Development of Cognitive Control across Childhood and Adolescence

Kiki Zanolie & Eveline A. Crone

INSTITUTE OF PSYCHOLOGY, LEIDEN UNIVERSITY, LEIDEN, THE NETHERLANDS

Abstract

This chapter describes recent progress in understanding the development of cognitive control in relation to brain development. Across childhood and adolescence, individuals learn to control thought and actions for the purpose of obtaining future goals. These changes in cognitive control have been linked to structural and functional changes of the prefrontal and parietal cortex. In this chapter, we describe the implications of these changes in three domains. The first domain concerns cognitive and adaptive control of thought and actions, with a focus on working memory, inhibition and performance monitoring. The second domain describes the role of cognitive control in affective decision-making, with a focus on delay of gratification. The third domain focuses on social decision-making, specifically how the development of control allows children and adolescents to consider fairness and reciprocity. Together, the findings are summarized in the context of current models of child and adolescent brain development.

Key Terms: cognitive control, brain development, adolescence, performance monitoring, response inhibition, working memory, fMRI, ERP

Introduction

One of the most salient changes during school-aged development is a pronounced increase in the ability to control thought and actions for the purpose of obtaining future goals, also referred to as cognitive control. School-aged development encompasses the period of late childhood (6-10 years) and adolescence (10-20 years), where adolescence is defined as a transitional phase between childhood and adulthood. During adolescence, there are significant

changes in physical, cognitive, emotional and social behavior (Blakemore, 2008). The onset of adolescence is marked by the start of puberty, during which hormone levels rise which trigger a cascade of physical and socio-emotional changes, preparing adolescents for independence (Shirtcliff, Dahl, & Pollak, 2009). Puberty starts approximately around the age of 10-12 years (on average 1.5 years earlier for girls than for boys), but there are large individual differences between children with respect to when they enter puberty. That is to say, some children may already start puberty at 8 years of age, whereas others do not start puberty until 13 years of age. The end phase of adolescence is less clearly defined, generally occurs around the age of 20-25-years, and is defined as the time when individuals obtain mature social goals (Crone & Dahl, 2012).

Of all cognitive processes, cognitive control is probably the latest to reach adult performance levels, with improvements that are observed over the whole period of child and adolescent development (Diamond, 2013; Huizinga, Dolan, & van der Molen, 2006). One reason for this protracted development is most likely because cognitive control relies on the combination of many lower and higher-level functions working together. That is to say, cognitive control refers to a set of cognitive abilities that enable you to control and regulate your behavior adaptively to meet current and future goals. Cognitive control is comprised of many different components, such as working memory, inhibition and performance monitoring (Miyake et al., 2000; Huizinga et al., 2006). Cognitive control is important for school-based functions such as reading and math, but also for the ability to control impulses, and for social interactions. All these functions have shown development improvements across childhood and adolescence.

In the last two decades, much new insight has been gained with respect to understanding the development of cognitive control by relating it to changes in the structure and function of the brain. Longitudinal research on changes in brain structure over development within individuals has shown that regions within the frontal, temporal and parietal cortex show maturational changes much longer than previously thought, with massive changes in grey matter volume and white matter connections until the early twenties (Gogtay et al., 2004; Mills, Lalonde, Clasen, Giedd, & Blakemore, 2014). Moreover, these studies have shown that different brain structures develop at different rates. For example, several studies have demonstrated that grey matter in cortical areas, reflecting neuronal density and the numbers of connections between neurons, follows an inverted U-shape over development, declining at different ages depending on the region (Gogtay et al., 2004). For this reason, grey matter loss is considered an index of the time course of maturation per region (Casey, Tottenham, Liston, & Durston, 2005). Intriguingly, the most protracted development is observed in prefrontal and parietal cortex, regions of the brain that are consistently implicated in cognitive control (Casey, 2015).

Although it is still debated what the underlying mechanisms associated with a reduction in grey matter volume in cortical areas are (see Paus et al., 2008), it is thought that these reductions reflect synaptic reorganization and/or increases in white matter integrity (Paus et al., 2008). This idea that cortices continue to undergo synaptic pruning across adolescence is supported by histological studies of the postmortem human brain (Huttenlocher & Dabholkar, 1997; Petanjek et al., 2011).

More direct ways to investigate the relation between brain development and cognitive control is through examining brain responses while individuals perform cognitive tasks. Two methods have been most useful to examine these relations, which are functional Magnetic Resonance Image (fMRI), a method with good spatial resolution (Huettell, Song, & McCarthy, 2004), and Event-Related Potentials (ERP) derived from the electroencephalogram (EEG), a method with good temporal resolution (Segalowitz, Santesso, & Jetha, 2010).

In this chapter we will discuss new insights on functional development of brain regions supporting key aspects of cognitive control and show that these do not only have consequences for academic achievement, but also for affective and social development, specifically social decision making which requires inhibiting selfish impulses for the purpose of fairness and reciprocity.

We will describe the development or three key aspects of cognitive control, which are working memory, inhibition, and performance monitoring. Whereas working memory and inhibition are important for keeping information in and out of mind, performance monitoring plays a central role in the development for behavioral adjustment. Performance monitoring is therefore particularly important for rapid adaptation to a variety of changing social environments, such as forming new friendships, changing schools, and making future-oriented choices.

Developmental Changes in Cognitive Control and the Role of the prefrontal cortex

Cognitive Control and Prefrontal Cortex

It has been well conceptualized for over a century that the prefrontal cortex plays an important role in cognitive control (Milner, 1963). Early studies of patients with prefrontal cortex showed that these patients have difficulties with cognitive flexibility. This was demonstrated using the now famous Wisconsin

Card Sorting Task (Milner, 1963). In this task, individuals are asked to sort desk using a certain criterion that they need to discover themselves, such as color, shape or number. Each sort is followed by positive or negative feedback, and as such the participant needs to pay attention to the outcomes of their behavior and use the feedback to discover rules in the task. After a certain number of correct sorts, however, the sorting rule changes (e.g., unbeknownst to the participants sorting to color no longer results in positive feedback, but the correct sorting dimension is now shape). The participant needs to respond flexibly to this change and needs to update behavior accordingly. It was found that especially patients with damage to the dorsolateral and medial prefrontal cortex have difficulty with updating their behavior (Barcelo & Knight, 2002). Interestingly, young children show similar deficits on this task (Crone, Ridderinkhof, Worm, Somsen, & van der Molen, 2004) and over the course of adolescence, children become more successful in performing the WCST (Huizinga et al., 2006). It is clear that this task requires many different control processes, such as working memory (keeping the sorting rule active), response inhibition (inhibit responding according to the old rule), and performance monitoring (paying attention to the feedback).

Many studies in adults have used neuroimaging to unravel how different regions in prefrontal cortex are involved in these separable processes involved in performing complex cognitive control tasks. These studies have consistently implicated that both the ventral and the dorsal lateral prefrontal cortex, along with the parietal cortex, are active during working memory tasks (see Figure 1; D'Esposito & Postle, 2015; Klingberg, 2010). In contrast, response inhibition typically engages the right ventrolateral prefrontal cortex and pre-SMA (Aron, Robbins, & Poldrack, 2014). Finally, performance monitoring typically engages both lateral and medial prefrontal cortex, although lateral prefrontal cortex is more strongly engaged in rule searching based on feedback, whereas medial prefrontal cortex is more strongly engaged in processing rule-violating feedback (Zanolie, Van Leijenhorst, Rombouts, & Crone, 2008).

Recently, developmental neuroimaging studies have examined how the regions within the prefrontal cortex are related to the development of cognitive control. Below, we describe these studies in the domains of working memory, inhibition and performance monitoring.

[Insert Fig 1 about here]

Development of Working Memory

One of the most studied components of cognitive control is working memory, which refers to the ability to keep information online while ignoring irrelevant information (Baddeley & Logie, 1999). The ability to keep information in mind is essential for a wide variety of cognitive abilities, including mathematical calculation, reading, problem-solving, and reasoning (Bayliss, Jarrold, Baddeley, & Gunn, 2005; Swanson, 2004). In fact, working memory capacity predicts school performance, such as reading and arithmetic (Hitch, Towse, & Hutton, 2001). Moreover, it has been demonstrated that working memory shows a strong connection to fluid intelligence (Engle, Tuholski, Laughlin, & Conway, 1999). The ability to keep information in working memory matures slowly during childhood and is thought to be the driving force behind cognitive development (e.g. Casey, Giedd, & Thomas, 2000; Diamond, 2002).

Many studies have used the model of Baddeley and Hitch (1974) as a framework for understanding working memory. According to this model working memory comprises of a central executive and two slave systems, the phonological loop and visuo-spatial sketchpad. The phonological loop is specialized in processing language-based information, whereas the visuo-spatial sketchpad is specialized in processing visuo-spatial information. Assessment of these two systems is usually made by means of short-term memory tasks in which small amounts of information are to be held and reproduced, with no additional cognitive demands (e.g. digit span, word recall, Corsi blocks and visual-patterns tasks). The central executive controls the allocation of resources between the phonological loop and the visuo-spatial sketchpad, and is able to update and manipulate the content of memory when new and relevant information is processed.

Assessment of the central executive typically involves experimental tasks that require participants to update or manipulate information currently held in working memory. Such tasks include the listening span, counting span, backward digit span and n-back task. In fMRI paradigms the n-back task is frequently used to investigate working memory capacity (see for a meta-analysis Owen, McMillan, Laird, & Bullmore, 2005). In the n-back task participants are presented with a series of stimuli (e.g. letters or words). The participant is required to maintain these stimuli online and compare it with *n* stimuli back. For example, in the 3-back letter version, the subject is required to compare each presented letter with the letter presented 3 before. The participant needs to indicate whether the letters are the same or different. In order to perform well on this task one needs to maintain information in memory and at the same time manipulate and update its content.

In adult brain imaging studies it is shown that maintenance and manipulation of information in working memory are associated with activation in the ventral and dorsal parts of the prefrontal cortex (PFC). Typically, the ventrolateral (VL) PFC is involved in maintenance of information in working memory, while the dorsolateral (DL) PFC is additionally recruited when manipulation of information is needed (Owen, Evans, Petrides, 1996; D' Esposito, Postle, Ballard & Lease, 1999; Smith & Jonides, 1999; Crone, Wendelken, Donahue, van Leijenhorst, & Bunge, 2006; Wagner, Maril, Bjork, & Schacter, 2001; Sakai & Passingham, 2002). Besides the DLPFC, also the superior parietal cortex is implicated in tasks involving manipulation (see meta-analysis Wager & Smith, 2003).

To test the neurocognitive development of working memory, studies have compared neural activity in children, adolescents and adults when they performed a working memory task in the scanner. One way of measuring working memory, is by varying the amount of time between stimulus presentations and retrieving information, or by varying the number of items that have to be held in working memory. This type of working memory is referred to as working memory *maintenance*. Several researchers have shown that activity in the lateral prefrontal cortex and parietal cortex during working memory *maintenance* increases from childhood to adulthood (Klingberg, Forssberg, & Westerberg, 2002; O'Hare, Lu, Houston, Bookheimer, & Sowell, 2008). Others have shown that in children activity is likely to be diffuse across different brain regions, whereas in adolescence it tends to be more restricted to the specific neural regions that show task-relevant activation as in adults. (Ciesielski, Lesnik, Savoy, Grant, & Ahlfors, 2006; Geier, Garver, Terwilliger, & Luna, 2009; Libertus, Brannon, & Pelphrey, 2009; Scherf, Sweeney, & Luna, 2006).

Age differences become even larger when participants are asked to reorganize the information in the working memory. This type of working memory is measured by the so-called manipulation task. One brain imaging study compared three age groups performing a working memory task in which three pictures were shown and needed to be remembered, children ages 8-12 years, adolescents ages 13-17 years, and young adults (Crone, Wendelken, Donohue, van Leijenhorst, & Bunge, 2006). In one condition, the forward condition, the participants were required to remember the pictures in the presented order during a short delay period (see Figure 2). In order to perform this condition well participants only needed to maintain the presented information in working memory. However, in the backward condition participants were required to remember the pictures in reversed order, therefore needing to manipulate besides maintain the information during the delay period. Maintenance of information in working memory (forward condition) was associated with increased VLPFC activation showing the same pattern for adults, adolescents and children. However, in the backward condition, when information needed to be manipulated, adults and

adolescents recruited the DLPFC in addition to the VLPFC, but the 8-12 year old children did not. It is important to note that increased brain activity does not reflect a stronger activation overall, but reflects a stronger brain activation for a specific contrast. In this study, for instance, activation during manipulating information was compared to maintaining information (backward condition > forward condition).

The number of correct responses in the backward condition correlated with the activation in the DLPFC, strengthening the hypothesis that the DLPFC is important for improvements in performance on working memory manipulation (Crone et al., 2006). In a subsequent study, it was found that this effect was independent of the number of items that had to be held within working memory, suggesting that the effects are specific for manipulation and not related to task difficulty (Jolles, Kleibeuker, Rombouts, & Crone, 2011). Similar results were obtained when researchers presented this task in a visuo-spatial n-back version. In this task it was found that both activity in the lateral prefrontal cortex and the parietal cortex increased linearly across ages 7-22 years (Kwon, Reiss, & Menon, 2002; Spencer-Smith et al., 2013), possibly related to adults being better able to activate these regions over a sustained period of time (Brahmbhatt, White, & Barch, 2010).

[Insert Figure 2 about here]

Together these studies provide evidence that the development of separable cognitive control functions within working memory are associated with differential maturational patterns of sub regions within the lateral PFC. The differential engagement of sub regions of the lateral PFC is in accordance with structural changes across development within the brain. Within the PFC, gray mater reduction is observed earlier for the VLPFC compared to the DLPFC, such that the VLPFC reaches mature levels at adolescence, whereas the DLPFC continues to have gray matter loss until young adulthood (Gogtay et al., 2004). More importantly, a study including 951 participants between ages 8-22 years showed that activity in lateral PFC mediates the relation between age and working memory (Satterthwaite et al., 2013), suggesting that children have more difficulty with working memory due to the protracted development of prefrontal cortex.

Apparent contradictive findings with regard to developmental brain activity patterns while maintaining information online might be due to task-specific processing requirements, such as visual spatial information processing (Klingberg et al., 2002) versus verbal information processing (Crone et al., 2006; O'Hare et al., 2008). Secondly, working memory load may account for differences in brain activity patterns (O'Hare et al., 2008).These task specific processes and

differences in working memory load may also contribute to differential developmental patterns in behavior. Although overall behavioral findings suggest that children and adolescents are capable of performing at adult levels, however, they still improve their ability to stay focused on the task and to monitor their behavior (Luna, Padmanabhan, & O'Hearn, 2010).

Development of Response Inhibition

Inhibition has been abundantly researched in development psychology. Researchers often use computer tasks to measure very precisely how children and adults succeed in stopping their responses. In the 'go/nogo' task (see for a review Hester, Fassbender, & Garavan, 2004), a participant is asked to press a button if a certain letter is shown, for example the letter X. This letter is shown in quick succession, but the participant is instructed that when the letter Y is presented, the button may not be pressed. This is especially hard for pre-schoolers (Diamond, 2013), but children up to the age of 12 or so also have more trouble inhibitig their behaviour than adults (Casey, 2015; Schel & Crone, 2013).

Another way of measuring inhibition is with the stop-signal task (Rubia, Smith, Taylor, & Brammer, 2007). In this task, the participant is instructed to respond to green arrows pointing left or right, by pressing a left or right button with their index fingers. But when the arrow turns red, the participant is not allowed to respond. This is relatively easy when the arrow turns red right away, but more difficult when the arrow remains green for a while first, and only turns red when participants are about to press the button. By varying the time between showing the arrow and turning the arrow red, researchers can determine how much time someone needs in order to be able to stop successfully. This time is called the Stop Signal Reaction Time (SSRT). Between the ages of 3 and 6, the SSRT is slow (Lee, Lo, Li, Sung, & Juan, 2015). However, the SSRT does not reach adult levels until the ages of 12-14 at least (van den Wildenberg & van der Molen, 2004). Until that age, children and adolescents have more difficulty stopping than adults (Schel, Scheres, & Crone, 2014).

When someone has damage to the right ventral area of the lateral prefrontal cortex, this leads to great difficulty with stopping (Aron, Robbins, & Poldrack, 2004). Healthy adults show activity in this area when performing a go/no go task or a stop-signal task (Aron et al., 2004, 2014).

Researchers have investigated the development of this inhibition area between the ages of 8-12, and the ages of 18-25 using go/nogo task or stop signal tasks. The

most important finding was that when 8-to-12-year-olds perform a go/no go task during an fMRI-scan, they show less activity in the right ventral part of the lateral prefrontal cortex than the 18-to-25-year-olds (Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002; Durston et al., 2006; Rubia et al., 2006; Tamm, Menon, & Reiss, 2002). Interestingly, these children often show additional activity in a different area of the prefrontal cortex, such as the dorsal area of the prefrontal cortex (Booth et al., 2003; Durston et al., 2006). Similar results have been obtained for the stop-signal task (Rubia et al., 2013; Rubia et al., 2007; Vink et al., 2014). These findings suggest again a shift from diffuse to localized activity.

Development of Performance Monitoring

Performance monitoring is of pivotal importance to rapidly adapt to a changing (social) environment. It is not only important to be able to monitor your performance in order to adjust your behavior after committing an error, but also when making future-oriented choices and forming new friendships. A wide variety of tasks have been used to study the neural processes involved in the development of performance monitoring, ranging from cognitive learning tasks (e.g. Hajcak, Moser, Holroyd, & Simons, 2006; Holroyd & Coles, 2002) to social-affective feedback tasks (e.g. Fareri & Delgado, 2014; Somerville, Heatherton, & Kelley, 2006). In performance monitoring studies participants typically have to make a single or binary choice when presented with a stimulus. Upon this choice performance feedback is given, which can either have a positive valence when the choice is correct or a negative valence when the choice is incorrect. Studies in adults have shown great involvement of the dorsal medial PFC, more specifically the pre-Supplementary Motor Area (pre-SMA) and the dorsal Anterior Cingulate Cortex (dACC) (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004).

Performance monitoring can be subdivided into internal and external feedback processing or monitoring. The Event-Related Potential (ERP) technique has proven to be very useful in investigating these types of monitoring, especially internal monitoring. ERP studies have shown that internal feedback processing, when errors are processed, is associated with a negative ERP component, the Error-Related Negativity (ERN), which peaks approximately between 50–100 ms after an error is committed. This component is visible even before external feedback may be presented. Traditionally the ERN is examined by means of speeded response tasks in which conflicting stimulus-response mappings are likely to occur equally, such as the Go/NoGo and Flanker tasks. In the Go/NoGo task prepotent responses to target stimuli need to be inhibited, while in the Flanker task stimuli need to be discriminated with congruent or incongruent flanking stimuli. The source of the ERN is estimated in the dACC by using source localization methods (Carter & van Veen, 2007; Holroyd & Coles, 2002).

Compared to the ERN, which reflects the activation of an internal feedback processing or monitoring system, the FRN reflects activity associated with external monitoring (Gentsch, Ullsperger, & Ullsperger, 2009). External feedback processing is associated with a negative ERP component, the Feedback-Related Negativity (FRN; also referred to as the Medial Frontal Negativity, MFN). This component peaks approximately 250-350 ms after feedback is presented. The source of the FRN has been estimated in both the dACC (van Noordt & Segalowitz, 2012) and in the basal ganglia (Foti, Weinberg, Dien, & Hajcak, 2011). These sources are consistent with the hypothesis that this component reflects activity of phasic increases and decreases in midbrain dopamine systems, which signal to the dACC that outcomes are better or worse than expected (Holroyd & Coles, 2002). However, there is an ongoing debate with respect to whether the FRN reflects a response to negative feedback (Segalowitz, Santesso, Murphy, Homan, & Chantziantoniou, 2010), reflects a reward-related positivity that is absent on negative feedback (i.e., nonreward) trials (Foti et al., 2011), or is a response to saliency of feedback irrespective of valence (Santesso, Dzyundzyak, & Segalowitz, 2011).

In fMRI paradigms it was previously found that processing negative feedback compared to positive feedback is associated with an increase in pre-SMA and dACC activity (Holroyd et al., 2004; Zanolie, Teng, et al., 2008), where neural responses are larger when negative feedback is unexpected (Zanolie, Van Leijenhorst, et al., 2008). Typically, activity in the pre-SMA and dACC during performance monitoring tasks is accompanied by activation in lateral parts of the PFC, which together have been interpreted as areas involved in behavioral adjustment (Carter & van Veen, 2007; Kerns et al., 2004). These results suggest that the dorsal mPFC is involved in cognitive error and negative feedback processing.

During adolescence, children and adolescents improve in the ability to monitor their own actions. Particularly, abilities to monitor, evaluate, and adjust behavior according to changing environmental and social demands improve rapidly. Internal monitoring of actions has been studied to a great extent using ERPs, by focusing on the ERN. Typically internal signals are activated whenever one notices that an error is committed (van Noordt & Segalowitz, 2012). Studies that have investigated the ERN in a developmental population have found that the ERN is present, but small, in children between ages 3-12 years (Grammer, Carrasco, Gehring, & Morrison, 2014; Torpey, Hajcak, Kim, Kujawa, & Klein, 2012; Richardson, Anderson, Reid, & Fox, 2011; van Meel, Heslenfeld, Rommelse, Oosterlaan, & Sergeant, 2012). Between late childhood (10-12 years) and early adulthood, the ERN after committing an error becomes larger (Santesso, Segalowitz, & Schmidt, 2006; van Meel et al., 2012). During late adolescence and adulthood there are continued changes in the pronunciation of the ERN

(Ladouceur, Dahl, & Carter, 2007; for a review, Tamnes, Walhovd, Torstveit, Sells, & Fjell, 2013).

The development of external feedback monitoring has been studied by measuring the FRN (e.g. Holroyd, Baker, Kerns, & Muller, 2008; van Meel, Oosterlaan, Heslenfeld, & Sergeant, 2005; Segalowitz et al., 2011; Crowley et al., 2009). Only few studies have directly compared the FRN in healthy, normally developing children with adults (Eppinger , Mock, & Kray, 2009; Santesso et al., 2011) while other studies only included an adolescent group of participants (Hämmerer, Li, Müller, & Lindenberger, 2011; Zottoli & Grose-Fifer, 2012; Crowley et al., 2013). Hämmerer et al. (2011) found that the FRN was largest in children and decreased with age. Also, the differences between FRN amplitudes after losses and gains were smallest in the youngest age group. Lastly, there seem to be latency differences in the FRN between age groups, such that the FRN peaks later in time for 10-12 and 13-14 year olds compared to 15-17 year olds (Crowley et al., 2013). Also, Zottoli and Grose-Fifer (2012) found a trend towards latency differences, where the FRN was later in time for 14-17 year olds compared to 22-26 year olds. These results seem to suggest that during childhood into adolescence the ability to use external feedback more efficiently is still developing, such that the neural processes underlying the FRN are still developing from childhood to adulthood. A tentative idea is that there might be age-related differences in the efficiency to differentiate between positive and negative feedback related to the developing dopamine system (Zottoli & Grose-Fifer, 2012)

External feedback monitoring has also been studied extensively using brain imaging techniques. Children and early adolescents (8-12 years) show remarkable improvements in behavioral adjustment after receiving cues or feedback signaling the need to change their current behavior. For example, Crone et al. (2008) measured the neural activity of three age groups (8–11 years, 14–15 years, and 18–25 years) while performing a rule-learning task, which was based on the principles of the WCST (Crone, Zanolie, Van Leijenhorst, Westenberg, & Rombouts, 2008). In this rule-learning task participants were required to sort a stimulus in one of four locations. After each sort participants received feedback whether the sort was correct (positive feedback) or incorrect (negative feedback). Participants had to use this trial-and-error learning in order to find the correct sorting rule. As soon as the rule was applied for a variable number of trials, the rule changed unexpectedly to a new rule. This signaled that participant that he needed to figure out the new rule by using the given feedback. Developmental comparisons showed that 8–11-year-olds activated the ACC/pre-SMA for all types of negative feedback, whereas 14–15-year-olds and 18–25-year-olds activated this region specifically after unexpected negative feedback signaling a rule shift and, therefore, a need to adjust current behavior. These results show that the pattern of activation changed between early- and mid-adolescence. Developmental increases in neural activity following negative feedback were also observed in the DLPFC,

however, this region showed a more protracted development with continued changes between mid-adolescence and adulthood (van den Bos, Guroglu, van den Bulk, Rombouts, & Crone, 2009; van Duijvenvoorde, Zanolie, Rombouts, Raijmakers, & Crone, 2008).

In a rule-learning paradigm Peters, Braams, Raijmakers, Koolschijn and Crone (2014) aimed to pinpoint the exact developmental time point at which the neural response after negative performance feedback reaches adult levels. To this end they included 268 participants in the age of 8 to 25 years. The researchers found that the developmental pattern in learning from negative feedback, and associated activity in dACC/pre-SMA and DLPFC following negative feedback, increased until age 14, after which it stabilized. Strong correlations between brain responses and behavior on the task showed that this dACC/pre-SMA and DLPFC network was involved in performing the task well, but there was also unique activity associated with age-related changes. These neural patterns of protracted development in dACC/pre-SMA and DLPFC have been observed in a variety of executive control paradigms, such as studies examining response inhibition and working memory, and are therefore be interpreted as the maturation of a cognitive learning process.

In conclusion, several studies examining performance monitoring based on internal monitoring (ERN) as well as external monitoring (FRN and processing feedback) have consistently shown a developmental growth in abilities. Not only the ability to monitor errors, but also distinguishing between different types of feedback develops from childhood through adolescence. More specifically, between childhood and adolescence the capacity for internal performance monitoring increases. Additionally, adolescents become more successful in filtering the informative value of feedback, and as a consequence use feedback more efficiently in order to learn. These behavioral improvements are accompanied by functional changes in the brain, such that activity in the dorsal mPFC (more specifically the dACC/pre-SMA) and lateral PFC increases across age. These developmental patterns have been attributed to changes in executive functions and protracted development of the dorsal mPFC and lateral prefrontal cortex.

Developmental Changes in Affective Decision-Making

<u>Delay of gratification</u>

Many of the decisions we make in daily life don't involve only simple deliberations. Many times our decisions are the result of a complex interplay between choosing immediate benefits or long-term outcomes. Specifically this weighing of short versus long-term consequences of choices seems to undergo pronounced developmental changes in adolescence. For example, in a card playing task in which children, adolescents and adults can choose between cards with an immediate high rewards but high long term losses, or immediate low reward but small long term losses, children prefer immediate rewards whereas adults prefer delayed rewards. This choice pattern changes during adolescence, when teenagers are learning to make long-term choices, but even in 16-to-18-year-olds, the choice pattern is not quite as targeted on the long term as it is in adults aged 20 to 25 (Cauffman et al., 2010; Crone & van der Molen, 2004; Hooper, Luciana, Conklin, & Yarger, 2004).

The orbitofrontal cortex in particular plays an important role in controlling responses to reward stimuli (O'Doherty, 2011), as was demonstrated in earlier in neuropsychological research, but which was confirmed in white matter tract studies in healthy adults (Peper et al., 2013; van den Bos, Rodriguez, Schweitzer, & McClure, 2014). Whereas function activation patterns inform us about activity in a specific region, white matter tracts inform us about the structural connections between regions. Other areas that play roles in weighing choices, however, are the lateral frontal areas, which are of considerable importance for keeping track of long-term goals (Casey, 2015). For example, when a choice has to be made between an immediate, quick reward or a possible, larger reward on the long term, the emotion-related areas of the brain are active when the quick reward is chosen, whereas the lateral frontal cortex areas are active when the long-term alternatives are chosen (McClure, Laibson, Loewenstein, & Cohen, 2004).

A well-known task that measures these types of decisions in the laboratory is the delay of gratification task (also known as temporal discounting task). This task asks participants to choose between a smaller immediate reward (for example 5 euros today) or a larger delayed reward (for example 8 euros in 2 weeks). The more impulsive individuals typically choose more for the immediate reward. It is often found that children make more impulsive choices and the ability to delay gratification (or make long term choices) increases over the course of adolescence (Achterberg, Peper, Van Duijvenvoorde, Mandl, & Crone, 2016; Banich et al.,

2013; Steinbeis, Haushofer, Fehr, & Singer, 2016). Interestingly, when adolescents make immediate choices, they show stronger activity in the ventral striatum/nucleus accumbens than adults (Christakou, Brammer, & Rubia, 2011). Overcoming responses to immediate reward is associated with strong functional coupling between the regulating dorsolateral prefrontal cortex and the reward-valuing ventromedial frontal cortex, a connections that becomes stronger with increasing age (Steinbeis et al., 2016).

Moreover, studies that have looked at white matter tracts between the striatum and the frontal cortex have shown that the stronger these connections, the less impulsive people are. This tract becomes stronger between childhood and adulthood, and explains, at least partly, the developmental changes in delay of gratification (Achterberg et al., 2016; Olson et al., 2009; van den Bos, Rodriguez, Schweitzer, & McClure, 2015). Thus, the development of prefrontal cortex, which is important for several aspects of cognitive control, is most likely also of crucial importance when making patient, long-term beneficial decisions.

Developmental Changes in Cognitive Control and Social Decision-Making

Development of the Social Brain

Adolescence is seen as a very important transition period for the development of concern for others and social values, which is strongly tied to the development of cognitive and social-affective abilities. Here, we present the argument that cognitive control is also involved in social decision-making. Before describing this in more detail, it is important to have a general overview of brain regions that are involved in social reasoning, which include mentalizing about thoughts of others, and mentalizing about own benefits.

Mentalizing, the ability to understand the mental state of oneself and another, is closely tied to cognitive and social-affective development. One of the most important milestones of mentalizing capacities is the development of social perspective-taking abilities (Saxe & Kanwisher, 2003). Perspective-taking refers to the ability to understand intentions, considerations and goals of others from the point of view of that other person. The core components of perspective-taking mature before a child reaches the age of 5, leading to a 'theory of mind' (Wellman, Cross, & Watson, 2001). However, development of these perspective-taking abilities does not stop there. In experimental designs it was shown that abilities to understand and consider intentions of others in social interactions gradually develops during childhood and adolescence. For example, Dumontheil,

Apperly, and Blakemore (2010) had participants view a set of shelves with objects, which they were instructed to move by instructing another person. However this other person was not able to see all the objects. Therefore, in order to correctly move the objects the participant needed use the perspective of the other person. They showed that the ability to view a certain situation from the point of view of another person continues to develop in adolescence. In adults, perspective taking is associated with activity in the Temporal-Parietal Junction (TPJ), Superior Temporal Sulcus (STS), and dorsal mPFC (Denny, Kober, Wager, & Ochsner, 2012; Van Overwalle, 2009).

The second important component of mentalizing is self-referential processing, which involves comparing consequences for oneself to consequences for others (Rilling & Sanfey, 2011). In adults, self-referential processing is associated with activity in the ventral mPFC (Amodio & Frith, 2006; Denny et al., 2012). Activation patterns in the ventral mPFC, TPJ, STS and dorsal mPFC, which together are referred to as the social brain, change remarkably across adolescence and may influence adolescents' perspective-taking and self-referential abilities in decision-making (Blakemore, 2008).

Interestingly, in this perspective the DLPFC is not only important for cognitive control and affective control, but has also been identified as one of the key brain regions associated with social decision-making. As such, the DLPFC may contribute to the differential pattern observed in childhood and adolescence regarding social decisions.

Here, we provide evidence for a role of cognitive control in one specific aspect of social decision-making, which is the consideration of fairness.

Development of self-other perspectives in consideration of fairness

Cognitive control is a very important component of social interactions. Several studies have demonstrated the role of cognitive control in studies that have made use of social dilemma's, or economic games. When goods need to be divided between two individual there are two motivational aspects of importance during such a social decision: interest in your own benefit and concern for others (Van Dijk & Vermunt, 2000). Over the past decades many studies have investigated the development of fairness in different types of bargaining contexts. These paradigms stem from social and economic psychology, and are particularly valuable in studying the role of cognitive control in considerations of fairness.

Trust Game: In the Trust Game, there are two players with a certain sum of money, the stake (see Figure 3; Berg, Dickhaut, & McCabe, 1995). The first

player decides independently either to divide the original stake or to trust the second player with the money. If the first player trusts the second player the stake is tripled. However, the second player now has the power to divide all of the money (the tripled stake) as he or she wishes. The second player can either reciprocate the trust given by the first player by dividing the money relatively fair between him- or herself and the first player. Or the second player defects and keeps the profit, therefore giving nothing or only a small amount of the money back to the first player. Though there are many variations to the game, it usually involves a single transaction with an unknown other to avoid reputation effects.

Adolescents typically repay the trust a little less frequently than adults and children are the least trustworthy. Children may reciprocate in about 30 per cent of cases, and adolescents in 40 per cent of cases. The percentage stabilizes at around 50 per cent during early adulthood. This means that as adolescents get older, they more often take the perspective of the person dividing the money, and they become more prosocial – that is to say, more concerned about others. Possibly, they also get better at controlling the impulse to choose selfishly (van den Bos, Westenberg, Van Dijk, & Crone, 2010).

[Insert Figure 3 about here]

Dictator Game: In the Dictator Game (DG) there also are two players that receive a certain sum of money (see Figure 3). The first player decides how to split this amount of money. The second player does not have the ability to reject the offer made by the first player. In other words, the proposed division is always divided as the first player suggested. The DG is thought to capture an objective indication of fairness orientation of the first player because there are no strategies that play a role in the decision how to divide the sum of money (Van Dijk & Vermunt, 2000).

As it turns out, most people will give some money to the other person. They don't give necessarily half of their budget, but usually 20 to 30 per cent and keep the rest of the money for themselves. Children aged 8-10 years already do this. Children are inherently social from a young age; they also care about what other people get (Guroglu, van den Bos, & Crone, 2009).

The Ultimatum Game (UG) is an economic exchange game played by two players, a proposer and a responder (see Figure 3; Güth, Schmittberger, & Schwarze, 1982). The proposer receives a given sum of money, the stake, and is asked to share the stake by offering a certain amount of the stake to the responder. If the responder accepts the offer, both players keep the amount allocated by the proposer. However, if the responder rejects the offer, both players go empty-

handed. Based on economic rationality hypothesis (Von Neumann, & Morgenstern, 1953), one would expect that responders accept all offers higher than nothing to maximize their personal gain. However, responders reject most offers lower than 30% of the share and exhibit a strong preference for fair offers hovering around a 50-50 split (Van Dijk, & Vermunt, 2000). This, too, is seen in young children - it seems that the sense of fairness is ingrained very early on. However, the intentions of the person making the offer make a difference. You children take intentions into account less than adults, and adolescents respond to intentions more than children but less than adults (Guroglu et al., 2009).

Neuroscience findings have offered exciting new perspectives on fairness considerations, and the developmental changes across childhood and adolescence. Again, we argue that cognitive control is a very important component in these processes.

Development of fairness perspectives

ERP studies have shown that receiving unfair compared to fair offers in an UG is associated with larger FRN. In these studies the FRN was referred to as the MFN, however, for reasons of clarity we will refer to the FRN; Alexopoulos, Pfabigan, Lamm, Bauer, & Fishmeister, 2011; Boksem & De Cremer, 2010; Campanhã, Minati, Fregni, & Boggio, 2011; Polezzi et al., 2008; Van der Veen & Sahibdin, 2011; Wu, Zhou, van Dijk, Leliveld, & Zhou, 2011). The FRN not only differentiates between fair and unfair, also the level of unfairness and individual differences modulate the FRN. More specifically, the FRN is more pronounced for highly unfair offers than moderately unfair offers (Polezzi et al., 2008; Hewig et al., 2011; Van der Veen & Sahibdin, 2011). Individual differences analysis showed that especially participants with a high concern for fairness showed higher FRN responses to receiving unfair offers (Boksem & De Cremer, 2010).

Up until recently (ERP) research has mainly focused on what happens when someone receives an unfair offer. However, in daily life we also encounter situations in which we propose a fair deal but the other party does not accept this deal. In an ERP experiment Zanolie, de Cremer, Güroğlu, and Crone (2015) tested whether the rejection of a fair offer would show a larger FRN compared to the acceptance of a fair offer or rejection of an unfair offer. Participants of two age groups, mid-adolescents of 14-17 years old and early adults of 19-24 years old, played an adapted version of the UG with another (computer-simulated) player. The participant always was the proposer and played multiple rounds with the same other player, by making a choice between an unfair distribution (7 coins for proposer and 3 for responder; 7/3) and one of two alternatives: a fair distribution (5/5) or a hyperfair distribution (3/7). Zanolie et al. (2015) found that the rejection

of a fair offer (5/5; alternative was 7/3) was associated with a larger FRN compared to acceptance of a fair offer *and* rejection of an unfair offer (7/3; alternative was 3/7). The neural responses did not differ for the two age groups, suggesting that the FRN reacts as an alarm system to social prediction errors, which is already in place during mid-adolescence.

This developing preference for fairness over self-interest across childhood is thought to partly depend on the acquisition of perspective-taking abilities, enabling children to take another person's view (Harbaugh et al., 2003; Takagishi et al., 2010). This progressing ability to take the perspective of others, which is defined here as the ability to understand thoughts and intentions by others and willingness to act on this understanding, can subsequently result in the development of strategic behavior. In order to examine strategic behavior the Ultimatum Game (UG) and Dictator Game (DG) have been used by looking at the behavior of the proposer.

A prior neuroimaging study indeed examined the development of fairness considerations from the proposer perspective. In this study, children and adolescents between the ages 6 to 13 years played both the Dictator Game and the Ultimatum Game as a proposer. Given that the Ultimatum Game requires participants to think about possible rejections by the receiver (whereas this is not the case for the Dictator Game), the differences between offers in the Ultimatum Game and the Dictator Game was seen as an index of strategic behavior. The researchers reported that when entering adolescence (between ages 6 and 13 years), participants more often made strategic choices. Moreover, an increase in strategic offers was associated with more activity in the dorsal lateral prefrontal cortex (Steinbeis, Bernhardt, & Singer, 2012). The researchers interpreted this as that the dorsal lateral prefrontal cortex is important for the control of our impulse to be self-centered.

Interestingly, when a comparison is made between receiving an unfair offer and a fair offer in a classic Ultimatum Game, adolescents and adults showed stronger activity in the lateral prefrontal cortex when receiving unfair offers. Possibly, the older participants were better able to inhibit initial impulses to reject, and they may have thought more about the intentions why someone made an unfair offer (Steinmann et al., 2014).

Finally, an fMRI study that manipulated the intentions for proposing unfair offers found that the lateral prefrontal cortex was differentially activated across adolescent development when the other player had no option but proposing an unfair split. The adults activated the lateral PFC and the temporal parietal junction if the dividing player had no other option; however, young adolescents did not yet activate these brain areas. Adolescents are taking the other person's perspective more and more during this game, which requires you to consider what is good for

you and what is good for someone else. Also, they make more and more use of the prefrontal cortex, the area of the brain that is important in directing behavior.

Taken together, research that made us of social dilemma paradigms combined with EEG or fMRI recordings provided evidence that besides social brain regions, also regions that are typically associated with cognitive control (such as the dorsal medial PFC and lateral PFC) were activated. More interestingly, especially these regions showed developmental changes when making social decisions, suggesting that cognitive control development may explain at least part of the changes we observe in making social decisions.

Future Directions

This chapter aimed to provide a review of neuroscience methods to understand changes in the development of cognitive control. Moreover, we have tried to summarize how these changes are important for understanding cognitive development, but also affective and social development.

Given that these results are based on several different paradigms and methods, future studies should examine the role of cognitive control in a more detailed way, for example by specifically manipulating cognitive control demands (e.g., by having participants perform a working memory task while making social decisions), or by training cognitive control and test the effects on social-affective decision-making (Steinbeis et al., 2012).

Other directions for future studies will be by focusing more on the role of individual differences. In the studies described in this chapter we did not take these into account, but some studies have reported that for example social-economic status has an effect on the development of response inhibition (Spielberg et al., 2015).

Finally, an important direction for future studies will be to use longitudinal methods. This is commonly done in behavioral research, but only recently researchers have started to use these methods also in neuroimaging designs. This type of analyses will prove especially useful for fitting growth trajectories (Ordaz, Foran, Velanova, & Luna, 2013), but also for prediction analyses (Dumontheil & Klingberg, 2012).

Conclusion

The last two decades have resulted in tremendous progress in understanding the neural correlates of the development of cognitive control. These studies have found that, across late childhood and adolescence, individuals become better at keeping information in working memory, inhibiting ongoing behavior and adjust behavior according to changing environmental demands. Interestingly, these changes are accompanied by differential recruitment of regions in the prefrontal and parietal cortex. Many studies reported that activation in task-relevant brain regions in adults (those are brain regions that correlate with successful performance) become increasingly active when children develop into adults. These studies also show that children and adolescents often show activation in adjacent areas in prefrontal cortex and show a more diffuse pattern of activation. One way this can be explained is by the interactive specialization. This theory suggests that the role of certain cortical brain regions, and the way they respond to stimuli in the environment, is the result of interaction and competition between these regions, to acquire their roles. Some brain regions may have broad functionality early on in development and are partially activated in a wide range of functions. During development, activity-dependent interactions make cortical regions become more specialized with development (Johnson, 2011).

However, besides these cognitive changes, a key aspect of adolescence is social-reorientation. Adolescents become increasingly more independent from their parents and orient themselves towards their peers. It is a period in which friendships become more important and they start forming new complex networks of peers. In order to navigate complex social environments, adolescents need to develop their social competencies. Furthermore, adolescents often weigh short term and long-term outcomes differently than adults.

We have reviewed studies that have shown that when adults make these complex affective (e.g. weighing short and long term outcomes and social fairness considerations) decisions, they recruit regions that are often associated with cognitive control, such as the prefrontal cortex. Interestingly, these regions increasingly contribute to social-affective decision-making when children and adolescents grow up. Obviously, many other brain regions play a role in affective decision-making (such as the ventral striatum, for example) and in social decision-making (such as regions in the social brain network). Nonetheless, we have provided evidence that cognitive control is also very important in making social-affective choices, and both EEG and neuroimaging methods provide valuable methods to understand these contributions in more detail.

Definitions and Terms (Optional)

<u>Term</u>

> Definition

```
type="list"
```

List of Abbreviations

- dACC: dorsal Anterior Cingulate Cortex
- DG: Dictator Game
- ERP: Event-Related Potentials
- ERN: Error-Related Negativity
- DLPFC: dorsolateral prefrontal cortex
- FRN: Feedback-Related Negativity
- mPFC: medial prefrontal cortex
- PFC: Prefrontal cortex
- pre-SMA: pre-supplementary motor area
- TG: Trust Game
- UG: Ultimatum Game
- VLPFC: ventrolateral prefrontal cortex
- WCST: Wisconsin Card Sorting Task

References

Achterberg, M., Peper, J. S., Van Duijvenvoorde, A. C., Mandl, R. C., & Crone, E. A. (2016). Fronto-striatal white matter integrity predicts development in delay of gratification: a longitudinal study. *Journal of Neuroscience*.

Alexopoulos, J., Pfabigan, D. M., Lamm, C., Bauer, H., & Fischmeister, F. P. (2012). Do we care about the powerless third? An ERP study of the three-person ultimatum game. *Frontiers in Human Neuroscience, 6*, 59.

Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Review Neuroscience, 7*, 268–277.

Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences, 8*(4), 170-177.

Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2014). Inhibition and the right inferior frontal cortex: one decade on. *Trends in Cognitive Sciences, 18*(4), 177-185.

Baddeley, A.D., & Hitch, G. (1974). *Working memory.* In G.H. Bower (Ed.), *The psychology of learning and motivation: Advances in research and theory* (Vol. 8, pp. 47–89). New York: Academic Press.

Baddeley, A. D., & Logie, R. H., (1999). *Working memory: The multiple component model.* New York: Cambridge University Press.

Banich, M. T., De La Vega, A., Andrews-Hanna, J. R., Mackiewicz Seghete, K., Du, Y., & Claus, E. D. (2013). Developmental trends and individual differences in brain systems involved in intertemporal choice during adolescence. *Psychology of Addictive Behaviors, 27*(2), 416-430.

Barcelo, F., & Knight, R. T. (2002). Both random and perseverative errors underlie WCST deficits in prefrontal patients. *Neuropsychologia, 40*(3), 349-356.

Barrouillet, P. (1996). Transitive inferences from set-inclusion relations and working memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 22,* 1408-1422.

Bayliss, D. M., Jarrold, C., Baddeley, A. D. & Gunn, D. M. (2005). The relationship between short-term memory and working memory: Complex span made simple? *Memory, 13,* 414–421.

Berg, J., Dickhaut, J., & McCabe, K. (1995). Trust, reciprocity, and social history. *Games and Economic Behavior, 10,* 122–142.

Blakemore, S. J. (2008). The social brain in adolescence. Nature Review Neuroscience, 9, 267–277.

Blakemore, S. J., & Mills, K. L. (2014). Is adolescence a sensitive period for sociocultural processing? Annual Review of Psychology, 65, 187– 207.

Boksem, M. A., & De Cremer, D. (2010). Fairness concerns predict medial frontal negativity amplitude in ultimatum bargaining. *Social Neuroscience, 5*(1), 118-128.

Booth, J. R., Burman, D. D., Meyer, J. R., Lei, Z., Trommer, B. L., Davenport, N. D., et al. (2003). Neural development of selective attention and response inhibition. *NeuroImage, 20*(2), 737-751.

Brahmbhatt, S. B., White, D. A., & Barch, D. M. (2010). Developmental differences in sustained and transient activity underlying working memory. *Brain Research, 1354,* 140-151.

Bunge, S. A., Dudukovic, N. M., Thomason, M. E., Vaidya, C. J., & Gabrieli, J. D. (2002). Immature frontal lobe contributions to cognitive control in children: evidence from fMRI. *Neuron, 33*(2), 301-311.

Bunge, S. A., & Wright, S. B. (2007). Neurodevelopmental changes in working memory and cognitive control. *Current Opinion in Neurobiology, 17*, 243-250.

Campanhã, C., Minati, L., Fregni, F., & Boggio, P. S. (2011). Responding to unfair offers made by a friend: neuroelectrical activity changes in the anterior medial prefrontal cortex. *The Journal of Neuroscience, 31*, 15569-15574.

Casey, B. J. (2015). Beyond simple models of self-control to circuit-based accounts of adolescent behavior. *Annual Review of Psychology, 66*, 295-319.

Casey, B. J., Giedd, J. N., & Thomas, K. M. (2000). Structural and functional brain development and its relation to cognitive development. *Biological Psychology, 54*, 241 – 257.

Casey, B. J., Tottenham, N., Liston, C., & Durston, S. (2005). Imaging the developing brain: what have we learned about cognitive development? *Trends in Cognitive Sciences, 9*(3), 104-110.

Carter, C. S., & van Veen, V. (2007). Anterior cingulate cortex and conflict detection: An update of theory and data. *Cognitive, Affective, & Behavioral Neuroscience, 7*, 367–379.

Cauffman, E., Shulman, E. P., Steinberg, L., Claus, E., Banich, M. T., Graham, S., & Woolard, J. (2010). Age differences in affective decision making as indexed by performance on the Iowa Gambling Task. *Developmental Psychology, 46*(1), 193-207.

Christakou, A., Brammer, M., & Rubia, K. (2011). Maturation of limbic corticostriatal activation and connectivity associated with developmental changes in temporal discounting. *NeuroImage, 54*(2), 1344-1354.

Ciesielski, K. T., Lesnik, P. G., Savoy, R. L., Grant, E. P., & Ahlfors, S. P. (2006). Developmental neural networks in children performing a Categorical N-Back Task. *NeuroImage, 33*(3), 980-990.

Crone, E. A., & Dahl, R. E. (2012). Understanding adolescence as a period of social-affective engagement and goal flexibility. *Nature Reviews Neuroscience, 13*, 636–650.

Crone, E. A., Jennings, J. R., & Van der Molen, M. W. (2004). Developmental change in feedback processing as reflected by phasic heart rate changes. *Developmental Psychology, 40,* 1228–1238.

Crone, E. A., Ridderinkhof, K. R., Worm, M., Somsen, R. J. M., & Van der Molen (2004). Switching between spatial stimulus-response mappings: A developmental study of cognitive flexibility. *Developmental Science, 7*, 443-455.

Crone, E. A., Somsen, R. J., Zanolie, K., & Van der Molen, M. W. (2006). A heart rate analysis of developmental change in feedback processing and rule shifting from

childhood to early adulthood. *Journal of Experimental Child Psychology, 95*, 99–116.

Crone, E. A., & van der Molen, M. W. (2004). Developmental changes in real life decision making: performance on a gambling task previously shown to depend on the ventromedial prefrontal cortex. *Developmental Neuropsychology, 25*(3), 251-279.

Crone, E. A., Wendelken, C., Donohue, S., van Leijenhorst, L., & Bunge, S. A. (2006). Neurocognitive development of the ability to manipulate information in working memory. *Proceedings of the National Acadamy of Sciences of the United States of America, 103*(24), 9315-9320.

Crone, E. A., Zanolie, K., Van Leijenhorst, L., Westenberg, P. M., & Rombouts, S. A. R. B. (2008). Neural mechanisms supporting flexible performance adjustment during development. *Cognitive, Affective, & Behavioral Neuroscience, 8,* 165-177.

Crowley, M. J., Wu, J., Crutcher, C., Bailey, C. A., Lejuez, C. W., & Mayes, L. C. (2009). Risk-taking and the feedback negativity response to loss among at-risk adolescents. *Developmental Neuroscience, 31*, 137-148.

Crowley, M. J., Wu, J., Hommer, R. E., South, M., Molfese, P. J., Fearon, R. M. P., & Mayes, L. C. (2013). A developmental study of the feedback-related negativity from 10-17 years: Age and sex effects for reward versus non-reward. *Developmental Neuropsychology, 38*, 595-612.

Denny, B. T., Kober, H., Wager, T. D., & Ochsner, K. N. (2012). A meta-analysis of functional neuroimaging studies of self- and other judgments reveals a spatial gradient for mentalizing in medial prefrontal cortex. *Journal of Cognitive Neuroscience, 24*, 1742–1752.

D'Esposito, M., Postle, B. R., Ballard, D., & Lease, J. (1999). Maintenance versus manipulation of information held in working memory: an event-related fMRI study. *Brain and Cognition, 41*, 66–86.

D'Esposito, M., & Postle, B. R. (2015). The cognitive neuroscience of working memory. *Annual Review of Psychology, 66*, 115-142.

Diamond, A. (2002). Normal development of prefrontal cortex from birth to young adulthood: Cognitive functions, anatomy, and biochemistry. In D. T. Stuss & R. T. Knight (Eds.), Principles of frontal lobe function (pp. 466 – 503). New York: Oxford University Press.

Diamond, A. (2013). Executive functions. *Annual Review of Psychology, 64*, 135-168.

Dumontheil, I., Apperly, I. A., & Blakemore, S. J. (2010). Online usage of theory of mind continues to develop in late adolescence. *Developmental Science, 13,* 331-338.

Dumontheil, I., & Klingberg, T. (2012). Brain activity during a visuospatial working memory task predicts arithmetical performance 2 years later. *Cerebral Cortex, 22*(5), 1078-1085.

Durston, S., Davidson, M. C., Tottenham, N., Galvan, A., Spicer, J., Fossella, J. A., & Casey, B. J. (2006). A shift from diffuse to focal cortical activity with development. *Developmetal Science, 9*(1), 1-8.

Eppinger, B., Mock, B., & Kray, J. (2009). Developmental differences in learning and error processing: Evidence from ERPs. *Psychophysiology, 46,* 1043-1053.

Engle, R. W., Tuholski, S. W., Laughlin, J. E., & Conway, A. R. (1999). Working memory, short term memory, and general fluid intelligence: A latent variable approach. *Journal of Experimental Psychology: General, 128*, 309-331.

Flagan, T., & Beer, J. S. (2013). Three ways in which midline regions contribute to self-evaluation. *Frontiers in Human Neuroscience, 7*, 450.

Fareri, D. S., & Delgado, M. R. (2014). Differential reward responses during competition against in- and out-of-network others. Social Cognitive and Affective Neuroscience, 9, 412–420.

Foti, D., Weinberg, A., Dien, J., & Hajcak, G. (2011). Event-related potential activity in the basal ganglia differentiates rewards from nonrewards: Response to commentary. *Human Brain Mapping, 32*, 2267–2269.

Geier, C. F., Garver, K., Terwilliger, R., & Luna, B. (2009). Development of working memory maintenance. *Journal of Neurophysiology, 101*(1), 84-99.

Gentsch, A., Ullsperger, P., & Ullsperger, M. (2009). Dissociable medial frontal negativities from a common monitoring system for self-and externally caused failure of goal achievement. *NeuroImage, 47,* 2023-2030.

Giedd, J. N. (2004). Structural magnetic resonance imaging of the adolescent brain. *Annals of the New York Academy of Sciences, 1021,* 77-85.

Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., et al. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences USA, 101(21),* 8174-8179..

Gunther Moor, B. G., van Leijenhorst, L., Rombouts, S. A., Crone, E. A., & Van der Molen, M. W. (2010). Do you like me? Neural correlates of social evaluation and developmental trajectories. Social Neuroscience, 5, 461–482

Güroĝlu, B., van den Bos, W., & Crone, E. A. (2009). Fairness considerations: increasing understanding of intentionality during adolescence. *Journal of Experimental Child Psychology, 104*(4), 398-409.

Grammer, J. K., Carrasco, M., Gehring, W. J., & Morrison, F. J. (2014). Age-related changes in error processing in young children: A school based investigation. *Developmental Cognitive Neuroscience, 9C*, 93–105.

Güth, W., Schmittberger, R., & Schwarze, B. (1982). An experimental analysis of ultimatum bargaining. *Journal of Economic Behavior & Organization, 3*, 367.

Guyer, A. E., Choate, V. R., Pine, D. S., & Nelson, E. E. (2012). Neural circuitry underlying affective response to peer feedback in adolescence. *Social, Cognitive, & Affective Neuroscience, 7,* 81–92.

Hämmerer, D., & Eppinger, B. (2012). Dopaminergic and prefrontal contributions to reward-based learning and outcome monitoring during child development and aging. *Developmental Psychology, 48*, 862-874.

Hämmerer, D., Li, S-C, Müller, V., Lindenberger, U. (2010). Life span differences in electrophysiological correlates of monitoring gains and losses during probabilistic reinforcement learning. *Journal of Cognitive Neuroscience, 23,* 579-592.

Hajcak, G., Moser, J. S., Holroyd, C. B., & Simons, R. F. (2006). The feedback-related negativity reflects the binary evaluation of good versus bad outcomes. Biological Psychology, 71, 148–154.

Hester, R., Fassbender, C., & Garavan, H. (2004). Individual differences in error processing: A review and reanalusis of three event-related fMRI studies using the GO/NOGO task. *Cerebral Cortex, 14*, 986-994.

Hewig, J., Kretschmer, N., Trippe, R. H., Hecht, H., Coles, M., Holroyd, C. B., & Miltner, W. H. (2011). Why humans deviate from rational choice. *Psychophysiology, 48*, 507-514.

Hitch, G. J., Towse, J. N. & Hutton, U. (2001). What limits children's working memory span? Theoretical accounts and applications for scholastic development. *Journal of Experimental Psychology: General, 130,* 184–198.

Holroyd, C. B., Baker, T. E., Kerns, K. A., & Müller, U. (2008). Electrophysiological evidence of atypical motivation and reward processing in children with attention-deficit hyperactivity disorder. *Neuropsychologia, 46,* 2234-2242.

Holroyd, C. B., & Coles, M. G. (2002). The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychological Review, 109,* 679–709.

Holroyd, C. B., Nieuwenhuis, S., Yeung, N., Nystrom, L., Mars, R. B., Coles, M. G., & Cohen, J. D. (2004). Dorsal anterior cingulate cortex shows fMRI response to internal and external error signals. *Nature Neuroscience, 7,* 497–498.

Hooper, C. J., Luciana, M., Conklin, H. M., & Yarger, R. S. (2004). Adolescents' performance on the Iowa Gambling Task: implications for the development of decision making and ventromedial prefrontal cortex. *Developmental Psychology, 40*(6), 1148-1158.

Huettell, S. A., Song, A. W., & McCarthy, G. (2004). *Functional Magnetic Resonance Imaging, 3rd Edition*. Massachusetts USA: Sinauer Associates Inc.

Huizinga, M., Dolan, C. V., & van der Molen, M. W. (2006). Age-related change in executive function: Developmental trends and a latent variable analysis. *Neuropsychologia, 44,* 2017–2036

Johnson, M. H. (2011). Interactive specialization: a domain-general framework for human functional brain development? *Developmental Cognitive Neuroscience, 1*(1), 7-21.

Jolles, D. D., Kleibeuker, S. W., Rombouts, S. A., & Crone, E. A. (2011). Developmental differences in prefrontal activation during working memory maintenance and manipulation for different memory loads. *Developmental Science, 14*(4), 713-724.

Kerns, J. G., Cohen, J. D., MacDonald, A. W., III, Cho, R.Y., Stenger, V. A., & Carter, C. S. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Science, 303*, 1023–1026.

Klingberg, T. (2010). Training and plasticity of working memory. *Trends in Cognitive Sciences, 14*(7), 317-324.

Klingberg, T., Forssberg, H., & Westerberg, H. (2002). Increased brain activity in frontal and parietal cortex underlies the development of visuospatial working memory capacity during childhood. *Journal of Cognitive Neuroscience, 14*(1), 1-10.

Kwon, H., Reiss, A. L., & Menon, V. (2002). Neural basis of protracted developmental changes in visuo-spatial working memory. *Proceedings of the National Acadamy of Sciences of the United States of America, 99*(20), 13336-13341.

Ladouceur, C. D., Dahl, R. E., & Carter, C. S. (2007). Development of action monitoring through adolescence into adulthood: ERP and source localization. Developmental Science, 10, 874–891.

Lee, H. W., Lo, Y. H., Li, K. H., Sung, W. S., & Juan, C. H. (2015). The relationship between the development of response inhibition and intelligence in preschool children. *Frontiers in Psychology, 6*, 802.

Libertus, M. E., Brannon, E. M., & Pelphrey, K. A. (2009). Developmental changes in category-specific brain responses to numbers and letters in a working memory task. *NeuroImage, 44*(4), 1404-1414.

Luna, B., Padmanabhan, A., & O'Hearn, K. (2010). What has fMRI told us about the development of cognitive control through adolescence? *Brain and Cognition, 72*, 101-113.

McClure, S. M., Laibson, D. I., Loewenstein, G., & Cohen, J. D. (2004). Separate neural systems value immediate and delayed monetary rewards. *Science, 306*(5695), 503-507.

Owen, A. M., Evans, A. C., & Petrides, M. (1996). Evidence for a two-stage model of spatial working memory processing within the lateral forntal cortex: A positron emission tomography study. *Cerebral Cortex, 6*, 31–38.

Mills, K. L., Lalonde, F., Clasen, L. S., Giedd, J. N., & Blakemore, S. J. (2014). Developmental changes in the structure of the social brain in late childhood and adolescence. *Social, Cognitive, & Affective Neuroscience, 9*(1), 123-131.

Milner, B. (1963). Effects of different brain lesions on card sorting. *Archives of Neurology, 9*, 100-110.

Miyake, A., Friedman, N. P., Emerson, M. J., Witzki, A. H., Howerter, A., & Wager, T. D. (2000). The unity and diversity of executive functions and their contributions to complex "frontal lobe" tasks: A latent variable analysis. *Cognitive Psychology, 41*(1), 49–100.

O'Doherty, J. P. (2011). Contributions of the ventromedial prefrontal cortex to goal-directed action selection. *Annuals of the New York Academy of Sciences, 1239*, 118-129.

O'Hare, E. D., Lu, L. H., Houston, S. M., Bookheimer, S. Y., & Sowell, E. R. (2008). Neurodevelopmental changes in verbal working memory load-dependency: an fMRI investigation. *NeuroImage, 42*(4), 1678-1685.

Olson, E. A., Collins, P. F., Hooper, C. J., Muetzel, R., Lim, K. O., & Luciana, M. (2009). White matter integrity predicts delay discounting behavior in 9- to 23-year-olds: a diffusion tensor imaging study. *Journal of Cognitive Neuroscience, 21*(7), 1406-1421.

Ordaz, S. J., Foran, W., Velanova, K., & Luna, B. (2013). Longitudinal growth curves of brain function underlying inhibitory control through adolescence. *Journal of Neuroscience, 33*(46), 18109-18124.

Owen, A. M., McMillan, K. M., Laird, A. R., & Bullmore, E. (2005). N-back working memory paradigm: A meta-analysis of normative functional neuroimaging studies. *Human Brain Mapping, 25*, 46-59.

Peper, J. S., Mandl, R. C., Braams, B. R., de Water, E., Heijboer, A. C., Koolschijn, P. C., & Crone, E. A. (2013). Delay discounting and frontostriatal fiber tracts: a

combined DTI and MTR study on impulsive choices in healthy young adults. *Cerebral Cortex, 23*(7), 1695-1702.

Peters, S., Braams, B. R., Raijmakers, M. E., Koolschijn, P. C., & Crone, E. A. (2014). The neural coding of feedback learning across child and adolescent development. *Journal of Cognitive Neuroscience,26,* 1705-1720.

Polezzi, D., Daum, I., Rubaltelli, E., Lotto, L., Civai, C., Sartori, G., & Rumiati, R. (2008). Mentalizing in economic decision-making. *Behavioural Brain Research, 190*(2), 218-223.

Richardson, C., Anderson, M., Reid, C. L., & Fox, A. M. (2011). Neural indicators of error processing and intraindividual variability in reaction time in 7 and 9 year-olds. Developmental Psychobiology, 53, 256–265

Ridderinkhof, K. R., Ullsperger, M., Crone, E. A., & Nieuwenhuis, S. (2004). The role of the medial frontal cortex in cognitive control. *Science, 306*, 443–447.

Rilling, J. K., & Sanfey, A. G. (2011). The neuroscience of social decision-making. *Annual Review of Psychology, 62,* 23–48.

Rubia, K., Lim, L., Ecker, C., Halari, R., Giampietro, V., Simmons, A., et al. (2013). Effects of age and gender on neural networks of motor response inhibition: from adolescence to mid-adulthood. *NeuroImage, 83*, 690-703.

Rubia, K., Smith, A. B., Taylor, E., & Brammer, M. (2007). Linear age-correlated functional development of right inferior fronto-striato-cerebellar networks during response inhibition and anterior cingulate during error-related processes. *Human Brain Mapping, 28*(11), 1163-1177.

Rubia, K., Smith, A. B., Woolley, J., Nosarti, C., Heyman, I., Taylor, E., & Brammer, M. (2006). Progressive increase of frontostriatal brain activation from childhood to adulthood during event-related tasks of cognitive control. *Human Brain Mapping, 27*(12), 973-993.

Sakai, K., & Passingham, R. E. (2002). Prefrontal interactions reflect future task operations. *Nature Neuroscience, 6*, 75–81.

Santesso, D. L., Dzyundzyak, A., & Segalowitz, S. J. (2011). Age, sex and individual differences in punishment sensitivity: Factors influencing the feedback-related negativity. *Psychophysiology, 48,* 1481–1489.

Santesso, D. L., Segalowitz, S. J., & Schmidt, L. A. (2006). Error-related electrocortical responses in 10-year-old children and young adults. *Developmental Science, 9*, 473–481.

Satterthwaite, T. D., Wolf, D. H., Erus, G., Ruparel, K., Elliott, M. A., Gennatas, E. D., et al. (2013). Functional maturation of the executive system during adolescence. *The Journal of Neuroscience, 33*(41), 16249-16261.

Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people: The role of the temporo-parietal junction in "theory of mind". *NeuroImage, 19,* 1835–1842.

Schel, M. A., & Crone, E. A. (2013). Development of response inhibition in the context of relevant versus irrelevant emotions. *Frontiers in Psychology, 4*, 383.

Schel, M. A., Scheres, A., & Crone, E. A. (2014). New perspectives on self-control development: highlighting the role of intentional inhibition. *Neuropsychologia, 65*, 236-246.

Scherf, K. S., Sweeney, J. A., & Luna, B. (2006). Brain basis of developmental change in visuospatial working memory. *The Journal of Cognitive Neuroscience, 18*(7), 1045-1058.

Segalowitz, S. J., Santesso, D. L., & Jetha, M. K. (2010). Electrophysiological changes during adolescence: a review. *Brain and Cognition, 72*(1), 86-100.

Segalowitz, S. J., Santesso, D. L., Murphy, T. I., Homan, D., Chantziantoniou, D. K., & Khan, S. (2010). Retest reliability of medial frontal negativities during performance monitoring. *Psychophysiology, 47,* 260–270.

Shirtcliff, E. A., Dahl, R. E., & Pollak, S. D. (2009). Pubertal development: Corresponde nce between hormonal and physical development. *Child Development, 80*, 327-337.

Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science, 283,* 1657–1661.

Somerville, L. H., Heatherton, T. F., & Kelley, W. M. (2006). Anterior cingulate cortex responds differentially to expectancy violation and social rejection. Nature Neuroscience, 9, 1007–1008.

Sowell, E. R., Thompson, P. M., Leonard, C. M., Welcomes, S. E., Kan, E., & Toga, A. W. (2004). Longitudinal mapping of cortical thickness and brain growth in normal children. *Journal of Neuroscience, 24(38),* 8223-8231.

Spencer-Smith, M., Ritter, B. C., Murner-Lavanchy, I., El-Koussy, M., Steinlin, M., & Everts, R. (2013). Age, sex, and performance influence the visuospatial working memory network in childhood. *Developmental Neuropsychology, 38*(4), 236-255

Spielberg, J. M., Galarce, E. M., Ladouceur, C. D., McMakin, D. L., Olino, T. M., Forbes, E. E., . . . Dahl, R. E. (2015). Adolescent development of inhibition as a function of SES and gender: Converging evidence from behavior and fMRI. *Human Brain Mapping, 36*(8), 3194-3203

Steinbeis, N., Bernhardt, B. C., & Singer, T. (2012). Impulse control and underlying functions of the left DLPFC mediate age-related and age-independent individual differences in strategic social behavior. *Neuron, 73*(5), 1040-1051.

Steinbeis, N., Haushofer, J., Fehr, E., & Singer, T. (2016). Development of Behavioral Control and Associated vmPFC-DLPFC Connectivity Explains Children's Increased Resistance to Temptation in Intertemporal Choice. *Cerebral Cortex, 26*(1), 32-42.

Steinmann, E., Schmalor, A., Prehn-Kristensen, A., Wolff, S., Galka, A., Mohring, J., . . . Siniatchkin, M. (2014). Developmental changes of neuronal networks associated with strategic social decision-making. *Neuropsychologia, 56*, 37-46.

Swanson, H. L. (2004). Working memory and phonological processing as predictors of children's mathematical problem solving at different ages. *Memory and Cognition, 32*, 648–661.

Tamm, L., Menon, V., & Reiss, A. L. (2002). Maturation of brain function associated with response inhibition. *Journal of the American Academy of Child and Adolescent Psychiatry, 41*(10), 1231-1238.

Tamnes, C. K., Walhovd, K. B., Torstveit, M., Sells, V. T., & Fjell, A. M. (2013). Performance monitoring in children and adolescents: A review of developmental changes in the error-related negativity and brain maturation. *Developmental Cognitive Neuroscience, 6,* 1–13.

Torpey, D. C., Hajcak, G., Kim, J., Kujawa, A., & Klein, D. N. (2012). Electrocortical and behavioral measures of response monitoring in young children during a Go/No-Go task. *Developmental Psychobiology, 54*, 139–150.

Van der Veen, F. M., & Sahibdin, P. P. (2011). Dissociation between medial frontal negativity and cardiac responses in the ultimatum game: Effects of offer size and fairness. *Cognitive, Affective, & Behavioral Neuroscience, 11*, 516-525.

Van Dijk, E., & Vermunt, R. (2000). Strategy and fairness in social decision making: Sometimes it pays to be powerless. *Journal of Experimental Social Psychology, 36*, 1-25.

van den Bos, W., Guroglu, B., van den Bulk, B. G., Rombouts, S. A., & Crone, E. A. (2009). Better than expected or as bad as you thought? The neurocognitive development of probabilistic feedback processing. *Frontiers in Human Neuroscience, 3*, 52.

van den Bos, W., Rodriguez, C. A., Schweitzer, J. B., & McClure, S. M. (2014). Connectivity strength of dissociable striatal tracts predict individual differences in temporal discounting. *The Journal of Neuroscience, 34*(31), 10298-10310.

van den Bos, W., Rodriguez, C. A., Schweitzer, J. B., & McClure, S. M. (2015). Adolescent impatience decreases with increased frontostriatal connectivity. *Proceedings of the National Acadamy of Sciences of the United States of America, 112*(29), E3765-3774.

van den Bos, W., Westenberg, M., Van Dijk, E., & Crone, E. A. (2010). Development of trust and reciprocity in adolescence. *Cognitive Development, 25*, 90-102.

van den Wildenberg, W. P., & van der Molen, M. W. (2004). Developmental trends in simple and selective inhibition of compatible and incompatible responses. *Journal of Experimental Child Psychology, 87*(3), 201-220.

van Duijvenvoorde, A. C. K., Zanolie, K., Rombouts, S. A. R. B., Raijmakers, M., & Crone, E.A. (2008). Evaluating the negative or valuing the positive? Neural mechanisms supporting feedback-based learning across development. *The Journal of Neuroscience, 28,* 9495-9503.

van Meel, C. S., Heslenfeld, D. J., Rommelse, N. N., Oosterlaan, J., & Sergeant, J. A. (2012). Developmental trajectories of neural mechanisms supporting conflict and error processing in middle childhood. *Developmental Neuropsychology, 37,* 358–378.

van Meel, C. S., Oosterlaan, J., Heslenfeld, D. J., & Sergeant, J. A. (2005). Telling good from bad news: ADHD differentially affects processing of positive and negative feedback during guessing. *Neuropsychologia, 43,* 1946-1954.

van Noordt, S. J., & Segalowitz, S. J. (2012). Performance monitoring and the medial prefrontal cortex: A review of individual differences and context effects as a window on self-regulation. *Frontiers in Human Neuroscience, 6,* 197.

Vink, M., Zandbelt, B. B., Gladwin, T., Hillegers, M., Hoogendam, J. M., van den Wildenberg, W. P., et al. (2014). Frontostriatal activity and connectivity increase during proactive inhibition across adolescence and early adulthood. *Human Brain Mapping, 35*(9), 4415-4427

Von Neumann, J., & Morgenstern, O. (1953). *Theory of Games and Economic Behavior.* Princeton: Princeton University Press.

Van Overwalle, F. (2009). Social cognition and the brain: A meta-analysis. *Human Brain Mapping, 30,* 829–858.

Wager, T. D., & Smith, E. E. (2003). Neuroimaging studies of working memory. *Cognitive, Affective, & Behavioral Neuroscience. 3,* 255–274.

Wagner, A. D., Maril, A., Bjork, R. A., & Schacter, D. L. (2001). Prefrontal contributions to executive control: fMRI evidence for functional distinctions within lateral prefrontal cortex. *NeuroImage, 14,* 1337–1347.

Wellman, H. M., Cross, D., & Watson, J. (2001). Meta-analysis of theory-of-mind development: the truth about false belief. *Child Development, 72,* 655-684.

Wu, Y., Zhou, Y., van Dijk, E., Leliveld, M. C., & Zhou, X. (2011). Social comparison affects brein responses to fairness in asset division: an ERP study with the ultimatum game. *Frontiers in Human Neuroscience, 5,* 1-8.

Zanolie, K., De Cremer, D., Güroğlu, B., & Crone, E. A. (2015). Rejection in bargaining situations: An event-related potential study in adolescents and adults. *PLOS One, 10,* e0139953.

Zanolie, K., Teng, S., Donohue, S.E., Band, G.P.H., Rombouts, S.A.R.B., & Crone, E.A. (2008). Switching between colors and shapes on the basis of positive and negative feedback: An fMRI and EEG study on feedback-based learning. *Cortex, 44,* 537-547.

Zanolie, K., Van Leijenhorst, L., Rombouts, S., & Crone, E. (2008). Separable neural mechanisms contribute to feedback processing in a rule-learning task. *Neuropsychologia, 46*(1), 117-126.

Zottoli, T. M., & Grose-Fifer, J. (2012). The feedback-related negativity (FRN) in adolescents. *Psychophysiology, 49*, 413-420.
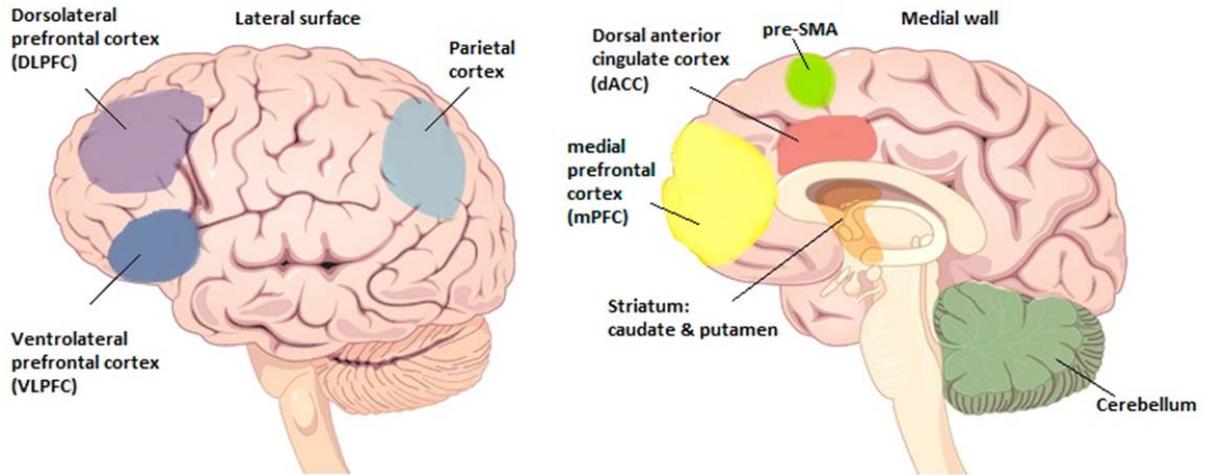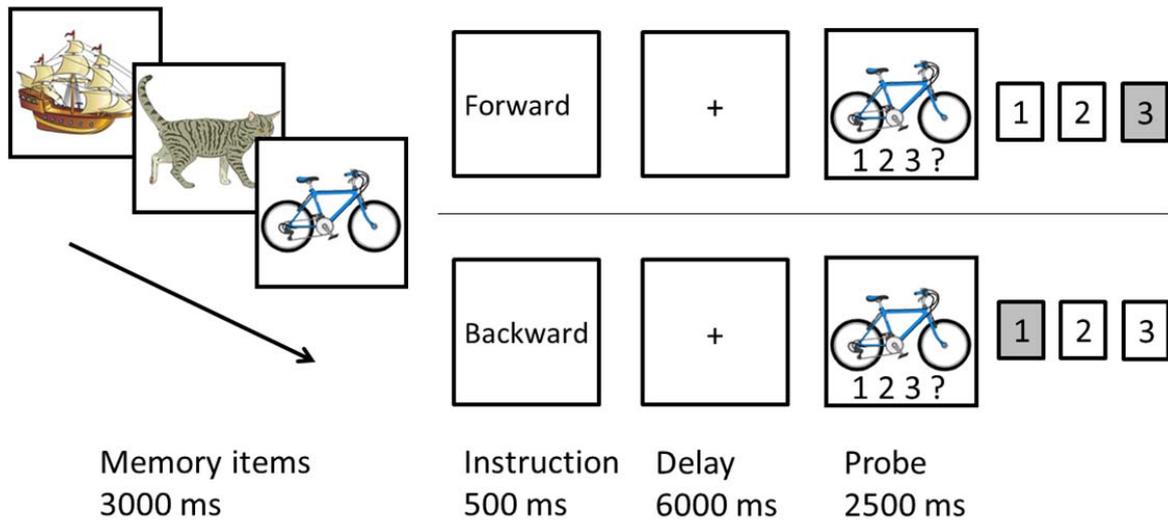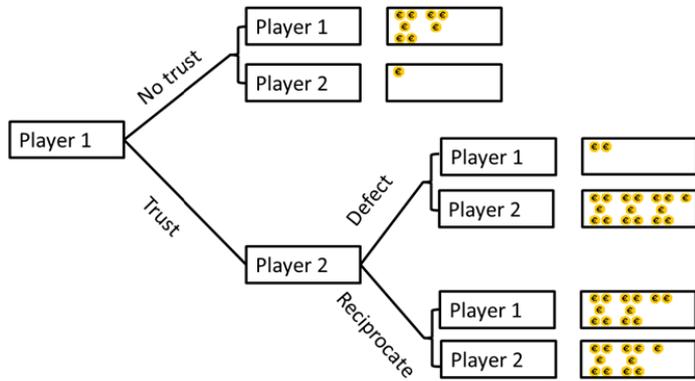
Figure 1.

Figure 2.
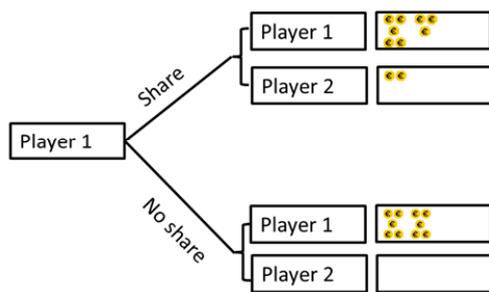

Memory items
3000 ms

Instruction
500 ms

Delay
6000 ms

Probe
2500 ms

Adapted from Crone et al., 2006

Figure 3.

Trust Game

Dictator Game

Ultimatum Game