Development of abstract thinking during childhood and adolescence: The role of rostrolateral prefrontal cortex

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ABSTRACT

Rostral prefrontal cortex (RPFC) has increased in size and changed in terms of its cellular organisation during primate evolution. In parallel emerged the ability to detach oneself from the immediate environment to process abstract thoughts and solve problems and to understand other individuals' thoughts and intentions. Rostrolateral prefrontal cortex (RLPFC) is thought to play an important role in supporting the integration of abstract, often self-generated, thoughts. Thoughts can be temporally abstract and relate to long term goals, or past or future events, or relationally abstract and focus on the relationships between representations rather than simple stimulus features. Behavioural studies have provided evidence of a prolonged development of the cognitive functions associated with RLPFC, in particular logical and relational reasoning, but also episodic memory retrieval and prospective memory. Functional and structural neuroimaging studies provide further support for a prolonged development of RLPFC during adolescence, with some evidence of increased specialisation of RLPFC activation for relational integration and aspects of episodic memory retrieval. Topics for future research will be discussed, such as the role of medial RPFC in processing abstract thoughts in the social domain, the possibility of training abstract thinking in the domain of reasoning, and links to education.

Contents

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1. Introduction

Abstract thoughts can be broadly defined as thoughts that are self-generated and stimuli-independent, in contrast to stimulus-oriented, perceptually-derived, information. Beyond this definition, two particular forms of abstraction can be considered (see Nee et al., 2014). Abstraction can be defined temporally: abstract thoughts are those that relate to long term goals, or past or future events. Alternately, abstraction can be defined relationally: abstract thoughts are those that focus on the relationships between representations rather simple stimulus features. A subset of cognitive processes has particularly high requirements of abstract thoughts manipulation, either within a single temporal or relational domain, or across both. These include the retrieval of past thoughts and memories (e.g. episodic or source memory retrieval), the manipulation of current task-related or task-unrelated self-generated information (e.g. relational reasoning and problem solving or mindwandering respectively) and the processing of thoughts linked to the future (e.g. planning, multitasking, prospective memory). Interestingly, the most anterior part of the lateral prefrontal cortex, the rostrolateral prefrontal cortex (RLPFC), has been found to show increased activations in paradigms testing this whole range of cognitive functions (e.g. see Badre, 2008; Burgess et al., 2007a; Ramnani and Owen, 2004 for review). The rostral prefrontal cortex (RPFC), as other parts of the frontal cortex and the temporal cortices, shows prolonged structural development during adolescence (e.g. see Dumontheil et al., 2008 for review). The relationship between abstract thoughts and RPFC, in particular the RLPFC, during late childhood and adolescence will be the topic of this review.

Adolescence starts at the onset of puberty and can be broadly defined as between the ages of 10 and 19 (Sawyer et al., 2012). Although brain and behavioural changes during this period are less pronounced than during infancy and childhood, adolescence is nevertheless an important period of development in terms of the acquisition of higher cognitive skills, as well as the onset of mental disorders (see Dumontheil et al. (2008) for a discussion of RPFC and developmental disorders). Adolescence emerges as a critical phase of reorganisation of regulatory systems, and may also be a period of extended brain plasticity and thus a relevant target for interventions (Steinberg, 2005).

The first section of this paper will focus on the association between lateral RPFC and the ability to attend to and manipulate abstract thoughts. I will then discuss the development of this ability during late childhood and adolescence and how structural and functional development of RPFC may underlie the behavioural changes observed during adolescence. I will then briefly relate these findings to studies of the development of medial RPFC function in social cognition tasks. Finally, I will discuss future avenues of research in this field as well as potential implications of these findings for education policy and practice. This review will focus on aspects of both relationally and temporally abstract thoughts (Nee et al., 2014), as identified from the research on RLPFC function in adults. Although an effort was made to gather relevant evidence, this review is unlikely to be exhaustive and is biased towards those fields where more developmental neuroimaging research has currently been published.

Recently Ferrer et al. (2009) summarised the development of fluid reasoning, which can be considered as a type of abstract thinking. Here the goal is to perform a more extensive review of the development of abstract thinking more generally, including recent studies on the topic. Although some aspects of metacognition are relevant to the domain of abstract thought and reasoning, there has been until now little cognitive neuroscience research done with a developmental focus (see Fleming and Dolan, 2012; Fleming et al., 2010) and thus metacognition will not be reviewed here (see Schneider, 2008 for a review of the development of meta-cognitive knowledge).

2. Rostral prefrontal cortex function

2.1. Rostral prefrontal cortex: cytoarchitecture and subdivisions

RPFC, which corresponds approximately to Brodmann area 10 (BA10), is a large brain region in humans and is thought to be subdivided into separate subregions distinct

in terms of cellular organisation and function (Christoff and Gabrieli, 2000; Gilbert et al., 2006a, 2006b). Two quite different types of cognitive ability have been associated with the RPFC. The lateral parts of RPFC (RLPFC) appear to support the ability to detach oneself from the environment and to elaborate, evaluate and maintain abstract rules and information, as it is involved in reasoning, problem solving, and more generally abstract thinking (Amati and Shallice, 2007; Christoff and Gabrieli, 2000; Christoff et al., 2009b; Gilbert et al., 2006b; Koechlin et al., 2003; Ramnani and Owen, 2004) (see below for further details). The medial aspect of RPFC, or medial prefrontal cortex (MPFC), is implicated in social cognition, that is, the understanding of other people's minds (Amodio and Frith, 2006; Blakemore, 2008; Van Overwalle, 2009).

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 and Pandya, 1999), anterior temporal cortex (Amaral and Price, 1984; Moran et al., 1987) and cingulate cortex (Andersen et al., 1985; Arikuni et al., 1994; Bachevalier et al., 1997; Morecraft and Van Hoesen, 1993). In addition, its projections to these other regions are broadly reciprocal (Passingham, 2002; see Ramnani and 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., 2011, 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 and Owen, 2004).

In line with these findings, Amati and Shallice (2007) proposed that RPFC may support a novel type of cognitive computational process required for "abstract projectuality", that may be behind the cognitive capacities specific to modern humans. They propose that this brain operation permits a fluent sequence of non-routine computational operations to occur over a prolonged timecourse. This qualitatively different type of brain operation may have emerged from increasing prefrontal cortical connectivity in the RPFC, induced by gradual (quantitative) genetic changes affecting RPFC structure and organisation over evolution (Amati and Shallice, 2007). This model fits well with current theories of RLPFC function which will be detailed in the next section.

2.2. RLPFC and abstract thinking

A number of theories of the functional organisation of the frontal lobes have been proposed in the last decade based on neuroimaging and lesion data. The broad consensus is that the frontal cortex may possess a rostro-caudal organisation whereby more rostral regions support cognitive control involving progressively more abstract representations (Azuar et al., 2014; Badre and D'Esposito, 2007, 2009; Badre, 2008; Botvinick, 2008; Christoff et al., 2009b; Koechlin and Jubault, 2006; Koechlin and Summerfield, 2007; Koechlin et al., 2003; Petrides, 2005). In this organisation, posterior PFC supports the control and manipulation of temporally proximate, concrete action representations, while anterior PFC supports the control of temporally extended, abstract representations (Badre, 2008). Fig. 1, adapted from Badre (2008), shows a representation of this organisation. Of interest here is the position of the RLPFC, at the top of this frontal lobe hierarchy, and the suggestion that this brain region is recruited when temporally extended, abstract representations are attended to or manipulated.

RLPFC indeed shows increased blood oxygen level dependent (BOLD) signal in a number of tasks that require such aspects of cognition, including the retrieval of episodic or source memory (e.g. Dobbins et al., 2004; Turner et al., 2008; see Gilbert et al., 2006b for review and Spaniol et al., 2009 for meta-analysis); prospective memory (Barban et al., 2013; Benoit et al., 2011; Burgess et al., 2007b); the manipulation of highly abstract information (Christoff et al., 2009b); the selection and maintenance of task rules (Bengtsson et al., 2009; Braver et al., 2003; Dumontheil et al., 2011; Sakai and Passingham, 2003, 2006); sub-goal processing or branching (Badre and D'Esposito, 2007; Braver and Bongiolatti, 2002; Koechlin et al., 2003); integration of information (Badre and Wagner, 2004; Wolfensteller and von Cramon, 2011); analogical and relational reasoning (Bunge et al., 2009; Geake and Hansen, 2005; Hampshire et al., 2011; Smith et al., 2007; Volle et al., 2010; Wendelken et al., 2008, 2012; Wright et al., 2008) – although note that medial dorsal RPFC has also been implicated in analogical reasoning (Green et al., 2006; Krawczyk, 2012; Volle et al., 2010); reality monitoring (Simons et al., 2008); and mind-wandering (Christoff et al., 2004, 2009a; Dumontheil et al., 2010a; Schooler et al., 2011).

Lesion studies also provide supporting evidence for a role of RPFC in the control of temporally extended abstract representations, although, by their nature, these studies rarely distinguish between lateral and medial aspects of RPFC, and therefore between the social cognition and cognitive control aspects of RPFC function (Burgess, 2000; Burgess et al., 2009; Gläscher et al., 2010; Roca et al., 2010; Shallice and Burgess, 1991; Volle et al., 2011).

3. Behavioural studies of the development of abstract thinking

Abstract thinking encompasses a number of different cognitive processes, but one definition adopted here is that abstract thinking can be considered as the manipulation of self-generated thoughts, or thoughts that are not directly connected to the environment. A distinction is made between relationally and temporally abstract thoughts. As described above, neuroimaging and lesion studies in adults suggest that RLPFC is thought to be specifically involved in the elaboration, evaluation and maintenance of abstract rules (Amati and Shallice, 2007; Christoff and Gabrieli, 2000; Christoff et al., 2009b; Koechlin et al., 2003; Ramnani and Owen, 2004), as well as in the ability to
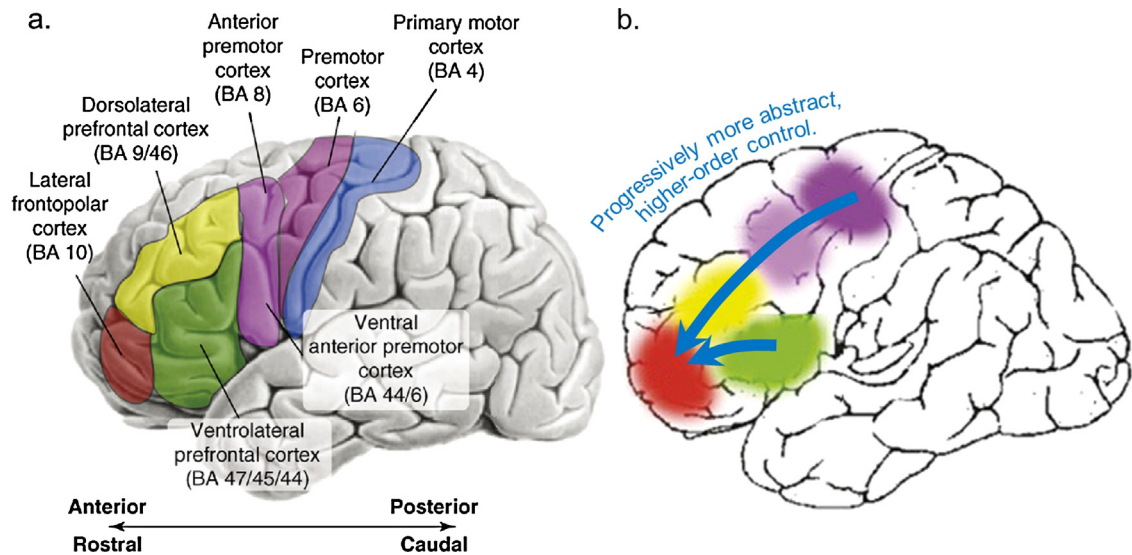
Fig. 1. Sub-divisions of the frontal lobes. (a) Schematic representation of the major anatomical sub-divisions of the frontal lobes. Following a caudal to rostral direction, labelled areas include motor cortex, dorsal and ventral premotor cortices, dorsal and ventral aspects of anterior premotor cortex, ventrolateral prefrontal cortex (VLPFC), dorsolateral prefrontal cortex (DLPFC), and lateral frontopolar cortex, also termed rostrolateral prefrontal cortex (RLPFC). Boundaries and Brodmann areas (BA) are approximate. (b) Schematic representation of the rostro-caudal gradient of the organisation of the prefrontal cortex. The consensus among diverse theoretical accounts of the organisation of the PFC is that progressively more anterior PFC regions support cognitive control of progressively more abstract and temporally extended representations (adapted from Badre, 2008).

flexibly control whether one selectively attends towards self-generated thoughts or the environment (Burgess et al., 2007a), whether this self-generated information is task-relevant, or task-irrelevant, i.e. when the mind wanders (Christoff et al., 2004, 2009a; Dumontheil et al., 2010a). A number of theorists have suggested that adolescents can operate at a new and more abstract level of thought because they can integrate the results of two different sorts of lower-order processing (Case, 1985; Fischer, 1980; Halford, 1982). This new intellectual potential emerging in adolescence builds on the idea that children can progressively handle first one new abstract element, then two, and then multiple abstract elements simultaneously (see Marini and Case, 1994, for review). Below are described behavioural studies investigating the development of the ability to flexibly attend towards self-generated thoughts, the development of the ability to reason logically and integrate relations or representations, and finally the development of the processing of self-generated thoughts that can be considered temporally abstract, and are related to past experiences (episodic memory) or future events (prospective memory). Although multitasking, or branching, has been a particular focus of neuroimaging and lesion research on RLPFC function in adults (Badre and D'Esposito, 2007; Braver and Bongiolatti, 2002; Burgess, 2000; Koechlin et al., 2003), this topic has not been specifically investigated in developmental psychology research.

3.1. 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., 2007a). In children, manipulation of SI thoughts has been studied in the context of fluid intelligence and relational reasoning (Crone, 2009; Wright et al., 2008; see below) and working memory (WM) tasks (Crone et al., 2006), while the ability to resist distracting SO information has been studied in perceptual (Booth et al., 2003; Bunge et al., 2002) and WM tasks (Olesen et al., 2007). In this latter study 13 year-old participants showed poorer accuracy than adults in visuospatial WM trials that included distraction relative to trials that did not.

In a recent study (Dumontheil et al., 2010b), we tested 179 female participants aged 7–27-year old on 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 participants were asked to continue going through the alphabet sequence in their head and continue responding (see Fig. 2a). 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 response speed improvements extending into late adolescence (see Fig. 2b). This development in the
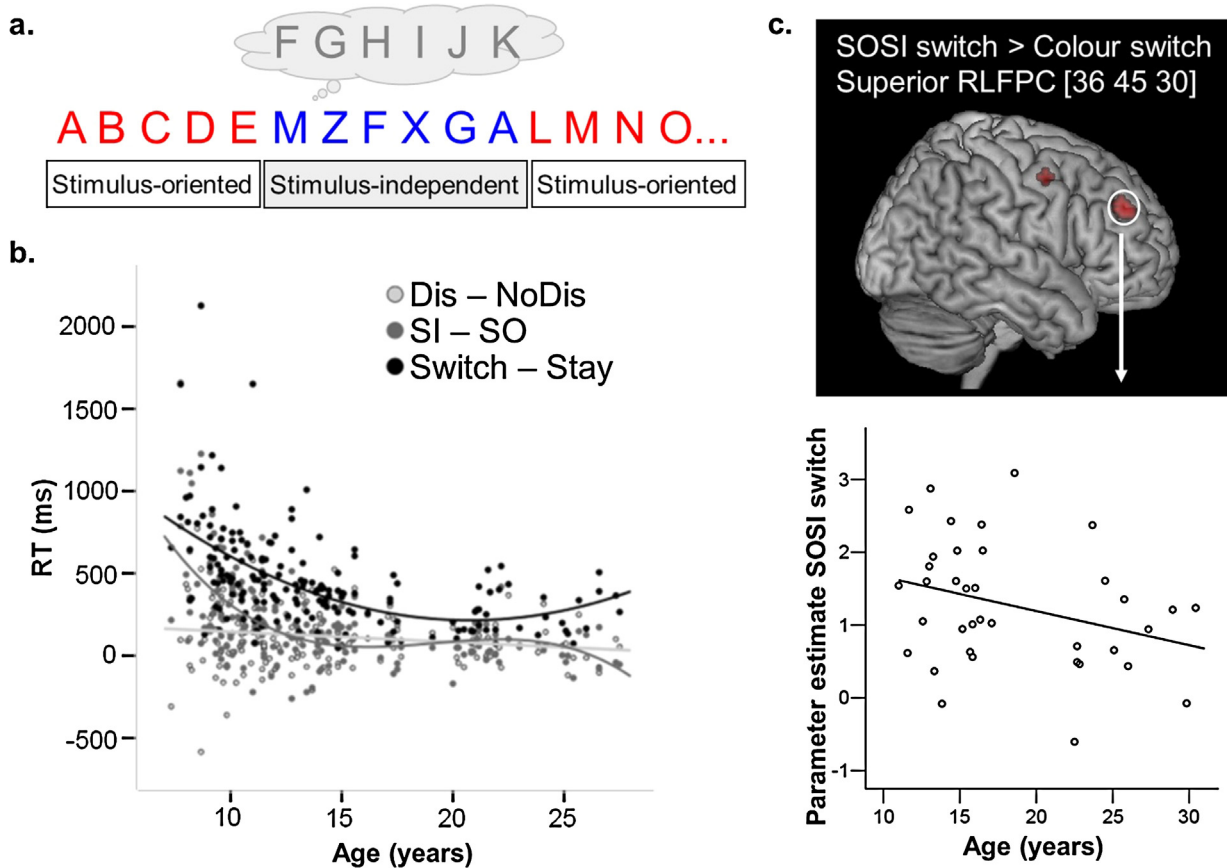
Fig. 2. Development of the flexible switching between selecting thoughts derived from the environment and abstract thoughts. (a) Alphabet task. Participants classify letters of the alphabet according to their shape (line or curve). When the letter is red, participants judge the letter presented on the screen (stimulus-oriented (SO) blocks). When the letter is blue (or when there is no letter) participants continue reciting the alphabet in their head and judge the shape of the letter in their head (stimulus-independent (SI) blocks), while ignoring the distracting letter presented on the screen (Distractor condition), or in the absence of a letter on the screen (No-distractor condition). Performance in the two types of blocks (SI vs. SO) and the two conditions (Distractor vs. No-distractor), and performance in switch trials (first trial of a SO or SI block) and subsequent trials (stay trials) were compared. (b) Behavioural results. The speed of responding in SI vs. SO, and in switch vs. stay trials continued to increase during adolescence. The speed of responding in the presence of Distractors also improved but followed a flatter linear developmental function (adapted from Dumontheil et al., 2010b). (c) Functional MRI results. The main effect of switching between SO and SI conditions vs. a simple change of colour of the stimuli over the whole age range is presented (family-wise error corrected $p < .05$), highlighting the right superior RLPFC activation (top). RLPFC activity in this contrast is plotted against age (bottom). There was a significant decrease in activity during adolescence, which was not purely a consequence of differences in performance and brain structure between the participants and could reflect the maturation of neurocognitive strategies (see Dumontheil et al., 2010b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

speed of manipulating self-generated thoughts and in the speed of switching between perceptually-derived and self-generated thoughts may underlie improvements during adolescence in planning, reasoning and abstract thinking, abilities that rely on the manipulation of thoughts that are not directly derived from the environment (Anderson et al., 2001; De Luca et al., 2003; Huizinga et al., 2006; Rosso et al., 2004). Below is described in more detail the particular case of the development of reasoning.

3.2. Development of logical reasoning

Problem solving by analogy requires the transfer of previously acquired solutions or strategies from one context or situation to another. Preschoolers (e.g. Holyoak et al., 1984) and even infants (e.g. Chen et al., 1997) exhibit

an ability to draw analogies and use a solution learned from a one problem to solve another problem. However older children are better able to detect the underlying similarities between the original problem and the novel problem situation (e.g. Chen and Daehler, 1992; Daehler and Chen, 1993; Holyoak et al., 1984; see Chen et al., 1997 for review). Experimental paradigms have tended to be action-based, requiring children to perform a particular action to achieve a goal. However, analogical reasoning is also assessed using verbal or pictorial stimuli in propositional analogy tasks (Ferrer et al., 2009), for example asking children to match the sequence "bread: slice of bread:: orange:?" with one of the following options: slice of orange, slice of cake, squeezed oranges, orange balloon, orange basketball. The relational shift hypothesis proposes that young children interpret analogy and metaphor first

in terms of object similarity, and then in terms of relational similarity. Support for this hypothesis is given for example by the observation that when relational similarity competes with object similarity, young children make object-similarity responses, while with increasing age/experience responses become in line with relational similarity (Rattermann and Gentner, 1998). This relational shift is thought to be not simply age-determined, but knowledge-related, which means it can occur at different ages in different domains. However, adults continue to use both object commonalities and relational commonalities in processing comparisons (see Rattermann and Gentner (1998) for discussion). In a recent computational study, Morrison et al. (2011) propose that the development of analogical reasoning during childhood is best explained by a combination of improved information processing, in particular working memory (which supports the maintenance of a greater number of relations) and inhibitory control (which supports the resistance to distraction by object commonalities), in combination with knowledge accretion.

Subsequent developmental changes have been observed during adolescence. Marini and Case (1994) show that a capacity for abstract reasoning begins to emerge in both social and non-social domains about the age of 11 or 12 and that further development of this ability is constrained by the number of abstract elements that can be coordinated at one time, independent of the particular content of these abstract elements. The task used required participants to predict the movement of a beam where both the weight and distance from the centre were relevant factors to be combined, or to predict a character's behaviour based on personality traits abstracted from a scenario. Similarly, Hatcher et al. (1990) observed development of abstract thinking between ages 10, 13 and 17-year old, using the balance beam task and a verbal analogical reasoning task. Using conditional reasoning (if... then... statement) tasks, De Neys and Everaerts (2008) showed that improvements in conditional reasoning observed during adolescence were not only related to the start of the formal reasoning stage around age 12, but also depended on the ability to retrieve alternatives from memory and to inhibit these alternatives when necessary. The authors note that according to other studies (see De Neys and Everaerts, 2008, for review) not all adolescents will show this ability to inhibit alternatives when they are irrelevant, leading to individual differences in conditional reasoning in adulthood.

These studies therefore suggest that logical reasoning depends on the interplay of the ability to maintain and manipulate information in working memory, the inhibition of irrelevant or incorrect alternatives, and domain-specific knowledge, in addition to the requirements of integrating multiple abstract representations.

3.3. Behavioural measures of relational reasoning development during adolescence

Although, as discussed above, relational processing can be recruited for analogical reasoning, a number of studies have focused more specifically on relational reasoning per se. 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 and Gentner, 1998). Further improvements during childhood and adolescence may relate to increased relational knowledge or increased working memory capacity (Crone et al., 2009; Sternberg and Rifkin, 1979; see Richland et al., 2006, for discussion). Indeed, Carpenter et al. (1990) argued that the processes leading to individual differences on relational reasoning tasks such as the Raven's matrices (Raven, 1998) are primarily the ability to extract abstract relations and to dynamically manage a large set of problem-solving goals in working memory. Thus, for relational reasoning as for logical reasoning, working memory is thought to play an important role in supporting the maintenance of multiple abstract thoughts to allow their comparison and integration.

Prolonged developmental changes in relational reasoning into adolescence have been observed in a few behavioural studies (see also the next section on neuroimaging studies). For example, although their age groups were small, Rosso et al. (2004) showed that accuracy in the matrix reasoning section of the WAIS-III increased with age in the range 9–19-year old. We recently employed a relational reasoning task initially developed by Christoff et al. (2003), to investigate relational reasoning development during adolescence in a large sample of healthy participants (Dumontheil et al., 2010c, Experiment 1). 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 response 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). One hundred and seventy nine female participants aged 7–27-year old participated in the study (same participant as Dumontheil et al. (2010b)). When comparing the relational integration (or 2-relational) condition of the task to a condition requiring the processing of only 1-relation (either shape, or texture), the results showed a non-linear pattern of improvement in accuracy across age. After an early improvement in accuracy, with 9–11-year olds performing at adult levels, performance dipped in the 11–14-year olds and gradually improved again to adult levels throughout late adolescence. Further analysis of these data using a combined measure of reaction time over accuracy to take into account a potential speed-accuracy trade-off suggests that in fact 2-relational vs. 1-relational performance in this task improved progressively during late childhood and mid-adolescence, with a significant improvement between the 7–9 and 14–17 years old age groups on this combined measure.

3.4. Development of episodic memory

Episodic memory refers to memories for specific episodes previously experienced. Memories for such events are often accompanied by the phenomenal experience of recollective experience (Tulving, 1983). Sander and colleagues have proposed that episodic memory relies on the combination of an associative and a strategic processing component (Sander et al., 2012). Raj and Bell (2010) have reviewed the development of episodic memory formation in childhood extensively and similarly contrast binding and source memory to source monitoring. It is generally believed that by the age of 4 years, children have an episodic memory system in place (Raj and Bell, 2010). The associative component, which relies primarily on mediotemporal and posterior brain regions (e.g. Simons and Spiers, 2003; see Raj and Bell, 2010 for review) is relatively mature by middle childhood (Gathercole, 1998; Rhodes et al., 2011). However, some studies still show continuing improvements in episodic memory performance between late childhood and adulthood (DeMaster and Ghetti, 2013; Lorsbach and Reimer, 2005), in particular in tasks requiring memory for combined features (e.g. objects and locations) (Lorsbach and Reimer, 2005).

In contrast, the strategic component, which refers to top-down control processes involved in the organisation and monitoring of memory representations mainly relies on prefrontal brain regions (Miller and Cohen, 2001), particularly for tasks requiring binding of feature information and source memory retrieval. This component shows more prolonged development in childhood, adolescence and until young adulthood. For example, in a longitudinal study following children between 4 and 10 years of age, different developmental timecourses were observed for the memory for individual items vs. a combination of source and facts (Riggins, 2014). Overall, younger children perform worse than adolescents on source discrimination tasks, and adolescents perform themselves worse than adults (De Chastelaine et al., 2007; DeMaster and Ghetti, 2013; Ghetti et al., 2010). Adults also perform better than children and adolescents on tasks requiring a recollection judgement, i.e. requiring the specific contextual details of a memory episode, but not in tasks requiring a recognition judgement, i.e. knowing that an item has been previously encountered (Billingsley et al., 2002; Ofen et al., 2007). Sander et al. (2012) showed that, similarly to adults, children and adolescents could benefit from mnemonic instruction and training in an episodic memory task, highlighting the role of strategy implementation in episodic memory performance.

Executive function (EF) abilities have been suggested to play a role in episodic memory performance. Indeed, higher EF scores are associated with better performance on source memory tests, and lower rates of source memory errors, particularly lower false alarm rates. Frontal lobe function may support the integration of item and source information, content and context, during encoding, and may also support contextual memory retrieval by guiding the search and monitoring processes and inhibition of feelings of familiarity (see Raj and Bell, 2010 for review). The specific role of RLPFC in episodic memory may be in supporting the coordination of search and monitoring processes during episodic memory retrieval (Spaniol et al., 2009), with BOLD signal increases in RLPFC possibly specific to intentional rather than incidental retrieval (Fletcher and Henson, 2001; Simons and Spiers, 2003).

Little research has been done to investigate the role played by EF during episodic memory development. In young children (4 and 6 years old), Rajan et al. (2014) found that language ability, and a composite measure of EF (combining inhibitory control, working memory and set shifting) uniquely predicted fact and source memory retrieval, however when the EF measures were considered individually, the only significant association was that inhibitory control predicted source recall. Rhodes et al. (2011) found that 10 and 11-year old children, but not 8 and 9-year olds, showed a relationship between episodic memory and verbal working memory, which differed from the observed relationship between episodic memory and spatial working memory in adults, and thus suggested that the relationship between episodic memory and executive (frontal) components of episodic memory retrieval changed over the period of adolescence. Picard et al. (2012) also found that EF contributed to changes in temporal and spatial context aspects of episodic memory during adolescence. Ruffman et al. (2001) found that in children aged 6, 8 and 10 years old, working memory was related to accuracy in source monitoring judgements, while inhibitory control uniquely predicted false alarm rates.

3.5. Development of prospective memory

Prospective memory (PM) is the ability to "remember to remember", and is particularly difficult when an individual is simultaneously engaged in other activities. Research suggests that active strategical monitoring is more likely to be required when the PM cues are non-focal, non-distinctive, when the task is non-demanding and non-absorbing, when high importance is given to the PM task and the interval retentions are short (McDaniel and Einstein, 2007). Although a number of studies have now investigated the development of PM in childhood, fewer studies have investigated later development during adolescence (McDaniel and Einstein, 2007).

Event-based PM can be observed in preschool aged children (e.g. Guajardo and Best, 2000), however performance tends to be poor when the ongoing task needs to be interrupted (e.g. Kliegel et al., 2008) or when the cue is non-focal, suggesting that children aged 5 or younger have not developed strategic monitoring processes or do not have the attentional resources to deploy them during ongoing task performance (see also McDaniel and Einstein, 2007 for review). Event-based PM continues to develop as children become more able to use external reminders to cue prospective remembering and to interrupt ongoing task performance when necessary (Kliegel et al., 2008). Time-based PM requires greater strategic monitoring than event-based PM. Although time-based PM has also been observed in young children (5–7-year olds, Aberle and Kliegel, 2010), it tends overall to be associated with poorer performance than event-based PM (e.g. in 7–12-year-olds Yang et al., 2011). Time-based PM has been shown to continue to develop in late childhood and early adolescence

(Yang et al., 2011) as children become increasingly proficient at using time-checking strategies (Kerns, 2000; Mackinlay et al., 2009; Voigt et al., 2011).

Developmental changes in PM performance are also observed further into adolescence, with more correct event-related PM responses made by adults than adolescents (aged 12 in Zöllig et al. (2007); aged 14 in Wang et al. (2006); but no difference observed with 13–14-year olds in Zimmermann and Meier (2006)). In a large online study, Maylor and Logie (2010) found (using a single event-based PM trial) that performance peaked in late adolescence (16–19-year old) and that females outperform males in early adolescence. Ward et al. (2005) showed that adolescents detected more PM cues than children, with similar performance to adults, however they relied more than adults on a remembering strategy described as "Thought about all the time/looked out for the cues", while adults used more frequently a strategy described as "Remembered only when saw the cues". This indicates that to achieve a similar performance, adolescents needed to use a more active monitoring strategy than the adults. In a realistic time-based PM task requiring participants to remember to take baking cakes out of an oven while playing a video game, 14-year-olds were better than 10-year-olds, even though both age groups were able to deploy strategic clock-monitoring strategies (Ceci and Bronfenbrenner, 1985). Consistent with the greater need for strategic monitoring, the development of PM abilities is mainly observed during adolescence when non-focal cues are used (Wang et al., 2011).

The realisation of delayed intentions is thought to rely on a prospective component, the detection or recognition of prospective cues, but also a retrospective component, the retrieval of an intention from memory following the recognition of a prospective cue (Simons et al., 2006). The retrospective component is likely to share many of the processes that support episodic memory, in particular the retrieval of contextual information from long-term memory. Zöllig et al. (2007) found that adolescents made more confusion errors than young adults, which the authors argue indicates that the retrospective component of PM is less efficient in adolescents. Similarly, Yang et al. (2011) report that 7–8-year-olds missed PM cues more often than 11–12-year olds, while 9–10-year olds showed a higher frequency of confusion (false-alarm and wrong responses) than 11–12-year olds suggesting differential developmental patterns of the PM and retrospective memory components. Maylor and Logie (2010) similarly observed earlier development of PM performance compared to retrospective memory performance in a lifespan study.

Successful PM is thought to rely on a range of other executive skills, however evidence is mixed regarding which aspects of EF are most relevant to PM development. A few studies have investigated this with time-based PM tasks. Aberle and Kliegel (2010) found that PM performance in 5–7 year olds was associated with processing speed and working memory. In older, 7–12 year old children, Mackinlay et al. (2009) found that the majority of the developmental changes in PM performance could be explained by planning and task switching performance measures, while Mäntylä et al. (2007) found children aged 8–12-year

old achieved similar accuracy to adults in a time-based PM task by checking the clock more often, and that while in children inhibition and updating (within a single "supervision" factor), but not shifting, predicted clock monitoring frequency, in adults they predicted timing error.

To summarise, similarly to the investigations of logical and relational reasoning, these studies highlight the role of working memory in supporting temporally abstract thinking. In addition, good performance on prospective and episodic memory tasks may depend on the use of appropriate strategies, themselves dependent on the ability to extract and evaluate abstract information regarding task rules, goals and performance monitoring. It is this higher level of abstraction, either in the relational or temporal domain, which is thought to be specific to RLPFC (Badre, 2008).

4. Functional neuroimaging studies of abstract thinking development

This section reviews the functional MRI findings on the development of abstract thinking during adolescence. The focus will first be on research on relationally abstract thinking, reviewing studies which have investigated the orientation of attention towards self-generated thoughts and the manipulation and integration of relations. Second, I will discuss findings related to the processing of temporally abstract thoughts, reviewing studies of episodic memory retrieval and prospective memory, although the evidence is more limited for the latter.

4.1. Neuroimaging study of the development of the flexible selection of self-generated thoughts

On the basis of studies in adults, Burgess et al. (2007a) have suggested that RPFC supports the flexible orientation of attention towards perceptually-derived information or self-generated thoughts. In a recent study, the Alphabet task described above, which contrasts SI and SO phases with very similar task requirements, was tested in a smaller group of participants aged 11–30 years old using functional MRI (fMRI). Two comparisons were performed using this task (Dumontheil et al., 2010b): SI vs. SO thought manipulation and switches between SO and SI phases versus switches of the colour of the letter stimuli. In this sample of 37 participants, the difference in performance between SI and SO trials did not change with age, however participants did become faster in the SO/SI switch trials with age. The comparison of SI vs. SO thought manipulation led to increased BOLD signal in a large fronto-parietal network of regions that extended into RLPFC bilaterally. Among this network, only the left anterior insula showed developmental changes, with a decrease in activation with age, which was independent of individual differences in performance. The comparison of SO/SI switches versus Colour switches led to a much smaller network of brain regions including the right superior RLPFC, precuneus and superior temporal gyrus (Fig. 2c). In this comparison only the RLPFC cluster showed a trend for a decrease in activation with age,

similarly not accounted for by individual differences in performance (Fig. 2c).

4.2. Neuroimaging studies of visuospatial relational reasoning development

Neuroimaging studies in adults have shown that a fronto-parietal network of brain regions is recruited during relational integration, i.e. when solving 2-relational problems, with activation in RLPFC, and in particular left RLPFC, specific to relational integrational demands (Bunge et al., 2009; Christoff et al., 2003; Smith et al., 2007; Wendelken et al., 2012). Four recent studies have investigated the development of relational reasoning between late childhood and adolescence or adulthood using fMRI (Crone et al., 2009; Dumontheil et al., 2010c; Eslinger et al., 2009; Wendelken et al., 2011). These four studies used paradigms of relational processing in the visuospatial domain. Dumontheil et al. (2010c) and Wendelken et al. (2011) used very similar tasks and compared 2-relational (i.e. relational integration), 1-relational, and fixation conditions. Crone et al. (2009) used problems derived from the Ravens Progressive Matrices (Raven, 1998) and included an additional 0-relational condition and a simple orientation of arrows task as baseline. Eslinger et al. (2009) used coloured geometrical shape sequences as stimuli and compared 2-relational and 1-relational conditions.

In terms of behaviour, Crone et al. (2009) found that 8–12-year old made more errors, but were not slower, than 18–25-year olds in 2-relational than 1-relational trials; Dumontheil et al. (2010c, Experiment 2) found that 11–14-year olds responded faster than 14–18-year olds in 2-relational than 1-relational trials, but neither group differed from the adult group, and there was no age group difference in accuracy; Wendelken et al. (2011) did not observe age differences in 2-relational vs. 1-relational performance over the age range of 7–18-year old using age as a continuous variable; Eslinger et al. (2009) do not report analyses of performance changes in the 8–19-year age range they studied. Thus the performance findings are mixed in these studies and performance was typically included as a covariate in the analyses.

Neuroimaging results of the first three studies, with a particular focus on the RLPFC findings, are described in Fig. 3. Crone et al. (2009) found increased specificity for 2-relational vs. 1-relational problems between childhood and adulthood in the left RLPFC (Fig. 3a) in the later part of the trial period, and increased specificity for 2-relational vs. 1-relational problems with age within the child group, aged 8–12-year old. Performance was not included as a covariate in these analyses, however the authors suggested that the fact that the left RLPFC in children showed increased BOLD signal in 2-relational trials compared to 1-relational in the initial part of the trial may be associated with the poorer performance observed in children in 2-relational trials. Dumontheil et al. (2010c) observed a trend for an increase in activation in the left RLPFC in 2-relational vs. 1-relational trials between early- and mid-adolescence, and a subsequent decreased activation in this region between mid-adolescence and adulthood (Fig. 3b). The early- to mid-adolescence increase did not

remain when performance was included as covariates, while the mid-adolescence to adulthood increase was only partially accounted for by accuracy differences. Wendelken et al. (2011) found decrease activation with age in 1-relational trials in the left RLPFC, which led to increased activation in 2-relational vs. 1-relational trials between the ages of 6 and 18 years old (Fig. 3c). This developmental effect remained significant when performance was covaried. Finally, Eslinger et al. (2009) report increases with age between late childhood and adolescence in the parietal cortex bilaterally and decreases in age across large parts of the frontal cortex, but no specific findings in RLPFC. The development of the relational integration of semantic stimuli will be described below, before a possible general pattern of developmental change observed in these studies is discussed.

4.3. Development of relational integration of semantic stimuli

Another study also investigated the development of relational integration, however the paradigm was an analogical reasoning task requiring the integration of semantic information (Wright et al., 2008). Stimuli were pictures of objects. In the analogical condition participants were, for example, presented with a bee and a bee's nest, and a spider, and had to pick the correct matching object (a spider's web) among other items. In the control semantic condition the participant had to pick the most closely related object to a presented target object (e.g. a baseball for a baseball bat). A group of 6–13-year old children and a group of 19–26-year old adults participated in this study. The children/young adolescents were overall slower and made more errors than the adults, and also made disproportionally more errors in the analogical problems. In addition, children's RT was affected to a greater extent than adults by lure which were semantically vs. perceptually related to one of the stimulus items. Overall the comparison of analogical and semantic problems did not show increased BOLD signal in RLPFC. However, further analyses showed (1) increasing RLPFC activation with age in children both for semantic and analogical problems, and (2) in adulthood, greater RLPFC activation in the right RLPFC associated with greater accuracy in analogical problems. The authors argue this suggests that RLPFC is first increasingly involved in the processing of 1-relational (semantic) and 2-relational (analogical) problems, while in adulthood, its activation becomes more specific to relational integration, i.e. the analogical problems. In addition, Wright et al. (2008) similarly to Crone et al. (2009) observed timecourse differences in RLPFC activity between the children and the adults, with respectively later and more prolonged activation observed in children.

The use of a paradigm recruiting the manipulation of semantic relations raises the question of the role of verbal abilities in relational reasoning, including visuospatial reasoning. As discussed below, a recent study investigated the domain specificity of relational integration (Wendelken et al., 2012), comparing visuo-spatial and semantic variants of the Shapes task described above. The results indicated that both tasks recruited left RLPFC specifically for
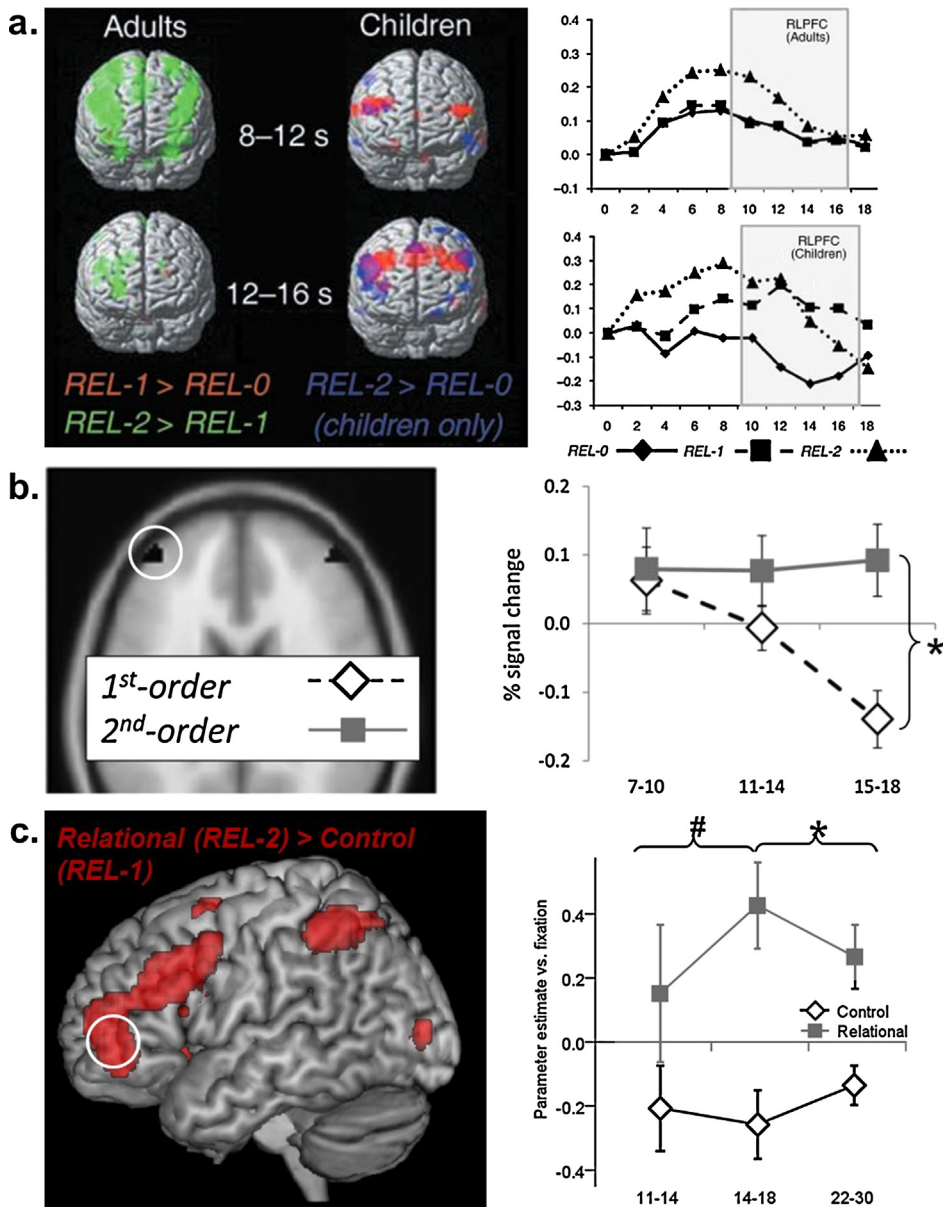
Fig. 3. Increased specificity of left RLPFC activation for relational integration (2nd order vs. 1st order relational processing) during development. Although the three studies summarised here used slightly different tasks, methods and age groups, the overall pattern shows an increased specificity of left RLPFC activation, in particular between late childhood and mid-adolescence. (a) RLPFC activation observed in adult ($N = 17$, age 18–25) and children ($N = 15$, age 8–12) performing problems following the general form of the Raven Progressive Matrices test (Raven, 1998), with a varying number of dimensions to be integrated. On the left are shown activations related to 1st order relational processing (REL-1 > REL-0) and relational integration (REL-2 > REL-1) in adults ($p < .001$ uncorrected) and children ($p < .005$ uncorrected) in the 8–16 s interval of a timecourse analysis. On the right are plotted the timecourses of activation from left RLPFC regions of interset in adults and children. In the later part of the timecourses, there was a significant interaction between age group and condition (grey highlight), with activations greater in REL-2 than REL-1 in adults, and greater in REL-1 than REL-0 in children (adapted from Crone et al., 2009). (b) Left RLPFC activation observed in three groups of children and adolescents (total $N = 85$) performing a task requiring 1st or 2nd order visuospatial relational processing. Analyses using age as a continuous variable show a significant decrease in left RLPFC associated with 1st-order relational processing only, resulting in a significant age × condition interaction (adapted from Wendelken et al., 2011). (c) Left hemisphere activation observed in a group of adult ($N = 13$, age 22–30) and adolescent ($N = 24$, age 11–18) participants performing a similar task to (b). In the left RLPFC, Relational > Control activation, i.e. that specific to 2nd vs. 1st order relational processing, increased marginally between early and mid-adolescence (#), while it decreased between mid-adolescence and adulthood (*) (adapted from Dumontheil et al., 2010a,b,c).

the relational integration condition vs. the processing of two relations without integration. This left hemisphere-specificity of relational integration activity may be related to a verbal recoding during relational reasoning. In terms of development, it has been shown that after age 7 children tend to recode visuospatial or pictorial information in a verbal format in working memory tasks (Conrad, 1971; Flavell et al., 1966), and that these processes are related to their use

of self-regulatory private speech (Al-Namlah et al., 2006). This shift to phonological recoding has been suggested to be part of a general transition towards verbal mediation of cognitive processes (Ford and Silber, 1994; Hitch et al., 1991). Articulatory suppression has been shown to affect performance of executive functions tasks more broadly (e.g. in task switching (Baddeley et al., 2001), or Tower of London tasks (Wallace et al., 2009)) and a diminished use of inner speech among individuals with autism spectrum disorders is thought to contribute to the executive dysfunction associated with these disorders (Wallace et al., 2009; Whitehouse et al., 2006). In addition, a large-scale lesion study in adults showed that performance deficits on the Raven's Colored Progressive Matrices, which is considered to be a non-verbal test of reasoning, were associated with lesions in temporal regions essential for language processing, as well as in the left inferior parietal lobule (Baldo et al., 2010).

Therefore, current results suggest that relational reasoning in adults relies on verbal recoding of the relations and specific activations in the left RLPFC, however whether verbal recoding becomes more prevalent with age during relational reasoning, as in certain EF tasks, has not yet been investigated, and more research will be necessary to further explore these issues.

4.4. Increasing specificity of RLPFC activation for relational integration during development

A common overall pattern of the studies described above was of an increased activation in 2-relational problems vs. 1-relational problems between childhood and adolescence, which may be specific to the left RLPFC. However, this pattern of increased specialisation may be similar in a broader network of brain regions. Indeed, Crone et al. (2009) found that left dorsolateral prefrontal cortex (DLPFC) and left parietal cortex showed similar increased specialisation of activation for 2-relational trials vs. 1-relational trials when comparing children and adults. Wendelken et al. (2011) also found increased specialisation, although weaker, in bilateral intraparietal lobules, but not in the DLPFC. When comparing adolescents to adults Dumontheil et al. (2010c) did not find age effects in either DLPFC or parietal cortex. It is possible that only more sensitive analyses looking at BOLD signal timecourse or including a large number of children and adolescent participants may be able to pick up specialisation of brain activation in these regions.

It is as yet unclear how much this increased specialisation may relate to changes in accuracy and reaction times in 2-relational trials. However, the pattern suggests specialisation of left RLPFC, and potentially DLPFC and parietal cortex for relational integration compared to relational processing during adolescence. Only one of these studies compared later adolescence to adulthood and the findings showed decreased activation in the 2-relational vs. 1-relational comparison (Dumontheil et al., 2010c), which was partly related to accuracy differences between these age groups.

The pattern of increasing specialisation of brain activation for relational integration was driven in some studies by decreasing activation for relational processing, which highlights the complexity of investigating fMRI data developmentally. In particular, it is unclear whether increased activation (e.g. in WM task, Klingberg et al., 2002) or decreased activation (e.g. in response inhibition tasks, Tamm et al., 2002) reflect "more efficient" neural processing. One interpretation is that increased activation reflects greater specialisation of the brain region for a particular cognitive process, while decreased activation may reflect the fact that with more efficient neural processing in other brain regions or increased connectivity between regions, a particular brain region is no longer necessary for a particular cognitive process (e.g. RLPFC for the processing of single relations). In this context, as is true in general for fMRI studies, the specific contrast investigated is particularly relevant, for example whether one is contrasting relational integration (2-Rel) to relational processing (1-Rel) or to a fixation control condition. Although RLPFC did not show an increased BOLD signal during a Raven reasoning task at the corrected threshold used, a recent study in adults by Perfetti et al. (2009) speaks to the fact that lower performance or abilities overall may be associated with less specific brain activations in fronto-parietal regions. Comparing high and low fluid intelligence (gf) participants, Perfetti et al. (2009) found that while the high gf group showed increased fronto-parietal activation in the analytical (more complex) problems compared to the figural problems, the low gf group showed greater activations in the figural condition than the high gf group, and a tendency for the activations in the analytical condition to be lower than in the figural condition. In the visual analogy task described above, Wright et al. (2008) found that in adults the specificity of RLPFC activations for relational integration was positively correlated with accuracy on the task. In another study, it was shown that high gf participants showed greater parietal activations than low gf participants in a relational integration task (Lee et al., 2006). This later result highlights the importance of processing in brain regions other than RLPFC for the performance of relational integration. The parietal cortex has been suggested to support the identification of the visuo-spatial relations that are the basis of relational integration (Ferrer et al., 2009).

In summary, fMRI studies have demonstrated changes in RLPFC activation during adolescence during the manipulation and integration of self-generated thoughts and their relations. The overall pattern suggests increasing specialisation of activations in the left RLPFC in particular, but also in the DLPFC and parietal cortex, which are thought to support the processing of single relations. More work will be needed to assess how these observed functional changes relate to developmental changes in performance. One factor that has been proposed to play a role is brain structure, which will be discussed in Section 4.7.

4.5. RLPFC and episodic memory retrieval during development

RPFC has been suggested to play a role in the control, and possibly processing, of temporally extended representation (Badre, 2008, Fig. 1), as suggested by its increased activation during branching or multitasking (Badre and

D'Esposito, 2007; Braver and Bongiolatti, 2002; Koechlin et al., 2003), prospective memory (Benoit et al., 2011; Burgess et al., 2007b), episodic memory, in particular episodic memory retrieval (Dobbins et al., 2004; Spaniol et al., 2009; Turner et al., 2008) and mindwandering (Christoff et al., 2009a, 2004; Dumontheil et al., 2010a; Schooler et al., 2011). Studies investigating the development of the neural correlates for episodic memory have tended to focus on the encoding phase of episodic memory, rather than episodic memory retrieval (Chiu et al., 2006; Ghetti et al., 2010; Ofen et al., 2007). However a few very recent studies investigated episodic memory retrieval using fMRI and event-related potentials (ERPs).

Findings regarding the development of the neural correlates of episodic memory in the hippocampus have been mixed. In contrast, more consistent findings have been observed in the frontal and parietal cortices thought to support memory retrieval (see DeMaster et al., 2013 for review). Paz-Alonso et al. (2008) focused on the development of true and false recognition and tested children age 8 and 12-year old, and 19–23-year old adults. The results showed region-specific developmental changes in the MTL, bilateral DLPFC, posterior parietal cortex, and right RLPFC. Adults, but not children, exhibited strongest right RLPFC activation for hits and those trials where a semantically-related lure was correctly rejected, i.e., according to the authors, those conditions in which monitoring was both required (due to the presentation of semantically relevant stimuli), and successful (leading to a correct response) (Fig. 4a).

DeMaster and Ghetti (2013) scanned children aged 8–11-year old and adults aged 18–25-year old who were asked whether a drawing shown on the screen had been presented before or not (item memory) and what colour was the border of the drawing during its first presentation (context or source memory). Activations associated with successful retrieval across age groups were observed in the right MTL, left posterior parietal cortex, left RLPFC and precuneus. In the RLPFC activation was observed across conditions and was unspecific to successful retrieval in children, while in adults the activation was greater for trials where the colour-drawing pair was successfully remembered than when the drawing was recognised but the colour not remembered, and in turn these trials show greater activation than for drawings correctly recognised as new (Fig. 4b).

In a second study, DeMaster et al. (2013) used a spatial context (drawing presented on the left or right of the screen) rather than a colour border and scanned children aged 8–9 or 10–12 years old and adults. Similarly to their previous study, DeMaster et al. (2013) observed an age × condition interaction in the left RLPFC (with a similar but weaker pattern in the right RLPFC). Adults showed greater activation for correct than incorrect source memory retrieval, and more activation for incorrect source memory retrieval (but correct old item recognition) than for correctly rejected items (new items) (Fig. 4c). In 10–11-year-olds, only the comparison correct vs. incorrect source memory retrieval was significant, while in 8–9-year olds activation was greater for correctly recognised items than for items correctly identified as new (Fig. 4c). A similar pattern of developmental changes was observed in the left parietal cortex and precuneus, but differed in the insula and DLPFC. The similar pattern observed between the parietal cortex and RLPFC further reinforces the idea that these two regions interact strongly during abstract thinking, as suggested in the relational abstract thoughts studies described above and in Section 5 below. Although DeMaster et al. (2013) point out that these two regions have been associated with different cognitive processes in the past, they suggest that further work needs to be done to disentangle their role during episodic memory retrieval development.

Contrary to the three studies described above (Fig. 4), Güler and Thomas (2013) did not observe developmental changes in RLPFC during episodic memory retrieval. However this study compared 9–10 and 12–13-year olds children and did not include an adult group, which may have limited the size of the developmental effect. In addition, the paradigm used was a paired-associate picture memory task rather than a source memory paradigm. Developmental differences in activation associated with successful recall were instead observed in a more posterior part of the left middle frontal gyrus (area 46/47), right middle temporal gyrus and cerebellum, left inferior parietal lobule and anterior cingulate gyrus (Güler and Thomas, 2013).

To summarise, recent studies investigating episodic memory development using neuroimaging methods show prolonged development of the neural correlates of item and source memory retrieval between late childhood and adulthood, with evidence of increased sensitivity of RLPFC activation to specific components of episodic memory (e.g. source vs. item memory, old vs. new item) in adults compared to children.

4.6. Neuroimaging studies of episodic memory and prospective memory during development

Only two studies have investigated the neural correlates of PM development. Both studies used event-related PM paradigms and collected ERP data. Mattli et al. (2011) tested children (mean age 10.3 years) and younger adults (mean age 31.4 years) (as well as an older adult group not discussed here). The N300 component reflects greater negativity for PM hits than PM misses and ongoing activity trials over the occipito–parietal region of the scalp. It is therefore thought to be associated with the detection of an event-based PM cue in the environment. Mattli et al. (2011) observed no difference in N300 amplitude for PM hits versus ongoing trials between the age group, however while adults showed greater N300 amplitude for PM hits than PM misses, children did not. According to the authors, this suggests that in children cue detection was not necessarily associated with realisation of the intention, possibly reflecting failure of executive processes associated with switching or disengaging from the ongoing activity. Reversely, a parietal positivity discriminated between PM hits and misses in children, but not in adults. No difference between age group was found between a frontal positivity which also discriminated between PM hits and PM misses. In a study including adolescent participants, Zöllig et al. (2007) observed larger N300 amplitudes in adolescents
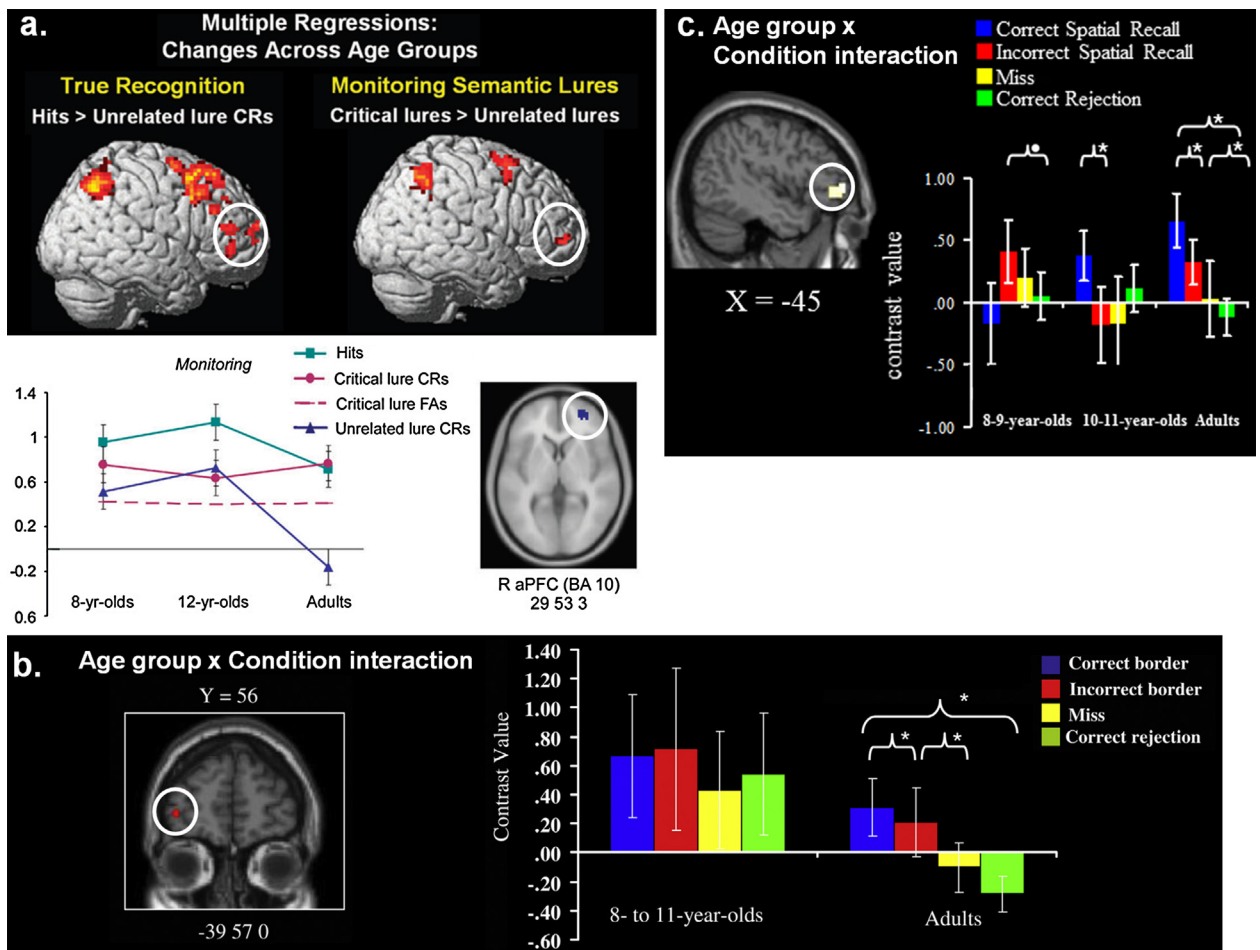
Fig. 4. Developmental changes in RLPFC activation during episodic memory tasks. (a) Neural correlates of episodic memory retrieval. Top left: increased activation with age associated with hit trials compared to trials with correctly rejected semantically unrelated lures; top right: increased activation with age associated with trials where a semantically related (critical) lure vs. an unrelated lure is correctly identified; bottom: region of interest analysis suggesting that in adults right RLPFC is involved in the monitoring of performance during episodic memory retrieval, with greater activation associated to correctly recognised semantically relevant items (hits or critical lures). CR: correct rejections; FA: false alarms; aPFC: anterior prefrontal cortex (adapted from Paz-Alonso et al., 2008). (b) Region of interest analysis of left RLPFC activation during source memory retrieval. The condition × age group interaction was significant, revealing increased RLPFC activation for increasingly amount of recollected information (correct border = both drawing and colour were remembered (source memory); incorrect border = the drawing but not its border colour was remembered (item memory); Miss = error trial; correct rejection = drawing correctly identified as not presented before) in the adults, but not the children, who showed similar RLPFC recruitment across trial types (adapted from DeMaster and Ghetti, 2013). (c) Region of interest analysis of left RLPFC activation during source memory retrieval. The condition × age group interaction was significant, revealing increased RLPFC activation for increasingly amount of recollected information (correct spatial recall = both drawing and its location were remembered (source memory); incorrect spatial recall = the drawing but not its location was remembered (item memory); Miss = error trial; correct rejection = drawing correctly identified as not presented before) in the adults, with a difference between source and item memory in the 10–11-year olds, but activation for item memory only for the 8–9-year olds (adapted from DeMaster et al., 2013).

than in adults when a PM intention had to be inhibited, and a larger parietal positivity between 600 and 800 ms when a PM intention had to be executed, as compared to ongoing trials. The latter effect is similar to that observed by Mattli et al. (2011). Source analyses suggested differences in current density between adolescents and adults for PM execution in mostly posterior brain regions, while ongoing trials were associated with greater right middle frontal gyrus activations in adolescents, which may be associated with some sort of anticipatory processing (Simons et al., 2006). However, adolescents also showed poorer performance in ongoing trials, limiting the inferences that can be made from these results. To summarise,

very little neuroimaging research has been done to investigate the development of PM during late childhood and adolescence. Further work, including fMRI studies, will be necessary to inform our understanding of the role played by RLPFC during PM development.

5. Association between structural changes during development and abstract thinking

RLPFC undergoes substantial structural changes during adolescence (see Dumontheil et al., 2008 for review). Research on developmental changes in brain structure have tended to consist of whole-brain analyses and do not

typically report analyses in anatomical subdivisons of the frontal cortex. Overall the results show increases in white matter volumes and decreases in grey matter volumes with age in the frontal cortex during adolescence (Barnea-Goraly et al., 2005; Giedd et al., 1999; Shaw et al., 2008; Sowell et al., 1999, 2004; Tamnes et al., 2010; Westlye et al., 2010). Behavioural and functional changes during development, and in particular late childhood and adolescence, are often interpreted as being a consequence of the structural changes that occur during this period (Crone and Dahl, 2012; Luna et al., 2010; Spear, 2000). Decreases in functional activations are considered to reflect developmental reductions in grey matter volume, presumably related to synaptic pruning. Increases are thought to relate to improved and more localised 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 (e.g. Lu et al., 2009; Olesen et al., 2003; Van den Bos et al., 2012). The association between structural changes during development and relationally abstract thinking will be described below, presenting data from recent studies which attempt to integrate brain and behavioural measures. No studies to date have investigated associations between brain structure and temporally abstract thinking during development.

Cortical thickness of RLPFC, in particular in females (e.g. Narr et al., 2007), and during adolescence (e.g. Shaw et al., 2006), has been shown to be positively correlated with standardised intelligence quotient (IQ). IQ is typically measured using tests such as the Wechsler intelligence scales (Wechsler, 1997), which include a variety of subtests testing verbal and performance intelligence. Some of these tests will require the manipulation of self-generated and abstract thoughts; however, it is as yet unclear whether this accounts for the observed link between RLPFC structure and IQ (Narr et al., 2007; Shaw et al., 2006). The finding by Shaw et al. (2006) that the developmental timecourse of cortical thickness changes was associated with IQ, rather than cortical thickness in early childhood or in adulthood, stresses the importance of studying developmental trajectories. However, very few research groups have the means to do so using large longitudinal samples and most of the data discussed below are cross-sectional.

Using the datasets described above, collected while participants performed the Alphabet and Shapes tasks (Dumontheil et al., 2010b, 2010c), we aimed to test the hypothesis that decreases in functional BOLD signal during adolescence may reflect the concomitant local decreases in grey matter volume. To do so we extracted local grey and white matter volumes in the brain regions showing functional developmental changes and entered these data into multiple regression analyses. The results revealed that the decrease in superior RLPFC during switching between self-generated and perceptually-derived information was not accounted for by local structural changes (Dumontheil et al., 2010b). Analyses of the relational integration data from the Shapes task (Dumontheil et al., 2010c) provided a

different picture, showing that the decreased BOLD signal between mid-adolescents and adults did not remain significant when local structural measures (and performance) were covaried. Further tests were performed to relate structural changes to the connectivity changes observed using dynamic causal modelling (DCM) (Bazargani et al., 2014). Grey matter volume in RLPFC and fixed connectivity (i.e. connectivity in 1-relational trials) between frontal and insular regions were both found to decrease with age. RLPFC grey matter volume was further found to predict short-range fixed connectivity. However, no significant mediation of the effect of age on short-range fixed connectivity by RLPFC grey matter volume was observed (Bazargani et al., 2014). RLPFC grey matter volume in addition predicted 2-relational vs. 1-relational accuracy (Bazargani et al., 2014). In the other study of relational integration development in children and adolescent participants described above, increased functional selectivity in the left RLPFC was partly accounted for by cortical thinning in the left inferior parietal lobule (Wendelken et al., 2011), with a positive correlation between inferior parietal lobule thickness and activation in the left RLPFC in 1-relational trials.

The first two sets of results, within the same participants, provide evidence for the complex relationships between developmental changes in task-related brain activity, performance and local changes in brain structure. Overall the results discussed above suggest that individual differences in grey matter, in RLPFC or the inferior parietal lobule, can play a role in the development of functional networks supporting relational integration. There is less evidence suggesting specific roles of individual differences or developmental changes in white matter in the development of relational reasoning. Indeed, a recent study has shown that developmental changes in whole-brain measures of white matter volume or fractional anisotropy predicted developmental improvements in visuospatial reasoning ability. However, this effect was mediated via processing speed and was not found to be specific to fronto-parietal white matter tracts (Ferrer et al., 2013). This suggests that, contrary to grey matter volume, the influence of structural developmental changes in white matter on reasoning ability may not be region-specific.

6. Questions for future research

6.1. Influence of puberty vs. chronological age

The role of puberty in the developing adolescent brain (Blakemore et al., 2010; Crone and Dahl, 2012) and whether changes observed during adolescence are a consequence of chronological age or puberty levels has been the topic of a few recent studies investigating structural changes (Goddings et al., 2014) and functional changes during a social cognition task (Goddings et al., 2012). Although in this latter study the functional changes observed in the MPFC were related to age rather than puberty level (in contrast to the functional changes observed in the temporal cortex), very little is known about the effect of puberty stage on the development of abstract thinking and the lateral parts of the prefrontal cortex during adolescence.

More generally, there is currently little evidence of gender differences in this age range in functional imaging data (e.g. Hatcher et al., 1990; Wendelken et al., 2011), however the available data is limited as some studies only included participants of one gender (e.g. Dumontheil et al., 2010b, 2010c), and others did not test for potential gender differences (e.g. DeMaster and Ghetti, 2013; Crone et al., 2009), likely because of sample size limitations. However, structural neuroimaging studies have shown that the RPFC is the region with the greatest difference in rates of cortical thinning between males and females between the ages of 9 and 22 years (Raznahan et al., 2010), and that there are sex differences in the relationship between cortical thickness maturation in the RPFC and in the superior frontal cortex in the same age range (Raznahan et al., 2011). These structural studies suggest investigating the possible consequences of these structural differences over chronological and pubertal development for RLPFC function maturation is warranted.

6.2. Investigation of the role of RLPFC in the development of temporally abstract thinking

As mentioned above, RLPFC has been implicated in prospective memory, episodic memory retrieval and mind-wandering, i.e. cognitive processes associated with the manipulation of temporally extended abstract information. Although recent neuroimaging work has started to investigate the neural correlates of episodic memory retrieval, only a couple of ERP studies have investigated PM, and no research has been done on mindwandering development. Future research on these topics will broaden our understanding of the development of adolescents' ability to retrieve past experience and think about the future, and how these abilities relate to the control of attention towards perceptually-derived vs. self-generated thoughts.

6.3. Abstract thinking in the social domain: the role of medial RPFC

Anatomical studies investigating the cytoarchitectonic properties of RPFC (e.g. Öngür et al., 2003) and meta-analyses of fMRI data (Gilbert et al., 2006b; Van Overwalle, 2009) suggest a distinction between the medial and lateral aspects of RPFC. Activations along the medial wall have mainly been observed in social cognition tasks, in particular those involving theory of mind, or mentalising, i.e. our ability to understand our own and other people's mental states (except in the most polar part of Brodmann area 10, see Gilbert et al., 2006b; Van Overwalle, 2009). In some situations another person's intention may be quite apparent on the basis of their overt behaviour, and our own mental states or feelings may be salient via e.g. increased heart beat frequency, sweat or stomach-ache in response to stress. In such cases, mentalising would rely on perceptually-derived information. In other situations, one may need to retrieve from episodic memory past behaviour of a friend, or to retrieve social scripts and semantic information in order to judge how they should respond to a friend's comment or behave in a novel social situation. In such cases, one would need to manipulate and integrate self-generated

information. Along these lines, Van Overwalle (2009) in his review describes MPFC "as a module that integrates social information across time and allows reflection and representation of traits and norms, and presumably also of intentionality, at a more abstract cognitive level".

Of particular interest for further research would therefore be the functional relationship between RLPFC and MPFC during abstract thinking, and whether there is anything special about the reasoning and manipulation of social vs. non-social information. A couple of recent studies speak to this. In one study, the storage and manipulation of social information in working memory was associated with activations in both the typical lateral fronto-parietal network associated with working memory and regions of the social brain, including the MPFC and temporo-parietal junction (Meyer et al., 2012). In contrast, the other study, using a relational reasoning task on social information (how pleasant or unpleasant the participant or a participant's friend finds a particular concept), did not observe greater medial PFC activation during relational integration compared to the manipulation of single relations, but did observe left RLPFC activation, consistent with the relational integration studies reported above (Raposo et al., 2011). Note however that neither study included a non-social comparison condition, which would be needed to assess activation patterns that are specific to the manipulation of self-generated information of a social nature.

In terms of development, adolescents typically show increased MPFC activation during social cognition tasks (Blakemore, 2008; Crone and Dahl, 2012), although we recently showed that a pattern of increasing specialisation for perspective taking compared to the processing of social stimuli could be observed between adolescence and adulthood (Dumontheil et al., 2012). Touching on the relationship between abstract thinking about social vs. non-social information, an older study reported complex links in participants aged 10, 13 and 17-year old between abstract reasoning and self- or other- mentalising measures, which were found to differ according to sex (Hatcher et al., 1990). Finally, results of a recent qualitative study suggest that older teenagers coordinate an increasing number of psychological components while telling stories about their family and themselves, and in so doing, create increasingly abstract and coherent psychological profiles of themselves and others (Mckeough and Malcolm, 2010). A better understanding of the link between abstract thinking and social cognition during development may thus inform our understanding of the development of the self-concept during adolescence.

7. Training studies and implications for education

Fluid intelligence can be defined as the use of deliberate mental operations to solve novel problems. These mental operations include drawing inferences, concept formation, classification, generating and testing hypothesis, identifying relations, comprehending implications, problem solving, extrapolating, and transforming information. Thus, fluid intelligence is tightly linked to abstract thinking and relational integration (Ferrer et al., 2009). Fluid intelligence is thought to be an essential component of cognitive

development (Goswami, 1992) and the basis for acquisition of abilities in various domains during childhood and adolescence (Blair, 2006; see Ferrer et al., 2009 for review). Fluid intelligence in childhood predicts achievements at school (e.g. in maths during early adolescence (Primi et al., 2010)), university and in cognitively demanding occupations (Gottfredson, 1997). Fluid intelligence is therefore a predictor of learning, especially in novel and complex situations. Consequently, a better understanding of the development of abstract thinking and reasoning during late childhood and adolescence, both in terms of behaviour and neuroscience, may have implications for education.

Of particular relevance are recent studies assessing the training of abstract thinking or reasoning skills. A few studies have investigating fluid reasoning training during childhood. For example, computerised non-verbal reasoning training was shown to improve fluid intelligence in a large sample of 4-year olds (Bergman Nutley et al., 2011), and fluid reasoning training emphasising planning and relational integration led to substantial improvement on performance IQ, but not speed of reasoning, in children aged 7–9-year old from low socioeconomic backgrounds (Mackey et al., 2011). A couple of studies in young adults further report that students taking a US Law School Admissions Test (LSAT) course offering 70 h of reasoning training showed a strengthening in fronto-parietal and parietal-striatal resting state connectivity compared to matched control participants (Mackey et al., 2013), as well as changes in white matter structure in the frontal and parietal lobes (Mackey et al., 2012). Very little work has been done investigating training of reasoning in adolescents, although Chapman and Gamino (2008) have developed the Strategic Memory and Reasoning Training (SMART) programme, designed to improve top down reasoning skills. The aim of this programme is to teach children how to learn rather than what to learn, by supporting higher-order abstraction of meaning from incoming details and world knowledge, and there is promising evidence that this training programme leads to improved gist-reasoning and fact-learning ability (Gamino et al., 2010).

Whether children and adolescents may benefit more from training than adults will be an important area of research. Relatively little is currently known about developmental differences in brain plasticity in response to training interventions, however research in this domain has greater potential for tailoring appropriate training interventions to different age groups (see Jolles and Crone, 2012 for discussion). Both childhood and adolescence may be "sensitive periods" for teaching, as significant brain reorganisation is taking place during these periods. Perhaps the aims of adolescents' education 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: abstract thinking and reasoning, and the ability to focus on one's own thoughts in spite of environmental distraction. However, training intervention may be limited by the current level of structural brain development and cognitive capacity (as pointed out in Jolles and Crone, 2012), in particular for those training interventions based on strategy rather than repeated performance.

8. Conclusion

Rostrolateral prefrontal cortex supports a wide range of cognitive processes, which may have in common their requirement of retrieval, maintenance, manipulation and/or integration of self-generated, or stimulus-independent thoughts, considered broadly here as abstract thoughts, either relationally abstract, or temporally abstract. This review focused on summarising the evidence from behavioural and neuroimaging studies of the development of RLPFC and its associated functions. Behavioural studies have shown prolonged changes in the speed and accuracy of attending towards and processing self-generated information, in particular in reasoning tasks. These developmental changes appear to build on working memory and inhibitory control functions, as well as the acquisition of domain-specific knowledge. This dependence on the maturation of other aspects of cognition, including working memory and inhibitory control, which are dependent on more posterior regions of the frontal cortex, reinforces the idea that the maturation of RLPFC function will be relatively more protracted. Certain aspects of episodic memory and prospective memory, namely those that rely on implementation of strategies for recollecting source memory, and for time-checking in prospective memory tasks also continue to develop during adolescence. Neuroimaging evidence suggests a possible developmental pattern of increasing specialisation of RLPFC for the integration of relational information, with complex relationships between developmental changes in structure, performance and brain activation, and increasing specialisation for the retrieval of source memory, and item memory information, compared to the processing of new items. A strong relationship between RLPFC and the parietal cortex was apparent across tasks, and further work, in particular using connectivity analyses, may inform our understanding of how the interplay between these brain regions permits the increasingly successful integration of relationally and temporally abstract thoughts over development. Future research could inform our understanding of development of reasoning and abstract thinking in the social domain, and whether functions associated with the RPFC could be trained, with potential benefits in the domain of education.

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