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DEVELOPMENT OF RESPONSE INHIBITION AND DECISION-MAKING ACROSS CHILDHOOD : A COGNITIVE NEUROSCIENCE PERSPECTIVE

Wery P. M. van den Wildenberg*[1] *and Eveline A. Crone
Laboratory of Neurobiology and Cognition, CNRS and Université de Provence,
Marseille, France
Department of Psychology, Universiteit van Amsterdam, the Netherlands
Center for Mind and Brain, University of California, Davis, CA, USA

ABSTRACT

Recent advances within the field of neuroimaging and psychophysiological recording techniques have enabled the identification of key brain regions that contribute to developmental changes in cognitive control and decision-making. This chapter will focus on two influential paradigms in the field of experimental cognitive neuroscience that have contributed to our understanding of the nature of the increasing ability in children to control their own thoughts and actions as they grow older. The first section reviews the current cognitive developmental theories of behavioral inhibition. Response inhibition comes into play when prepotent, overlearned, or ongoing responses have to be suppressed in favor of executing an alternative response and is generally considered an important element of cognitive control and flexibility. These theories are supported by neuroimaging studies that identify the lateral prefrontal cortex as being relevant in tasks that require the on-line manipulation of information and the suppression of responses. The second part of this chapter provides an account of the development of cognitive processes involved in decision-making. Decision-making is required for a variety of behavior and often involves the consideration of multiple alternatives and reasoning about distant future consequences. According to the somatic-marker theory, the possible outcomes of a choice are mediated by emotions that are accompanied by anticipatory somatic activity. The theory underlying emotional self-regulation assigns an important role to the ventromedial prefrontal cortex. Finally, the examination of developmental changes in cognitive control functions from the perspective of cognitive neuroscience has also led to better characterizations of behavioral deficits found in disordered child populations.

1. INTRODUCTION

Cognitive developmental theories have provided important insight into developmental changes in children's hypothetical thought, organizational strategies, and the emerging ability to introspect and self-monitor, which underlie age-related improvements in a broad range of intellectual and social behaviors. However, remarkably little is known about cognitive and neurophysiological dimensions of childhood and adolescent maturational processes. This issue is starting to be an important drive for recent progress in the field of developmental science. That is, we are now starting to examine developmental changes in cognitive control functions from the perspective of cognitive neuroscience. This chapter aims to provide an overview of recent advances in the study of cognitive development across childhood from a cognitive neuroscience perspective. We describe studies that were inspired by an understanding of neural systems contributing to the development of cognitive control and complex decision-making. This unified approach has the potential to move cognitive developmental theories toward incorporating the effects that neural system interactions have on reasoning, self-monitoring, and decision-making. Additionally, this unification may lead to integrating our understanding of normal cognitive functions with disordered processes, observed, for example, in children with impulse control disorders (e.g., Attention-Deficit Hyperactivity-Disorder; AD/HD), and may lead to better characterizations of behavioral deficits found in disordered child populations.

In this chapter, we argue that the prefrontal cortex is a key brain region contributing to developmental changes in cognitive control and decision-making. The frontal lobes comprise a substantial area of the human brain, and there is evidence that these regions have reached their maximum size in humans compared to other organisms, therefore allowing for a greater complexity in intellectual abilities (Grafman, 1994). Moreover, this region of the brain is proposed to be the latest to fully develop, reaching full maturation only in adolescence (Casey et al., 1997; Dempster, 1993; Stuss, 1992; van der Molen and Ridderinkhof, 1998).

Recently, many neuroimaging studies have investigated processes that are relevant for cognitive control functions in adults, such as inhibition, manipulating complex information in memory, reward processing, guessing, and planning. These functions can be broadly captured under the umbrella's *inhibitory control* (also referred to as 'cold cognition') and *affective decision-making* (also referred to as 'hot cognition'). These studies emphasize the importance of the prefrontal cortex in higher cognitive processing, and also point out that this region may be fractionated according to separate subprocesses, reflected in distinct neural connectivity between prefrontal and other brain regions. The lateral prefrontal cortex, for example, appears to be relevant in motoric response inhibition, manipulating information on-line, considering options, and updating performance outcomes (Fletcher, Frith, and Rugg, 1997; Goel and Dolan, 2000; Goldberg, Podell, Harner, Riggio, and Lovell, 1994; Robin and Holyoak, 1995). The ventromedial prefrontal cortex, in contrast, is presumed to be involved in best-guess estimations, and emotional experience associated with gains and losses (Breitner, Aharon, Kahneman, Dale, and Shizgal, 2001; Elliott, Rees, and Dolan, 1999; Knutson, Westdorp, Kaiser, and Hommer, 2000; Rogers, et al., 1999). Studies of humans with ventromedial brain

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[1] Correspondence can be addressed to the first author at the CNRS - LNC, 31 chemin Joseph Aiguier, 13402 Marseille, cedex 20, France (e-mail: *wery@dds.nl*)

injury and neuroimaging studies indicate that this region is highly relevant for processing many types of reward and punishment, and making rapid changes in behavior to accommodate to environmental change. Both the lateral and ventromedial prefrontal cortex are thought to have close connections with the anterior cingulate cortex, which is involved in conflict processing and outcome relevant processing (Botvinick, Nystrom, Fissell, Carter, and Cohen, 1999; Carter et al., 1998).

This fractionation should not be taken to suggest that separate regions carry out functions in isolation, but rather that different areas of the prefrontal cortex appear to be engaged in separable neural systems involved in separable cognitive functions, while interacting with many other brain areas. Within this context, the goal of this chapter is to describe recent advances made in the investigation of developmental changes in subprocesses that rely on lateral prefrontal cortex, subserving inhibitory control, and the ventromedial prefrontal cortex, subserving affective decision-making).

2. DEVELOPMENT OF RESPONSE INHIBITION

2.1 Inhibition in Developmental Theories

In accounting for cognitive development, traditional theories have emphasized the role of changes in the capacity to store and process information (e.g., Case, 1985; Halford, 1993; Pascual-Leone, 1970). More recently, the concept of *inhibition* emerged from the literature (Howe and Pasnak, 1993) as a key construct in explaining cognitive development (Bjorklund and Harnishfeger, 1995; Dempster, 1993; van den Wildenberg and van der Molen, 2004; van der Molen, 2000). Moreover, deficient inhibition is central to current theories of childhood psychopathology (e.g., Barkley, 1997; Gray, 1987; Quay, 1997). Inhibitory control is postulated as an important mechanism that comes into play when the selected action has to compete for activation with strong alternatives. The general concept of inhibition appears in many different guises and is measured in many different ways and in many different experimental paradigms. Therefore, we propose the following working definition throughout this chapter. Inhibition is described as: “the mechanism or set of processes that result in the containment of prepotent behavioral responses when such actions are reflex-like, premature, inappropriate, or incorrect” (according to Burle, Vidal, Tandonnet, and Hasbroucq, 2002).

Within the field of developmental psychology, the term inhibition covers a variety of constructs that can be broadly divided into two categories (e.g., Smith, 1992). One cluster of theories refers to a form of hierarchical control in which a lower force is controlled (e.g., activated or inhibited) by a higher force. This top-down form of cognitive control is also referred to as “deliberate inhibition” (Logan, 1994). This notion seems central to Dempster’s theorizing that the resistance to interference contributes to diverse expressions of cognitive development (Dempster, 1993). His work is based on a synthesis of developmental research and neuropsychological research, both indicating that the frontal lobes are critically involved in interference-sensitive tasks. Dempster’s *susceptibility to interference model* emphasizes active suppression as a key construct and stresses the role of cognitive control functions that rely on prefrontal parts of the brain. An example taken from the cluster of developmental theories that denote inhibition as the competitive interaction between two processes rather than active suppression is the *inefficient inhibition model* (Bjorklund and Harnishfeger, 1995). This theory holds that inhibitory processes become more efficient during childhood. As a result, less irrelevant information enters working memory, thereby increasing its functional capacity. Processing efficiency is conceptualized here in terms of activation speed and inhibition, and inhibitory control is exerted as a process blocking the spread of activation (see a

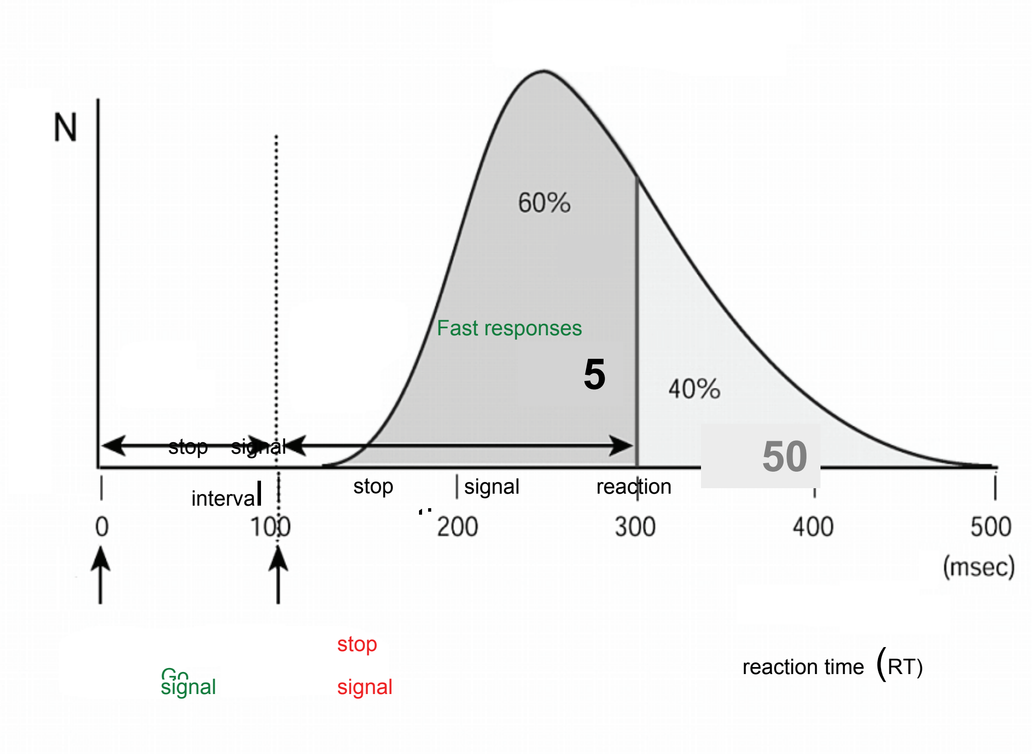


Figure 1. The estimation of stop-signal RT according to a race model (Logan and Cowan, 1984; Logan, 1994). The curve depicts the distribution of RTs on Go trials (trials without a stop signal) representing the finishing times of the response processes. Assuming independence of Go and stop processes, the finishing time of the stop process bisects the choice-RT distribution. Given that the button-press response could be withheld in 50% of all stop trials, stop-signal RT (200 ms) is calculated by subtracting mean stop-signal delay (100 ms) from the median choice RT (300 ms).

2.2 Measuring the Ability to Stop a Prepotent Motor Response: The Stop-Signal Paradigm

An influential paradigm that has been used successfully to investigate the development of inhibitory motor control is the *stop-signal procedure* (Lappin and Eriksen, 1966; Logan and Cowan, 1984; Ollman, 1973; for an overview see Logan, 1994). The stop-signal paradigm provides a useful tool to investigate the development of the covert cognitive processes that constitute inhibitory motor control. Conceptually, the type of inhibition manifested in the stop signal paradigm is one of several intentional acts of control that is required in many real-life situations, like stopping for a red traffic light, and that is exercised by a higher order executive system (e.g., Norman and Shallice, 1986). In the stop-signal paradigm, the participant usually performs a computerized choice reaction time (RT) task that requires the discrimination between two visual stimuli. For example, subjects may be instructed to press a response button with the left index finger to the presentation of a left-pointing arrow and to press another button with the right index finger to a right-pointing arrow. This primary RT task is referred to as the *Go task* and arrow signal are referred to as *Go signals*. During the execution of the Go task, a stop signal (usually a brief tone) is presented occasionally and unpredictably in a proportion, say 25%, of the trials. These trials are called *stop-signal trials*. The subject is instructed to put an effort into canceling his or her pending button-press response to the Go stimulus when faced with a stop signal. Usually, a staircase-tracking algorithm dynamically adjusts the timing of the stop-signal delay, that is, the interval between the presentation of the Go signal and the onset of the stop signal, working towards 50% successfully inhibited stop-signal trials (Levitt, 1971; Logan, Schachar, and Tannock, 1997). The advantage of the stop-signal paradigm is that it allows a precise measurement of the latency of the internally generated inhibitory process - *the stop-signal RT* - even though successful inhibition produces no overt behavior (see Figure 1).

2.2.1 Developmental Trends in Simple Inhibitory Control

The stop-signal RT as the dependent measure of inhibitory control has served developmental psychologists well. Developmental studies using the stop-signal paradigm have yielded evidence of age-related change in the speed of inhibitory processes. It has turned out that healthy young adults are able to stop whatever they are doing in about 200 to 250 ms, indicative of a very close control over their actions. Initially, studies that included children from different age groups failed to demonstrate clear systematic age-related changes in stop-signal inhibition (e.g., Band, van der Molen, Overtoom, and Verbaten, 2000; Jennings, van der Molen, Pelham, Brock, and Hoza, 1997; Oosterlaan, 1996; Schachar and Logan, 1990). However, Monte Carlo simulations suggested that these null findings can be explained through a lack of power, due to modest samples of subjects or insufficient experimental trials (Band, van der Molen, and Logan 2003).

More recent experimental studies were more successful in characterizing developmental changes in the ability to inhibit prepotent motor responses (e.g., Ridderinkhof, Band, and Logan, 1999; van den Wildenberg and van der Molen, 2004; Williams, Ponesse, Schachar, Logan, and Tannock, 1999). For example, Williams and colleagues (1999) used the stop task to examine the development of inhibitory control in a large sample that covered the life span. They reported a significant age-related change in stop-signal RT that decreased from 274 ms for 7-year-olds, and 223 ms for 10-year-olds, to 198 ms for 15-year olds, and 209 ms for young adults (see Figure 2). This significant developmental trend in stopping speed (i.e., the RT to stop signals) could be distinguished from the age-related change in response speed (i.e., the RT to Go signals), suggesting that different mechanisms are involved in stopping and executing a response (see also Ridderinkhof et al., 1999).

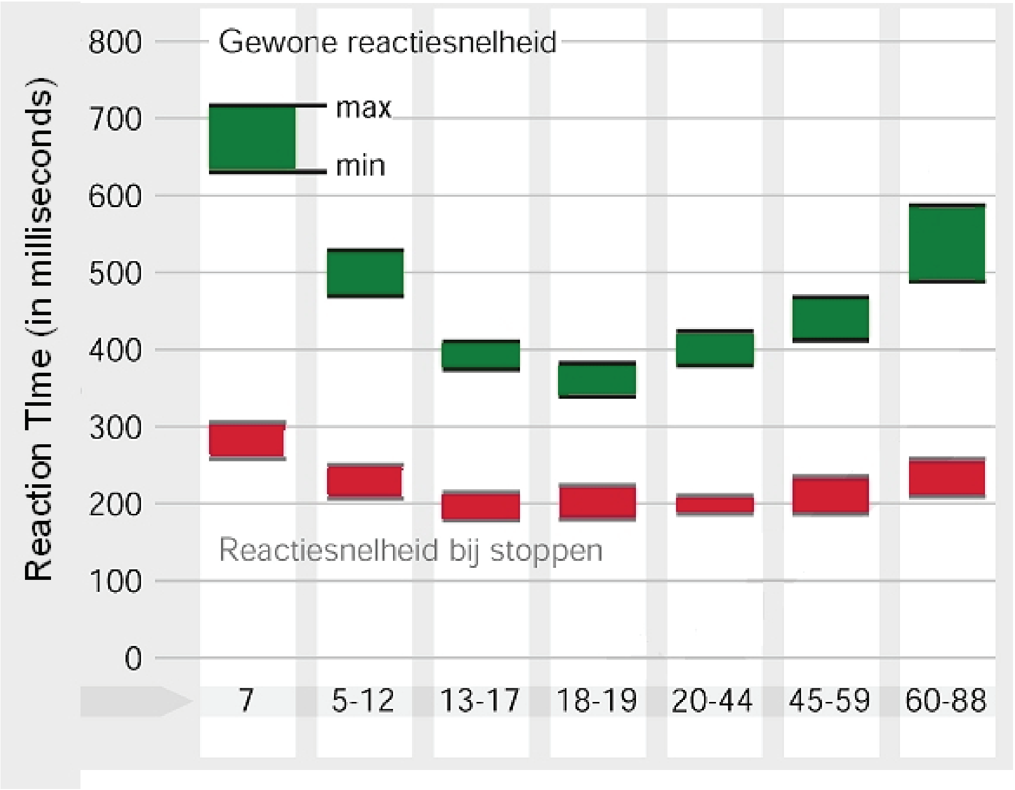


Figure 2. Depicted are the reaction times (RT) to the Go signal (green areas), representing the speed of executing a motor response, and the RT to the Stop signal (red areas), respresenting the time it takes to stop the motor response. As can be seen, the two cognitive processes follow distinct developmental trends. [Data reported by Williams et al., 1999].

2.2.2 Developmental Trends in Selective Inhibitory Control

The studies described above measured children's ability to abort ongoing action in a non-selective manner, also indicated as *simple inhibition*. In the typical stop task, the execution of whatever motor response had to be aborted whenever a stop signal was presented. Modifications of the standard stop-signal paradigm were used to track the development of more subtle manifestations of stopping control, dubbed *selective inhibition* (Logan, 1994). For example, the stop process has been made more complex at the perceptual end by requiring discrimination between two or more stop signals. Bedard and colleagues were the first to examine the development of selective inhibition by manipulating the perceptual component of stop-signal processing by adding a second stop tone to the typical stop-signal task (Bedard et al., 2002). Their subjects, in the range of 6 to 82 years of age, were instructed to inhibit the planned motor response if presented with the valid stop signal (e.g., the high-pitched tone) but not to the invalid signal (e.g., the low-pitched tone). Again, like in the simple stopping experiments by Williams and colleagues (1999), there was a marked development throughout the life span in the execution of go responses. Specifically, response speed increased throughout childhood (see also Cerella and Hale, 1994; Kail, 1991; 1993).

First, they observed that selective stopping gets faster with increasing age throughout childhood. That is, stop-signal RT speeded up from 456 ms in early childhood (6-8 years) and 336 ms in middle childhood (9-12 years) to 261 ms in adolescence (13-17 years) to 248 ms in young-adulthood (18-29 years). Again, the developmental trends in selective inhibitory control were unique and differed from the developmental trends in the ability to execute an overt response. Typically, selective stopping latencies are substantially longer than simple stopping latencies, because of the inclusion of the additional cognitive processing involved in decision "to stop or not to stop".

2.2.3 Further Specification of Developmental Trends

Van den Wildenberg and van der Molen (2004) conducted a developmental experiment in which they directly compared selective inhibitory control as measured by the selective stop-signal task with simple (nonselective) inhibitory control. In the simple stop condition, a button-press response indicated by the direction of an arrow had to be stopped on some trials if both flanking squares turned red (see Figure 3). The selective stop condition differed from the selective stop task used by Bedard et al., who focused on perceptually defined selective inhibitory control that required discrimination between auditory tones. Instead, the task used by van den Wildenberg and van der Molen draws upon motor-based selective inhibitory control by requiring the selection of the appropriate motoric response. The stop signal in the selective condition required the inhibition of the response, but only if the stop signal was presented at the same side as the instructed response to the go signal (see Figure 3).

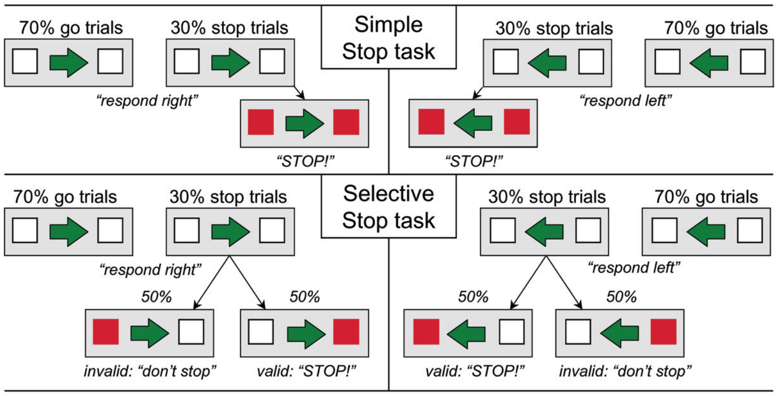


Figure 3. Schematic of the trial structures in the simple stop and the selective stop conditions used by van den Wildenberg and van der Molen (2004). The Go task in the simple and selective stop was to issue a button-press response with the hand indicated by the direction of the green arrow. In the simple stop task, participants were instructed to stop their response to the arrow if the two squares turned red. In the selective stop task, participants inhibited their response to valid stop signals but not to invalid stop signals (see text for further details).

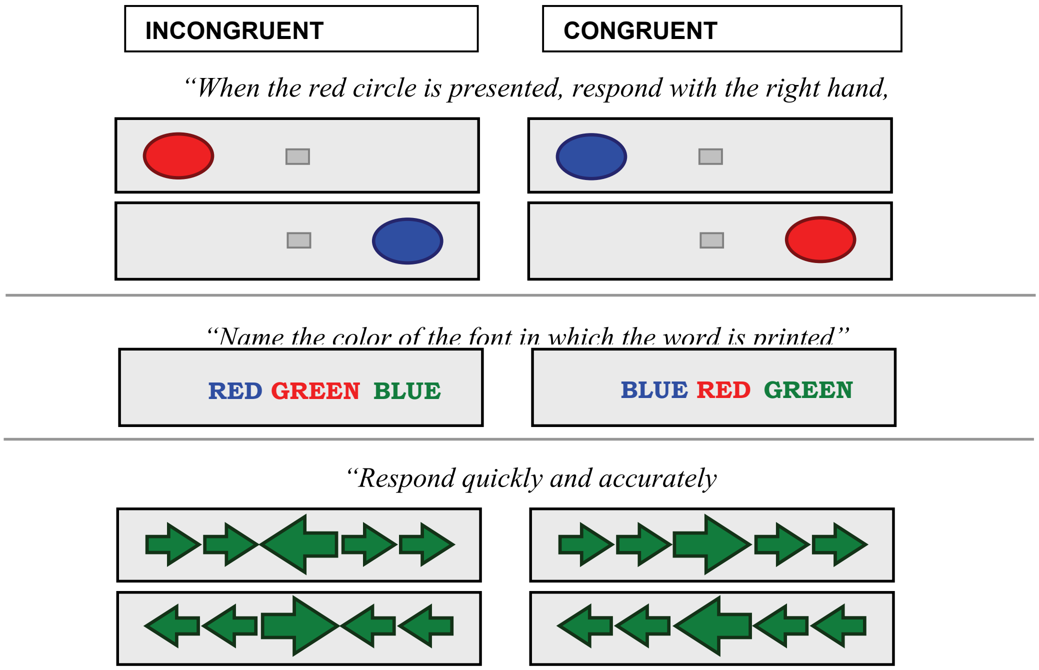
First, their simple stop results replicated the findings reported in previous developmental studies showing that the speed of simple inhibition improved throughout childhood (Ridderinkhof et al., 1999; Williams et al., 1999). The speed of simple inhibition increased from 275 ms in 7-year-olds, to 248 ms in 10-year-olds, to 207 ms in young adults. Second, the results of the selective stopping task showed that the speed of selective inhibition increased with advancing age. Selective stop-signal RTs decreased from 327 ms in the 7-year-olds, to 300 ms in the 10-year-olds, to 237 ms in the young adult group. It should be noted that Bedard and colleagues (2002) found a larger change in stop-signal RTs between ages 7 and 9 to 12 years and found a smaller change between ages 9 to 12 and 22 years, precisely the opposite of the pattern observed by van den Wildenberg and van der Molen. The apparent discrepancy is most likely due to a difference in design. Bedard and colleagues manipulated perceptual processes related to selective inhibition, instructing participants to discriminate between two auditory stop signals. The relatively small difference in selective stopping speed that they observed between ages 9 to 12 and 22 years seems to suggest that inhibition processes drawing on perceptual processes reach mature levels during adolescence. In contrast, the experimental design employed in the current study focused on response-related processes involved in selective stopping, as participants were required to base their stopping response on the mapping between the stop signal and the go response. Apparently, inhibitory control drawing on response-related processes develops relatively late, that is, beyond adolescence. Third, and most importantly, analyses of shared variance indicated that, even after removing the age-related change in simple stopping speed, the developmental trend in selective stopping speed continued to explain a significant proportion of the variance. This finding suggests distinct developmental trends in the speed of selective stopping versus simple stopping.

2.2.4 Maturation of Neural Substrates Underlying Response Inhibition

Developmental neuroimaging studies suggest that similar brain circuitry is recruited in children and adults during performance of inhibition tasks, but the magnitude of activity is typically greater and more diffuse in children relative to adults (Casey, Davidson, and Rosen, 2002; see Casey, Giedd, and Thomas, 2000 for overviews). Casey et al. (1997) performed one of the first studies examining development of inhibitory control using fMRI. They found that inhibitory processes in a go/nogo task were associated with increased activation that was distributed across both dorsolateral and orbitofrontal cortices, and the volume of activation was significantly greater for children relative to adults. Similarly, Tamm, Menon, and Reiss (2002) found that performance on a go/nogo task was positively associated with age in the left interior frontal gyrus, insula, orbitofrontal gyrus, and negatively in the left middle/superior frontal gyri. These results suggest that children activate discrete regions of the prefrontal cortex more extensively than adults, whereas adults show increased focal activation in specific regions associated with response inhibition. Using an oculomotor response-suppression task, Luna et al. (2001) reported increased activation in frontal, parietal, striatal, and thalamic regions when inhibition was required, and prefrontal activation was more active in adolescents than in children or adults. These results were interpreted suggesting that efficient modulation of reflective acts might not be fully developed until adulthood.

2.3 The Ability to Resist Interfering Response Activation - Conflict Tasks

The above-mentioned studies focused on developmental changes in motor inhibition. Another aspect of the construct of inhibition comes into play in tasks that study interference control or response conflict; the so-called conflict tasks. For matters of clarity, we will refer to this inhibition of irrelevant information as interference suppression, to distinguish it from motor inhibition. Various experimental paradigms have been designed to investigate response suppression. For instance, suppression of irrelevant information is often thought to be invoked in conflict tasks, such as the Stoop task, the Simon task, and the Eriksen Flanker tasks (see Figure 4).



"When the red circle is presented, respond with the right hand,

"Name the color of the font in which the word is printed"

"Respond quickly and accurately

Figure 4. Signal displays in the Simon conflict task (upper display), the Stoop task (middle display), and the Eriksen flanker task (lower display). The dependent measure is the difference in RT between responses to incongruent trials (to the left) and congruent trials (to the right).

2.3.1. The Simon Conflict Task

The Simon task makes use of the general finding that, in choice reaction tasks, RT is shorter and error rate lower when the position of the signal corresponds to the position of the required response, even if the position of the stimulus is completely irrelevant for the task. For example, when subjects have to issue a right hand response to a green signal (and a left hand response to a red signal), RT is generally shorter on congruent trials with a green signal appearing on the right of fixation than on incongruent trials with a green signal appearing on the left (Figure 4, upper display). Although subjects are instructed to respond as a function of the stimulus color (relevant stimulus dimension), the position of the signal, entirely irrelevant, affects response speed. The RT difference between congruent and incongruent responses is often termed the Simon effect (Hedge and Marsh, 1975; see Simon, 1990 for a review). Developmental studies with the Simon task are scarce.

2.3.2 The Stroop Task

The Stroop task (Stroop, 1935) requires subjects to name the font color of color words (e.g., ‘red’) that are printed in an incongruent color ink (e.g., blue). Reading the word interferes with naming the color, inference that should be suppressed. This induces a conflict between the tendency to read the color word and the actual task of naming the color of the font (see Figure 4, middle display). This conflict is characterized by slower responses to incongruent color-ink words than to congruent or neutral color-ink words. Early behavioral studies indicated that Stroop interference declines during development, which could be taken to indicate maturation of cognitive control functions like the ability suppress processing of task-irrelevant information (Comalli, Wapner, and Werner, 1962; Daniel, Pelotte, and Lewis, 2000; Schiller, 1966).

Adleman et al. (2002) report a positive correlation between age and Stroop-related interference activation in the left lateral prefrontal cortex, the left anterior cingulate, and the left parietal and parieto-occipital cortices. A recent developmental study recorded brain activity during Stroop task performance in different age groups with a technique called functional near-infrared spectroscopy, or fNIRS (Schroeter, Zysset, Wahl, and von Cramon, 2004). Analyses of mean RT revealed that the ability to suppress the automatic tendency to read the color word improved gradually from childhood (aged 7-13) to adolescence (ranged 19-29 years old). This finding suggests that young children have more difficulty than young adults in suppressing response activation that comes from task-irrelevant information in the environment. This behavioral difference was further related to an increase in brain activation to Stroop interference that was most pronounced in the dorsolateral prefrontal cortex (Schroeter et al., 2004), suggesting that the development of interference control as measured by Stroop task relies on the development of frontal brain structures.

2.3.3 The Eriksen Flanker Task

Finally, in the Eriksen flanker task the designated response is indicated by one aspect of the stimulus display. Additionally, other aspects of the stimulus display may elicit competing response tendencies, even if these are to be ignored (Eriksen and Eriksen, 1974). The typical observation is that responses are slowed when to-be-ignored stimulus features are associated with the response opposite to (rather than the same response as) the response assigned to the target stimulus feature. For instance, in the arrow version of the Eriksen the subject’s task is to execute a discriminative response according to the direction of a central target arrow, and to ignore flanking arrows (Figure 4, lower display). Responses are typically slowed in incongruent trials, that is, when the flanking arrows point in the direction opposite to, rather than in the same direction as the target arrow, as in congruent trials. Developmental studies by Ridderinkhof et al., (1999) and by Bunge, Dudukovic, Thomason, Vaidya, and Gabrieli (2002) used the Eriksen task and showed that children were more susceptible to interference from the environment than were adults. During task performance, Bunge and colleagues (2004) measured brain activity using functional Magnetic Resonance Imaging (fMRI). They showed that during interference suppression, 8-12-year-old children and adults both recruit the lateral prefrontal cortex. However, in adults this activation was associated with the right hemisphere, whereas in children activity was apparent in the left hemisphere. Both age groups exhibited brain-behavior correlations for homologous areas in the right and left hemisphere, respectively. A subset of children whose flanker-task performance was as good as adults (i.e., the best performers) still recruited left lateral prefrontal cortex, showing that this effect was not associated with performance differences, but rather reflects a qualitatively different recruitment of prefrontal cortex. These findings relate brain functions with cognitive abilities in children, indicating that the development of the ability to suppress interference is associated with differential recruitment of the prefrontal cortex (Dempster, 1993; Goldman-Rakic, 1987).

2.4 Deficient Inhibition and Childhood Pathology: AD/HD

As mentioned in the introduction, deficient inhibition is central in current theories of childhood psychopathology. This section focuses on attention deficit hyperactivity disorder (AD/HD), which is among the most prevalent and most extensively studied childhood pathologies. Mainstream theories of neurocognitive deficits associated with AD/HD currently focus on the role of impulsivity and response inhibition (e.g., Aron and Poldrack, 2005; Barkley, 1997; Nigg, 2001). A vast number of clinical applications of the stop-signal paradigm, described earlier, showed that children diagnosed with AD/HD exhibited slower stopping latencies than children diagnosed with other psychopathologies and normal control children (Jennings et al., 1997; Oosterlaan, Logan, and Sergeant, 1998; Oosterlaan and Sergeant, 1995; Overtoom et al., 2002; Schachar and Logan, 1990; for reviews of AD/HD studies with the stop-signal paradigm see Nigg, 2001). Next to distinguishing between groups like AD/HD versus non-pathological controls, stop-signal RT has been reported to discriminate AD/HD children tested under different conditions. Stopping latencies improved after administration of the stimulant drug *methylphenidate* (also known as Ritalin®) compared with administration of a placebo in children with AD/HD (Tannock, Schachar, Carr, Chajczyk, and Logan, 1989).

Ridderinkhof, Scheres, Oosterlaan, and Sergeant (2005) have presented an original approach to the study of cognitive deficits, particularly deficient response suppression, typically associated with AD/HD. They compared RT performance of children diagnosed with AD/HD with that of age-matched controls on an arrow version of the Eriksen flanker task. The principal distributional technique used is a graphical representation known as “the delta-plot”, showing the magnitude of interference effects as a function of response speed (see also Ridderinkhof, van den Wildenberg, Wijnen, and Burle, 2004). In the Eriksen task, the interference effect is defined as the difference between RTs to incongruent and congruent trials. The slope of the delta plot visualizes the time-course of response suppression. The slopes between quantile points turn from positive to more negative relatively late when response suppression is relatively weak, and progressively earlier when the suppression is stronger. The delta plots obtained by Ridderinkhof et al. (2005) showed that in AD/HD, the slopes of especially the slower segments of delta plots for RT were more negative-going for controls than for children with AD/HD, suggesting that response inhibition in the latter group is slower to operate (see Figure 5). These observations are in line with current mainstream theories that hypothesized AD/HD to involve a response-inhibition deficit (e.g., Barkley 1997; Nigg, 2001).

Complementary to the above-mentioned behavioral studies, Casey et al. (1997) found that the volume of the right frontal cortex correlated with behavioral measures of response inhibition in AD/HD children. Recent imaging studies linked deficits in inhibitory motor control to significant reduction in the right inferior prefrontal cortex (Durston et al., 2004). These fMRI studies are paralleled by studies using the electroencephalogram (EEG) to show that the amplitude of the N2, a component hypothesized to be a marker of behavioral inhibition, is significantly attenuated in AD/HD (Pliszka et al., 2000). Summarizing, several sources of evidence are consistent with the notion that deficits in response inhibition seen in AD/HD are related to functional and volumetric changes in the right inferior frontal cortex (see also Aron and Poldrack, 2005).

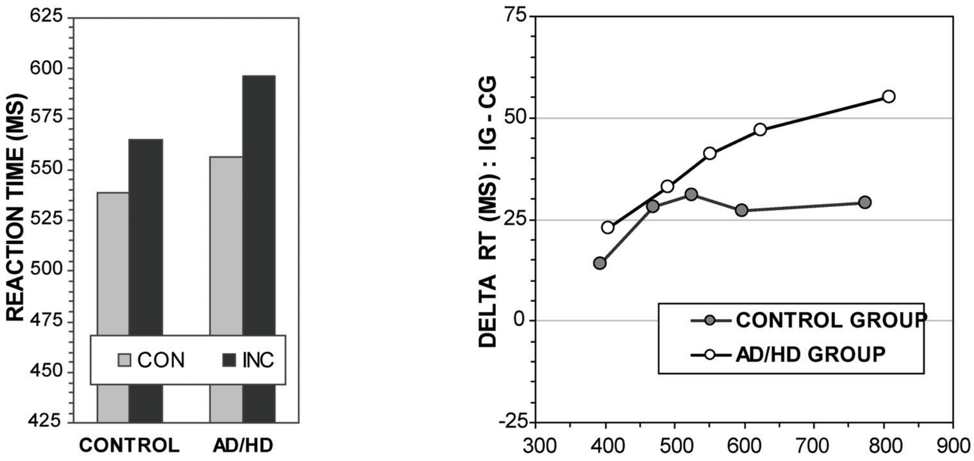


Figure 5. The left panel shows the overall RTs on congruent (CON) and incongruent (INC) task blocks for both AD/HD and control groups. The right panel displays the effect size (i.e., the magnitude of the flanker congruence effect) as a function of response speed as expressed in RT quintile score. Most importantly, the delta slopes diverge in the later segments of the RT distribution, with more-negative going slopes in the control group. This observation has been taken to suggest deficient suppression of activation elicited by irrelevant information in children with AD/HD.

Note. Adopted from, and with kind permission from, K. R. Ridderinkhof (2005).

3. DEVELOPMENT OF DECISION-MAKING

3.1 The Somatic Marker Hypothesis

For a long time, developmental research of cognitive control functions only focused on ‘cold cognition’, including developmental changes in inhibitory control and working memory. Recently, however, there is an increased interest in developmental changes in affective decision-making processes in both infancy and childhood. These studies were inspired by Damasio’s somatic marker hypothesis (1994), which is based on patient studies indicating that the ventromedial prefrontal cortex is important for forming relations between somatic responses associated with previously learned outcomes of situations and the reinstatement of these somatic states when a resembling decision has to be made. These associations hold the potential to reactivate an emotion by acting on the appropriate cortical or sub-cortical structures and become highly relevant in situations where future outcomes cannot be easily predicted on the basis of logical cost-benefit comparisons.

Given a certain situation, the ventromedial prefrontal cortex establishes a simple linkage between the aspects of the situation and the disposition for the type of emotion that in the past has been associated with the situation. The somatic markers normally help constrain the decision-making space by making that space manageable for logic-based cost-benefit analyses. Such constraints help an individual to decide efficiently in situations in which there is uncertainty about future outcomes. However, in the absence of somatic markers, options and outcomes become virtually equalized and the process of choosing will depend entirely on logic operations over many option-outcome pairs. This strategy is slow and may fail to take into account previous experience, and is often seen in ventromedial patients, who tend to engage in random and impulsive decision-making.

3.2 Measuring Decision-Making : The Iowa Card Gambling Task

The Iowa Card Gambling Task has been used as a test for assessing somatic markers that are experienced in real-life situations (Bechara, Damasio, Damasio, and Anderson, 1994). That is, the task resembles real-life in the way it factors reward, punishment, and uncertainty about future outcomes. The participant's task is to pick cards from four options; two options are followed by a high reward and, unpredictably, an even higher loss (disadvantageous options) and two other options are followed by a small reward but the unpredictable loss is also small (advantageous options). The participant should learn to differentiate between disadvantageous and advantageous choices. An important aspect of the task is that participants should use the outcome of their decisions to adjust their strategy. Interestingly, previous studies showed that besides immediate somatic responses following reward and loss, intact individuals develop anticipatory somatic "warning" markers preceding disadvantageous choices. This warning signal is missing for patients who have damage to the ventromedial prefrontal region (Bechara, Tranel, Damasio and Damasio, 1996).

3.2.1 Behavioral Studies

In a series of studies, Crone and colleagues (Crone, Vendel, and van der Molen, 2003; Crone and van der Molen, 2004; Crone, Bunge, Latenstein, and van der Molen, in press) showed that children's performance on a child version of the Iowa Gambling Task (the Hungry Donkey Task) resembled performance of patients with ventromedial prefrontal damage (see also Hooper, Luciana, Conklin, and Yarger, 2004; Overman, 2004). They examined children between the ages of 6 to 18 and consistently reported a pronounced developmental increase in the ability to learn to differentiate between disadvantageous and advantageous choices. Given that the task is complex, they considered the contribution of inductive reasoning, inhibitory control and working memory in the process of affective decision-making, but none of these functions could explain the developmental changes observed on the Hungry Donkey Task. Interestingly, however, in one study Crone et al. (in press) manipulated both the number of choice options as well as the frequency with which loss were given. The most important results from this study were that children as young as six years old were able to dissociate between disadvantageous and advantageous choices when the frequency with which delayed punishment was given was high, independent of whether the task included two or four response options. When the delayed punishment was infrequently given (but high in magnitude), children kept preferring the disadvantageous choices, also when there were only two choice options. Together, these results were interpreted to suggest that children's performance resembles that of patients with ventromedial prefrontal damage, and their decision-making impairment is most prominent when there is high uncertainty about future outcomes. This interpretation is consistent with Damasio's somatic marker hypothesis, suggesting that somatic markers are most relevant when the decision-making space is large. Similar results have been reported in studies focusing on 3-4-year olds and 3-6-year-olds (Garon and Moore, 2004; Kerr and Zelazo, 2004), suggesting that developmental changes in affective decision-making are already prominent during infancy.

3.2.2 Imaging Studies

To date, only two studies have examined the neural aspects of developmental changes in decision-making, and these studies both focused on changes during adolescence. May et al. (2004) reported that adolescents and adults recruit similar brain regions in a guessing game, including ventrolateral and medial prefrontal cortex. These regions were more active when participants received reward compared to punishment feedback. Bjork et al. (2004) reported similar findings, showing that adolescents and young adults do not differ in neural responses to positive and negative feedback. Interestingly, this study reported a strong relation between age and *anticipatory* neural activity in ventral striatum, insula, dorsal thalamus, and dorsal midbrain when participants prepared for a risky gamble. These results are largely consistent with the somatic marker hypothesis, which states that decision-making impairments in patients with ventromedial prefrontal damage are associated with reduced somatic activity when anticipating a risky decision, rather than deficient outcome processing. In an unpublished study, Crone et al. (2005) found that children and adolescents do not differ in autonomic activity (heart rate and skin conductance) when receiving punishment, but children showed reduced autonomic responses in preparation of a risky decision in comparison to adolescents. Thus, developmental changes in decision-making may be associated with reduced anticipatory warning signals before making a high-risk decision, as evidenced by reduced autonomic activity (Crone et al., 2005) and reduced neural activity in reward-associated brain regions (Bjork et al., 2004).

4. CONCLUSION

We examined two aspects of cognitive control development, inhibitory control, purportedly mediated by the lateral prefrontal cortex, and affective decision-making, purportedly mediated by the ventromedial prefrontal cortex. Both domains of control do not reach adult levels of performance until middle childhood, suggesting protracted maturation of brain regions associated with these functions.

Obviously, the parallelism proposed between brain maturation and developmental changes in performance on tasks presumed to rely on these regions can be readily criticized. For example, many studies do not measure direct brain activity, and the studies presented were largely cross-sectional. However, the perspectives derived from this research are supported by new approaches that were previously applicable only to adults and that have begun to be available for the study of how brain development and behavior change with growth and experience. Using functional MRI, researchers have become able to trace behavior-related changes in cortical areas (see Casey, 2002). By integrating these new noninvasive methods with techniques from developmental cognitive neuroscience, it is now possible to begin systematic research programs to directly test hypotheses of neurodevelopment.

One of the avenues taken in this chapter is to describe developmental changes in processes presumed to rely on prefrontal cortex in terms of the experimentally controlled subfunctions, instead of using complex neuropsychological tasks based on patient literature. Previous studies examining the development of prefrontal functioning typically used complex tasks (such as the Wisconsin Card Sorting Task) and used different measures to describe developmental changes. One of the major virtues of decomposing functions of the prefrontal cortex is that this method may allow assessment of each function in terms of its anatomical basis and psychophysiological manifestation. With the reviewed experimental paradigms as a basis, this future line of research is expected to increase our understanding of the development and functional role of cognitive control and decision-making systems and to identify the neural substrates potentially involved in pathophysiology of impulse disorders.

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