C. D., & Burgess, P. W. (2006). Performance-related activity in medial rostral prefrontal cortex (area 10) during low demand tasks. *Journal of Experimental Psychology: Human Perception and Performance*, 32, 45–58.
- Gilbert, S. J., Spengler, S., Simons, J. S., Frith, C. D., & Burgess, P. W. (2006). Differential functions of lateral and medial rostral prefrontal cortex (area 10) revealed by brain-behavior correlations. *Cerebral Cortex*, 16, 1783–1789.
- Gilbert, S. J., Spengler, S., Simons, J. S., Steele, J. D., Lawrie, S. M., Frith, C. D., et al. (2006). Functional specialization within rostral prefrontal cortex (area 10): A meta-analysis. *Journal of Cognitive Neuroscience*, 18, 1–17.
- Gilbert, S. J., Williamson, I. D. M., Dumontheil, I., Simons, J. S., Frith, C. D., & Burgess, P. W. (2007). Distinct regions of medial rostral prefrontal cortex supporting social and nonsocial functions. *Social Cognitive and Affective Neuroscience*, 2, 217–226.
- Grant, D. A., & Berg, E. A. (1948). A behavioural analysis of degree of reinforcement and ease of shifting to new responses in a Weigl-type card-sorting problem. *Journal of Experimental Psychology*, 38, 404–411.
- Gujardo, N. R., & Best, D. L. (2000). Do preschoolers remember what to do? Incentive and external cues in prospective memory. *Cognitive Development*, 15, 75–97.
- Iacoboni, M., Lieberman, M. D., Knowlton, B. J., Molnar-Szakacs, I., Moritz, M., Throop, C. J., et al. (2004). Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. *Neuroimage*, 21, 1167–1173.
- Johnson, S. C., Baxter, L. C., Wilder, L. S., Pipe, J. G., Heiserman, J. E., & Prigatano, G. P. (2002). Neural correlates of self-reflection. *Brain*, 125, 1808–1814.
- Kliegel, M., McDaniel, M. A., & Einstein, G. O. (2008). *Prospective memory: Cognitive, neuroscience, developmental, and applied perspectives*. Mahwah, NJ: Erlbaum.
- Kloo, D., & Perner, J. (2003). Training transfer between card sorting and false belief understanding: Helping children apply conflicting descriptions. *Child Development*, 74, 1823–1839.
- Koechlin, E., Basso, G., Pietrini, P., Panzer, S., & Grafman, J. (1999). The role of anterior prefrontal cortex in human cognition. *Nature*, 399, 148–151.
- Kosslyn, S. M., Thompson, W. L., Kim, I. J., & Alpert, N. M. (1995). Topographical representations of mental images in primary visual cortex. *Nature*, 378, 496–498.
- Lane, R. D., Finnk, G. R., Chau, P. M. L., & Dolan, R. J. (1997). Neural activation during selective attention to subjective emotional responses. *Neuroreport*, 8, 3969–3972.
- Lockl, K., & Schneider, W. (2007). Knowledge about the mind: Links between theory of mind and later metamemory. *Child Development*, 78, 148–167.
- Luria, A. R. (1966). *Higher cortical functions in man*. London: Tavistock.
- Mitchell, J. P., Banaji, M. R., & Macrae, C. N. (2005). General and specific contributions of the medial prefrontal cortex to knowledge about mental states. *Neuroimage*, 28, 757–762.
- Monsell, S. (1996). Control of mental processes. In V. Bruce (Ed.), *Unsolved mysteries of the mind* (pp. 93–148). Hove, UK: Erlbaum/Taylor & Francis.
- Ochsner, K. N., Knierim, K., Ludlow, D. H., Hanelin, J., Ramachandran, T., Glover, G., et al. (2004). Reflecting upon feelings: An fMRI study of neural systems supporting the attribution of emotion to self and other. *Journal of Cognitive Neuroscience*, 16, 1746–1772.
- O'Craven, K. M., & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *Journal of Cognitive Neuroscience*, 12, 1013–1023.
- Okuda, J., Fujii, T., Yamadori, A., Kawashima, R., Tsukiura, T., Fukatsu, R., et al. (1998). Participation of the prefrontal cortices in prospective memory: Evidence from a PET study in humans. *Neuroscience Letters*, 253, 127–130.
- Ozonoff, S., Pennington, B. F., & Rogers, S. J. (1991). Executive function deficits in high-functioning autistic children: Relationship to theory of mind. *Journal of Child Psychology and Psychiatry*, 32, 1081–1105.
- Penfield, W., & Evans, J. (1935). The frontal lobe in man: A clinical study of maximal removals. *Brain*, 58, 115–133.
- Perner, J., Lang, B., & Kloo, D. (2002). Theory of Mind and Self-Control: More than a Common Problem of Inhibition. *Child Development*, 73, 752–767.
- Ramnani, N., & Owen, A. M. (2004). Anterior prefrontal cortex: Insights into function from anatomy and neuroimaging. *Nature Reviews Neuroscience*, 5, 184–194.
- Schmitz, T. W., Kawahara-Baccus, T. N., & Johnson, S. C. (2004). Metacognitive evaluation, self-relevance, and the right prefrontal cortex. *Neuroimage*, 22, 941–947.
- Schulz, K. P., Fan, J., Tang, C. Y., Newcord, J. H., Buchsbaum, M. S., Cheung, A. M., et al. (2004). Response inhibition in adolescents diagnosed with attention deficit hyperactivity disorder during childhood: An event-related fMRI study. *American Journal of Psychiatry*, 161, 1650–1657.
- Semendeferi, K., Armstrong, E., Schleicher, A., Zilles, K., & Van Hoesen, G. W. (2001). Prefrontal cortex in humans and apes: A comparative study of area 10. *American Journal of Physical Anthropology*, 114, 224–241.
- Shallice, T. (1982). Specific impairments of planning. *Philosophical Transactions of the Royal Society of London B*, 298, 199–209.
- Shallice, T. (1988). *From neuropsychology to mental structure*. Cambridge, UK: Cambridge University Press.
- Shallice, T., & Burgess, P. W. (1991). Deficits in strategy application following frontal lobe damage in man. *Brain*, 114, 727–741.

- Simons, J. S., Davis, S., Gilbert, S. J., Frith, C. D., & Burgess, P. W. (2006). Discriminating imagined from perceived information engages brain areas implicated in schizophrenia. *Neuroimage*, *32*, 696–703.
- Simons, J. S., Schölvink, M., Gilbert, S. J., Frith, C. D., & Burgess, P. W. (2006). Differential components of prospective memory? Evidence from fMRI. *Neuropsychologia*, *44*, 1388–1397.
- Sodian, B., & Hülken, C. (2005). The developmental relationship of theory of mind, metacognition and executive functions: A study of advanced theory of mind abilities in ADHD-children. In W. Schneider, R. Schumann-Hengsteler, & B. Sodian (Eds.), *Interrelationships among working memory, theory of mind, and executive functions* (pp. 175–187). Hillsdale, NJ: Erlbaum.
- Sowell, E. R., Thompson, P. M., Holmes, C. J., Jernigan, T. L., & Toga, A. W. (1999). In vivo evidence for post-adolescent brain maturation in frontal and striatal regions. *Nature Neuroscience*, *2*, 859–861.
- Stroop, J. R. (1935). Studies in interference in serial verbal reactions. *Journal of Experimental Psychology*, *18*, 643–662.
- Stuss, D. T., & Knight, R. T. (2002). *Principles of frontal lobe function*. Oxford, UK: Oxford University Press.
- Wang, L., Kliegel, M., Yang, Z., & Liu, W. (2006). Prospective memory performance across adolescence. *Journal of Genetic Psychology*, *167*, 179–188.
- Ward, H., Shum, D., McKinlay, L., Baker-Tweney, S., & Wallace, G. (2005). Development of prospective memory: Tasks based on the prefrontal-lobe model. *Child Neuropsychology*, *11*, 527–549.