

Chapter 24

The neural correlates of cognitive control and the development of social behavior

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This chapter reviews the extant literature on the neural correlates of cognitive control across development, with an emphasis on relations to social behavior, motivation, and individual differences. Increasingly, researchers have sought to identify the subprocesses that make up cognitive control, with “monitoring” and “control instantiation” being the primary divisions of this construct, along with partitions based on the domains within which monitoring and control operate. In this chapter, we adopt this more nuanced approach to describing and understanding how the cognitive control system develops. Broadly, cognitive control has been found to develop nonlinearly, with rapid development across childhood and approaching maturity in adolescence. At the neural level, improvements in these abilities are generally associated with maturation of a frontoparietal network. Alongside such neurocognitive developments in cognitive control, changes in limbic-related motivation processes also exhibit stark developmental changes, particularly during the periadolescence period. In this chapter, we review the neurocognitive development of cognitive control and relations to motivation and social behavior. Additionally, how these functions differ across individuals, as a function of temperament and psychopathology, as well as cross-cultural variation, is reviewed.

24.1 The development of cognitive control and its neural basis

With development, children and adolescents improve in their ability to control their thoughts, behavior, and impulses, working toward goals while ignoring distracting information (Casey et al., 2005; Diamond, 2002; Zelazo, 2004). This ability has been termed *cognitive control* (Bunge and Crone, 2009; Nigg, 2017). Broadly, cognitive control can be divided into two distinct, but highly related, processes, including (1) *monitoring*, which detects situations where control might be needed, and (2) *control instantiation*, which biases neurocognitive activity to achieve task goals. Despite this distinction, monitoring and control instantiation are highly related and, in healthy adults, typically work together in tandem to allow for cognitive control. That is, monitoring is only useful if it is followed by control instantiation, and similarly, control instantiation would be aimless in the absence of monitoring to signal when control is required. Nonetheless, there are situations in adults where monitoring and control do not always closely track one another (Buzzell et al., 2017a; Van Der Borgh et al., 2016), and from a developmental perspective, there are some indications that these two processes exhibit

distinct, albeit highly contingent developmental trajectories. Monitoring and control instantiation can further be partitioned based on what is being monitored or how neural activity is being controlled. With this in mind, this chapter focuses primarily on error monitoring and inhibitory control, as specific examples of monitoring and control instantiation, respectively.

The chapter begins with a description of monitoring, leveraging more recent conceptualizations inspired by work in adults, and then provides a review of what is known about the development of monitoring at the behavioral and neural levels. Next, we expand on current conceptualizations of control instantiation, again leveraging recent adult work, before charting its developmental course. With a picture of the two core subdomains of cognitive control and their development in place, the chapter then turns to the highly related concept of motivation and motivation-control relations. Given that social rewards and social contexts represent one of the most common forms of human motivation, we then review what is known about the developmental relations between social behavior and cognitive control. Finally, the last portion of this chapter expands the review to explore how the development of cognitive control is related to individual differences in temperament and psychopathology, as well as cross-cultural variation. This chapter focuses mostly on childhood and adolescence given that majority of research into the neural correlates of cognitive control has been conducted for this age range. Moreover, cognitive control is known to develop markedly during this period.

24.1.1 Error monitoring

Monitoring, also referred to as “performance monitoring,” refers to the human brain’s ability to evaluate its own responses, or external stimuli, to determine whether adaptations are required to maintain goal-directed behavior (Ullsperger et al., 2014b). Critically, monitoring is not a unitary construct, nor mapped directly onto a single neural structure. Rather, monitoring is better characterized as a set of processes that all share the common function of detecting when control is needed, and a common anatomical hub in the medial–frontal cortex (MFC), to include the dorsal anterior cingulate cortex (dACC) (Shenhav et al., 2013). The three most common domains for which monitoring has been studied are (1) *conflict monitoring*, referring to interference and interactions between different information processing pathways in the brain at the level of stimulus or response-related neural activity (Braver et al., 2001); (2) *error monitoring*, referring to the detection of self-directed actions that deviate from task goals (Gehring et al., 1993); (3) *feedback monitoring*, referring to the processing of feedback related to task performance or the presence/absence of rewards and punishments (Holroyd and Coles, 2002). This chapter focuses on error monitoring.

Methodological considerations and adult studies. In the following, we focus our review of monitoring on the domain of error monitoring. However, before doing so, it is important to note inherent difficulties in the study of monitoring and cognitive control more generally. To study monitoring in the laboratory, computer-based tasks that require children or adults to make relatively quick decisions and responses are typically employed. One approach that has been proposed and widely used to studying error monitoring in children is to assess how quickly participants respond on the trials immediately following errors. A common finding is that individuals slow down on trials that follow errors, and this has traditionally been interpreted as reflecting the monitoring system first detecting the mistake, followed by subsequent control instantiation to respond more cautiously on the following trial (Botvinick et al., 2001; Danielmeier and Ullsperger, 2011). Thus, *posterror slowing* (PES) had been used as an index of monitoring. However, there are two issues with such an approach. First, it remains debated as to whether PES actually reflects more cautious responding or not (Danielmeier and Ullsperger, 2011; Jentsch and Dudschig, 2009; Notebaert et al., 2009), with the possibility that what PES reflects differs across tasks (Danielmeier and Ullsperger, 2011), and perhaps, even across development. Second, even if slowing always reflects increased response caution as the result of error monitoring detecting a mistake, this presents a measure of monitoring that is confounded with control instantiation. Given the confounded nature of behavioral metrics, a complementary approach to assessing monitoring is to leverage neuroimaging techniques, which can sometimes provide a more direct assessment of monitoring itself. However, such neural measures can also sometimes be confounded by overlapping neural processes or a lack of certainty as to what they index. Therefore, in studying the development of monitoring, it is important to consider both behavioral and neural metrics, while keeping in mind the limitations of each approach.

As previously mentioned, adult work finds that the monitoring system includes a network of brain regions, with a hub in MFC (Shenhav et al., 2013; Ullsperger et al., 2014a). Critically, activation of the monitoring system can be measured using the two most commonly employed noninvasive measures of neural activity: functional magnetic resonance imaging (fMRI) and electroencephalography (EEG). For example, when errors occur, conflict is detected, or negative feedback processed, increased activation of the MFC is typically observed via fMRI (Ridderinkhof et al., 2004). Moreover, a similar pattern of event-related potentials (ERPs) in the EEG is observed following conflict, errors, and feedback, consisting first of a rapid negativity over frontocentral scalp regions (i.e., the N2, error-related negativity [ERN], and feedback negativity,

respectively) and a slower positivity over more centroparietal scalp regions (i.e., the P3, Pe, and feedback P3, respectively; Ullsperger et al., 2014b). Source analysis studies suggest that the frontocentral negativities tend to share a common neural hub within MFC (Debener, 2005; Hauser et al., 2014; van Veen and Carter, 2002). Additionally, time–frequency analyses of EEG demonstrate that monitoring is associated with oscillatory changes within the theta band over frontocentral regions (Cavanagh et al., 2012).

To summarize, adult work suggests that monitoring reflects a class of processes that operate across domains, with a common neural hub within the MFC. Although monitoring activity can be indirectly inferred via behavioral metrics, neuroimaging approaches can also be used and may sometimes provide a more direct assessment of monitoring. With a basic understanding of adult monitoring in place, we now turn to a review of how monitoring develops across childhood and adolescence, with an emphasis on error monitoring.

Error monitoring development. Behavioral studies generally suggest that error monitoring emerges early in childhood. Using PES as a way to indirectly assess monitoring in children, Backen Jones et al. (2003) found that as 3- to 4-year-old children's performance on a Simon Says-type task improved, they tended to show PES. However, using a more fast-paced task-switching paradigm, Davidson et al. (2006) failed to find evidence of PES in 4- to 5-year-old children. Typically, younger children make more errors than adults and may be less aware of them; some studies have shown that children are able to detect errors but are unable to correct them. For example, Bullock and Lutkenhaus (1984) found that 18- and 24-month-old children could distinguish between correctly and incorrectly built towers, even when they themselves failed to build the towers correctly. In a study designed to examine this question with preschool children, Jacques et al. (1999) presented 3-year-old children with the dimensional change card sort, in which children are shown two target cards (e.g., a blue rabbit and a red boat) and are asked to sort a series of test cards (e.g., red rabbits and blue boats) first according to one dimension (e.g., color) and then according to the other (e.g., shape). Most 3-year-olds persevere during the postswitch phase, continuing to sort test cards by the first dimension (e.g., Zelazo et al., 2003). To assess error detection, Jacques et al. (1999) asked children to evaluate the sorting of a puppet. When 3-year-olds watched the puppet persevere, they judged the puppet to be correct, whereas when they saw the puppet sort correctly, they judged the puppet to be wrong. This pattern of results suggests that 3-year-olds' perseverating performance and error detection are closely linked in this task.

When studying PES in slightly older, school-aged children, mixed findings have been reported. On the one hand, a study of 6- to 10-year-olds found that PES increased from ages 6 to 7 years but then steadily decreased from ages 7 to 10 years (Gupta et al., 2009). On the other hand, across a wide age range (7–25 years), Davies et al. (2004) identified the presence of PES for all age groups, albeit no significant age-related changes emerged. Bearing the known limitations of using PES as an index of monitoring, the literature appears to support the relatively early emergence of error monitoring within the first few years of life, some evidence for an initial increase in monitoring into the early school years, but less development during adolescence.

Electrophysiological studies in young children have provided additional support for the early emergence of error monitoring. For example, EEG studies have demonstrated the presence of an ERN, thought to reflect activation of the monitoring system, as young as 4 years of age (Brooker et al., 2011). Moreover, this same study provides some evidence that the ERN increases in magnitude from 4 to 8 years, particularly for girls (Brooker et al., 2011). Other work has demonstrated the continued development of the ERN from ages 8 to 13 years (Meyer et al., 2012). Additionally, in one of the most extensive investigations of error monitoring development, a study by Davies et al. (2004) found that error monitoring generally increases throughout adolescence. However, the authors also found that such age-related changes were nonlinear and qualified by sex interactions, with females tending to show earlier changes than males. A more detailed review of developmental changes in the ERN specifically can be found elsewhere (Tamnes et al., 2013).

As previously mentioned, prior work in adults has consistently demonstrated a primarily cingulate-based source for the ERN, providing a direct link between this electrophysiological measure and the monitoring system (Debener, 2005; Hauser et al., 2014; van Veen and Carter, 2002). Similarly, developmental studies demonstrate that the ERN also includes a primarily cingulate-based source (Mathewson et al., 2005; Ladouceur et al., 2007; Santesso and Segalowitz, 2008), providing a direct link between developmental changes in the ERN and monitoring activity within the cingulate (MFC). Indeed, fMRI investigations have also found increased error-related MFC activation in adults, compared with children (Fitzgerald et al., 2010; Rubia et al., 2007). However, it is worth noting that the majority of source analysis studies have leveraged an approach that does not readily allow for identifying multiple sources of ERN activity across the brain and have employed approaches with limited spatial resolution. A more recent ERN source localization study in a sample of 9- to 35-year-olds employed individual MRI constraints and a distributed source model approach to build on this prior work in two important ways (Buzzell et al., 2017b). First, it was confirmed that across the age range studied, a primarily cingulate-based source was again identified, and critically, no significant changes across adolescence were found within

this core region of the monitoring system. Second, age-related changes in the ERN were localized to ventral–frontal neural regions that make up the extended error monitoring network: the insula, orbitofrontal cortex, and more caudal portions of the inferior frontal gyrus (frontal operculum; Buzzell et al., 2017b). Collectively, these data provide corroborating evidence for developmental increases in error monitoring through adolescence and even into early adulthood; however, at least for increases in error monitoring at these later stages of development, neural regions more closely tied to salience and emotional processing within ventral–frontal brain regions seem to be the focus of developmental change. These findings are consistent with structural (MRI) and functional (fMRI) studies that point to continued development and reorganization of widespread areas of the brain throughout adolescence and into adulthood, particularly those areas linked to higher cognitive functions like cognitive control (Sowell et al., 1999; Gogtay et al., 2004; Tamm et al., 2002). Moreover, these more extended changes within the monitoring system are consistent with other investigations of executive function development reporting marked changes in network dynamics with increasing age (Fair et al., 2007, 2009).

Studies of the ERN generally support the notion that error monitoring emerges early and exhibits continued development across childhood and adolescence, findings that are corroborated by source analyses, behavioral assessments of PES, and fMRI-based investigations. However, such studies leave open the question as to whether such development reflects increases in the underlying brain activity driving the ERN, i.e., signal strength, or whether developmental changes are better characterized by more efficient and synchronous neuronal firing. Leveraging time–frequency analyses of EEG data, DuPuis et al. (2015) demonstrated that developmental increases in the ERN from ages 5 to 7 years were best described by increases in signal consistency, as opposed to signal strength. Specifically, these authors demonstrated that theta band power (signal strength) and theta phase synchrony (signal consistency) both predicted the ERN but that longitudinal increases in the ERN were predicted by theta phase synchrony increases, whereas theta power actually exhibited decreases across this time period (DuPuis et al., 2015). These data suggest that error monitoring development, at least in the early school years, is best characterized by improved efficiency of the monitoring system. Future work will be needed to further characterize how theta band dynamics change across childhood and adolescence.

To summarize, error monitoring seems to emerge early, as supported by behavioral and electrophysiological data, and demonstrates rapid development during childhood but also continues to change throughout adolescence and even into adulthood. A general principle of such error monitoring development appears to be increased efficiency of this system, characterized by increased fMRI activations within error-specific brain regions, along with increased synchrony of such activations, as opposed to an overall increase in signal strength. Finally, at least for later development of this system throughout adolescence and into adulthood, development appears to be driven most prominently by the extended monitoring network in more ventral–frontal brain regions, as opposed to continued changes within the central MFC hub.

24.1.2 Control instantiation

Detecting when something goes wrong, monitoring, is only advantageous if the brain can do something about it and engage control instantiation. Specifically, control instantiation refers to top-down control over the brain and behavior to achieve task goals (Miller and Cohen, 2001). However, much like monitoring, control instantiation is not a unitary construct, nor mapped to a single neural structure. Instead, control instantiation refers to a broad class of neurocognitive processing that allows for maintaining goal-directed behavior. For example, inhibiting unwanted responses (Aron, 2007), increasing attention (Desimone and Duncan, 1995), and switching from one task to another (Braver et al., 2003) reflect a few examples of control instantiation. Thus, control instantiation can be partitioned as a function of the domain within which control operates; in this review, we focused primarily on inhibitory control, with some discussion of attentional control and task switching as well. We first describe adult work briefly, as an introduction to the neural basis of control instantiation and its relations with monitoring. We then turn to a review of how control instantiation develops across childhood and adolescence.

Control instantiation in adults. Control instantiation can be readily assessed using behavioral metrics. Simply put, if participants are asked to perform a task that is believed to require a particular form of control instantiation for successful completion, then accuracy and real-time performance can be taken as a measure of control instantiation. However, such behavioral approaches to the study of control instantiation are not without limitation. First, control instantiation rarely occurs in the absence of monitoring first detecting that control is required. Thus, behavioral measures of control instantiation are necessarily confounded by monitoring. Second, when attempting to study a specific domain of control instantiation, such as inhibitory control, it is essentially impossible to design a task that does not also involve other forms of control to be performed properly. For example, a “go/no-go” task involves making repeated responses to frequently presented stimuli, and then infrequently withholding responses to others, believed to require inhibitory control (Bokura et al., 2001). This task is known to rely heavily on inhibitory control for successful completion; nonetheless, this task also

requires some degree of attentional control for successful performance (Schröger, 1993), yielding an imperfect metric of control instantiation. To summarize, similar to the limits of behavioral assessments of monitoring, behavioral approaches for studying control instantiation are also imperfect. However, here again, neural measures can be leveraged to provide a complementary method for studying control instantiation.

Work in adults generally supports the notion that whereas monitoring relies primarily on midline frontal structures, like the cingulate and MFC more generally, control instantiation is more closely linked to lateral prefrontal structures, along with superior parietal regions (Dosenbach et al., 2008; Miller and Cohen, 2001; Petersen and Posner, 2012). Moreover, given that monitoring and control typically work together in concert to allow for goal-directed behavior, a common observation is the dynamic interaction between these two cognitive control subprocesses. For example, following errors or other events that signal a need for control instantiation, initial activation of the MFC, associated with monitoring, is typically followed by activation of lateral—prefrontal cortical regions associated with control instantiation (MacDonald et al., 2000). This dynamic interplay between medial and lateral frontal structures has been observed using fMRI (MacDonald et al., 2000), as well as EEG (Cavanagh et al., 2009) by observing increased coupling within the theta band between these two regions. Despite these general themes of monitoring and control instantiation relations, the neural correlates of control instantiation also exhibit a high degree of domain specificity. For example, inhibitory control has been linked to a relatively specified frontostriatal network, including the inferior frontal cortex (Aron et al., 2004). In contrast, attentional control is more closely associated with a frontoparietal network that includes dorsolateral prefrontal cortex (PFC), the frontal eye fields, and superior parietal cortex (Petersen and Posner, 2012). Activation of these regions, linked to the sources of inhibitory and attentional control, can thus be taken as evidence for domain-specific control instantiation.

To summarize, control instantiation often emerges shortly after monitoring processes reach their peak, and direct interactions between monitoring and control instantiation emerge through medial—lateral communication within the frontal cortex. Moreover, control instantiation exhibits a high degree of domain specificity, which can be leveraged to more closely track changes in particular forms of control. With this basic understanding of control instantiation in place, we now turn to a review of how these processes develop. In particular, we place an emphasis on the study of inhibitory control, but studies relating to attentional control and task switching are also discussed.

Development of inhibitory control. Inhibitory control, as defined earlier, is the ability to inhibit a dominant response in favor of a more appropriate response or no response at all (Aron, 2007; Rothbart et al., 2003). At the behavioral level, inhibitory control has a well-characterized developmental course, with improvements in children's ability to inhibit prepotent responses detected during toddlerhood (Gerardi-Caulton, 2000), along with improvements in inhibitory control occurring during the preschool years (e.g., Gerstadt et al., 1994; Rueda et al., 2004; Zelazo, 2006). Moreover, marked improvements in inhibitory control continue during middle childhood (e.g., Simonds et al., 2007) and adolescence (e.g., Anderson, 2002; Huizinga et al., 2006).

Regarding changes in neural activation during inhibitory control tasks, research has pointed to several changes that occur with development. As noted earlier, a core region involved in inhibitory control, particularly for inhibition of motor responses, is the inferior frontal cortex (IFC; Aron et al., 2004). Using a go/no-go task to study longitudinal development of inhibitory control across ages 9–11 years, Durston et al. (2006) found activation of the right IFC to increase across the two time points studied. More importantly, the IFC was found to be associated with improved inhibitory performance and that this region in particular exhibited increased activation with increasing age, whereas developmental decreases in activation were found in prefrontal regions that were not relevant for task performance. These findings are in line with another study that employed a modified go/no-go task, observing increased right IFC activation in adults, compared with children (age 8–12 years). Specifically, Bunge et al. (2002) had participants perform a go/no-go task that included an additional manipulation so that some trials required only motor inhibition of infrequent responses (similar to a classic go/no-go task), whereas other trials required participants to ignore distracting information. As an aside, tasks that require participants to ignore distracting information are said to involve “distractor suppression,” which not only likely involves attentional control to minimize processing of the distracting information but also likely involves inhibitory control of motor responses associated with the distracting information. Critically, the authors found that across both conditions, children failed to recruit the right IFC. Given the close link between IFC activity and inhibitory control, this suggests that the feature shared by each condition of this modified task—inhibitory control of motor responses—was less developed in children. It is also worth noting that children appeared to adopt different neural strategies, compared with adults, for each condition of this task. Specifically, children recruited the opposite prefrontal hemisphere (left) for successful performance of the condition involving distractor suppression, whereas they recruited more posterior brain regions, but not frontal, for successful performance in the condition similar to the classic go/no-go task (Bunge et al., 2002).

Beyond developmental changes within the IFC, studies have generally indicated that activation in the PFC becomes more focal with age (e.g., Bunge et al., 2002; Durston et al., 2006; Luna et al., 2001). In a study by Rubia et al. (2006),

functional brain activation was compared between adolescents and adults during three different executive tasks measuring inhibitory control (go/no-go), cognitive interference inhibition (Simon task, for which the spatial location of stimuli conflict with the proper response location), and attentional set shifting (switch task, during which interference from a previous stimulus–response association has to be inhibited). In all three tasks, adults recruited portions of the PFC, the anterior cingulate cortex (ACC), and the striatum more strongly than adolescents. Additionally, adults engaged the inferior parietal cortex more strongly than adolescents on the Simon and switch tasks, a finding similar to that reported for the go/no-go task by Bunge et al. (2002). Additional evidence for focalization comes from a study by Luna et al. (2001), who administered an antisaccade task to children (7–12 years), adolescents (13–17 years), and young adults (18–22 years). This task requires participants to suppress looking at a visual target that appears suddenly in the peripheral visual field and instead look away from the target in the opposite direction. These authors found that a network of regions thought to be involved in inhibitory control and spatial attention was increased for adults, relative to children and adolescents. In particular, adults exhibited increased activity within the frontal eye fields (FEFs), intraparietal sulcus, thalamus, superior colliculus, and regions of the cerebellum. However, adolescents exhibited a marked increase in striatal activity compared with children, as well as increased dorsolateral prefrontal cortex (DLPFC) activation relative to either children or adults (Luna et al., 2001). As will be discussed further in the section on motivation, these findings regarding the striatum and DLPFC might point to the unique developmental changes in motivation and cognitive control that occurs during adolescence.

In sum, research examining the neural correlates of inhibitory control development suggests that, with age, improvements in this ability are associated with increased focalization and efficiency in recruitment of the PFC. Thus, with development, brain regions that are not relevant for task performance decrease in their activation, whereas regions relevant for the task increase in their activation. This focalization of the PFC has been consistently found with various tasks that tap inhibitory control, as well as for tasks that require other forms of control instantiation. These changes in functional activation of inhibitory control that occur with development may reflect disengagement from immature neural circuits used by children and adolescents and recruitment of more mature, alternative networks. However, the differences in activation patterns between children and adults may also reflect children's reliance on different cognitive strategies, ongoing strategy-learning processes, or differ from adults in their efforts to complete the tasks (Ernst and Mueller, 2008).

24.2 The role of cognitive control in decision-making, motivation, and social behavior

24.2.1 Motivation, decision-making, and cognitive control

Cognitive control would be aimless in the absence of motivation. That is, while cognitive control is what allows humans to sustain goal-directed behavior through monitoring and control instantiation, motivation is what provides a direction to behavior. Therefore, to better understand cognitive control and its developmental trajectory, it is critical to also consider the development of motivation. Existing work supports the idea of a frontostriatal network linking cognitive control and motivation during decision-making (see Somerville and Casey, 2010). However, few studies have examined the developmental neuroscience of motivation–control relations. Here, behavioral studies have more frequently been employed, as will be discussed further. Nevertheless, recent years have shown an increase in the number of studies exploring the neural basis of motivation–control relations, and critically, how such processes develop; these studies will be reviewed as well.

A simple paradigm that has been used to assess relations between motivation and cognitive control with young children is the delay-of-gratification task, which measures children's ability to give up an immediate reward in favor of a larger reward later (Mischel et al., 1972). For example, participants are seated in front of a piece of candy while an experimenter leaves the room. If they wait for the experimenter to return, they get two treats; otherwise they get only one (Mischel et al., 1972). Variations of the standard delay-of-gratification paradigm have shown developmental differences throughout the preschool years. For example, in one study (Kochanska et al., 1996), children were asked to hold candy in their mouth without eating it until they were told to do so. In a second task, children were asked not to peek while they could hear that the experimenter was wrapping a gift for them. Children's ability to delay gratification increased significantly from 3 to 4 years of age. In a study linking delay of gratification and decision-making, Prencipe and Zelazo (2005) examined children's delay of gratification for self and other (the experimenter). Three-year-olds typically chose an immediate reward for themselves and a delayed reward for others (the experimenter). According to Prencipe and Zelazo (2005), these findings suggest that 3-year-olds are capable of adaptive decision-making but still have difficulty regulating their own approach behavior in motivationally salient situations. According to these authors, it is possible that their behavior is driven by the relatively automatic processes rather than by more deliberate prefrontal networks. The findings can be explained in light of Barresi and Moore's (1996) model of the development of perspective-taking. It is possible that 3-year-olds may have made

impulsive choices in the self-condition because they took an exclusively first-person perspective on their own behavior and had difficulty adopting a more objective, third-person perspective according to which delay would be preferred. In contrast, 3-year-olds may have chosen delayed rewards in the other condition because they took an exclusively third-person perspective and had difficulty appreciating the experimenter's subjective perspective (i.e., his or her own desire for immediate gratification).

In more complex situations, individuals are often required to make approach-avoidance decisions in the face of uncertainty. One common measure of complex decision-making in adults is the Iowa gambling task (IGT; [Bechara et al., 1994](#)). In this task, participants are asked to choose cards from four decks that contain a different number of cards that could lead to their winning or losing money. During the task, the participants learn that some decks are more advantageous than others. [Kerr and Zelazo \(2004\)](#) modified the IGT to create a version for children that included two decks of cards, one advantageous and one disadvantageous. Feedback on participants' decisions was provided in the form of happy (reward) and sad (loss) faces. Choosing cards from the disadvantageous deck resulted in more rewards on every trial but also with occasional (unpredictable) large losses. Three-year-olds failed to develop a preference for the advantageous deck. However, 4- and 5-year-olds were able to make advantageous decisions ([Kerr and Zelazo, 2004](#)).

Although these studies suggest a steady improvement in delay of gratification during early childhood, motivation–control relations do not appear to follow a linear pattern of development throughout development. For example, [Figner et al. \(2009\)](#) used a gambling task in which reward feedback was given either during or after decision-making. The findings revealed that adolescents made riskier choices compared with adults, but only in the condition in which the reward was given during the decision. Another study examined participants between the ages of 10 and 30 years and used a delay discounting task ([Steinberg et al., 2009](#)) in which participants were asked to choose between an immediate reward of less value (e.g., \$400 today) and a variety of delayed rewards of more value (e.g., \$700 1 month from now or \$800 6 months from now). The findings indicate that, before age 16 years, children exhibited a greater willingness to accept a smaller reward immediately than a large reward that was delayed. In a third study, [Cauffman et al. \(2010\)](#) obtained similar results examining the same age range with a modified version of the IGT. Results indicate that approach behaviors (a tendency to choose from the advantageous decks) display an inverted U-shape relation to age, peaking in mid- to late adolescence. In contrast, avoidance behaviors (a tendency to refrain from choosing from the disadvantageous decks) increased linearly with age, with adults avoiding disadvantageous decks at higher rates than both preadolescents and adolescents. Taken together, these studies show that risky choices tend to peak between 14 and 16 years of age, followed by a decline in risky behavior. Critically, this pattern of behavior on laboratory tasks matches reports that adolescence is characterized by heightened rates of risky behavior, such as drug use and risky sexual conduct ([Casey et al., 2005](#); [Steinberg, 2008](#)).

The behavioral findings described earlier appear to suggest that while cognitive control might improve across childhood and adolescence, selective impairments on cognitive control tasks might occur during the adolescence period. These behavioral patterns have led several researchers to propose that such apparent deficits in adolescent cognitive control arise from a mismatch between cognitive control and motivation processes during this period ([Luciana and Collins, 2012](#); [Luna and Wright, 2016](#); [Somerville and Casey, 2010](#); [Steinberg, 2010](#)). These theories predict that due to different developmental trajectories of cognitive control and motivational processes, the adolescent period reflects a developmental window within which motivational processes are more salient relative to cognitive control ability. Thus, researchers have suggested that although adolescents show improvements in cognitive control relative to children, their goal-oriented behavior can be diminished in light of motivational cues of potential reward ([Cauffman et al., 2010](#); [Figner et al., 2009](#); [Steinberg et al., 2009](#)). Indeed, fMRI studies examining the role of the striatum in salient and motivational contexts support the idea that adolescents show enhanced sensitivity to incentives relative to children and adults ([Ernst et al., 2005](#); [Galvan et al., 2006](#); [Geier et al., 2010](#); [May et al., 2004](#)). For example, [Ernst et al. \(2005\)](#) used a monetary reward task and found stronger activation among adolescents than adults in the left nucleus accumbens, a structure in the striatum thought to be involved in reward processing. In addition, a reduction in amygdala response to reward omission was larger for adults than for adolescents. Moreover, in line with the importance of motivation–control interactions for effective cognitive control behavior, research has shown that connection strength between frontal and striatal regions is associated with cognitive control ability in typically and atypically developing individuals.

In addition to the developmental mismatch between motivation and control during the adolescent period, which can lead to apparent control deficits, motivation is also known to have a facilitative effect on cognitive control. For example, when participants were promised a financial reward for accurate performance on certain trials of an antisaccade task, cognitive control was improved for adolescents more than adults ([Jazbec et al., 2006](#)). [Geier et al. \(2010\)](#) studied the neural underpinnings of reward processing and its influence on cognitive control in adolescence using a modified version of an antisaccade task. The results indicated that faster correct inhibitory responses were made on reward trials than on neutral trials by both adolescents and adults. Additionally, fewer inhibitory errors were committed by adolescents. For reward

trials, activation was attenuated within the ventral striatum in adolescents during cue assessment. This was followed by overactivation in adolescents during response preparation (i.e., during fixation after the reward cue) in the ventral striatum, as well as the precentral sulcus, which is important for controlling eye movements. These findings suggest enhanced activation in adolescents in control regions as a result of reward anticipation (Geier et al., 2010).

In sum, studies examining the development of cognitive control in decision-making have pointed to an inverted U-shaped trend in the development of motivation (see Somerville and Casey, 2010). Studies with young children show steady improvements in the ability to delay gratification (e.g., Prencipe and Zelazo, 2005) as well as more effective decision-making (e.g., Kerr and Zelazo, 2004). However, studies have shown a greater propensity for risky decisions during adolescence in light of motivationally salient situations (e.g., Cauffman et al., 2010). Additionally, fMRI studies examining the link between cognitive control processes and motivation have found enhanced activation during adolescence in brain regions associated with cognitive control during anticipation of reward (Geier et al., 2010).

24.2.2 Cognitive control and social behavior

Research has increasingly focused on the relations between cognitive control and social behavior. Following our review of motivation development more generally, we first overview how social stimuli can serve as motivating factors that directly influence cognitive control. Next, we discuss how social stimuli can be the focus of cognitive control, such as when social rejection is processed by the monitoring system. Furthermore, we review research across each of these domains to illustrate the emerging neuroscience on the relations between cognitive control and social behavior.

It has long been known that, at least at the behavioral level, social stimuli or social contexts can serve to motivate behavior (Triplett, 1898; Zajonc and Paulus, 1980; Zajonc, 1965).

In line with this notion, similar to the finding that cognitive control performance is improved in the presence of monetary rewards (Jazbec et al., 2006), similar findings have been reported for social rewards, such as happy faces (Kohls et al., 2009). Social observation can also serve as a form of motivation, and researchers have shown that the presence of others leads to an increase in error monitoring, as measured by the ERN (Hajcak et al., 2005). Critically, work has recently demonstrated that the effects of social observation on error monitoring differ across development. For example, Barker et al. (2018) had a group of participants between the ages of 8–17 years perform a cognitive control task under two conditions, once while being watched by peers, and once alone. The authors found that this social observation manipulation only led to an increase in the ERN for the younger adolescents, with no effect present for the older adolescents. Moreover, age-related changes in error monitoring were diminished when this effect of social context was considered (Barker et al., 2018). Consistent with these findings, another study by Barker et al. (2015) did not find evidence for social-related changes in the ERN for a sample of adults (unless social anxiety was also considered), whereas a third study in children aged 12 years did identify such an effect (Buzzell et al., 2017c). Earlier, we reviewed how the error monitoring system develops across childhood and adolescence; however, such work did not consider the role of social context; these more recent data suggest that age-related changes in error monitoring may be more complex, with social context playing a critical role.

Beyond the influence that social context can have on cognitive control, research has also investigated how social feedback itself is processed by the brain, investigating direct relations between the monitoring system and social behavior. Using a feedback processing paradigm similar to other investigations of the monitoring system, Somerville et al. (2006) found that while expectancy violations and social rejection are both processed by the MFC, social rejection was exclusively associated with more ventral activation of the MFC. Whereas this initial study was performed in adults, subsequent work has studied how the processing of social feedback differs across age. For example, a similar study by Gunther Moor et al. (2010) found that across ages 8–25 years, increasing activation of not only ventral regions of the MFC, but also the orbitofrontal cortex, lateral regions of the frontal cortex, and the striatum, was found when processing rejection feedback. Similarly, other work has shown that when participants participate in a virtual game, which is manipulated so that the participants feel left out, social distress is similarly associated with increased activity within the ventral MFC (Gunther Moor et al., 2010). Critically, younger participants, aged 10–12 years, showed increased activation within the ventral MFC, specifically the subgenual anterior cingulate cortex, compared with older adolescents and adults (Gunther Moor et al., 2010).

To summarize, research has demonstrated that monitoring and control can be upregulated by the presence of others, effects that change over the course of development. In particular, increases in monitoring that are driven by the presence of others appear to be strongest during young adolescence. Similarly, younger adolescents appear to uniquely demonstrate activation of the subgenual ACC during social exclusion, suggesting that this reflects a critical developmental period in terms of the monitoring of social contexts. More generally, the processing of social rejection appears to associate with increased ventral MFC activity more broadly. Having reviewed the relations between cognitive control and social behavior, we now turn to a discussion of how cognitive control differs across individuals. Here, we continue a social focus, reviewing relations with other socioemotional factors such as temperament, social anxiety, and cross-cultural differences.

24.3 Individual differences in cognitive control

24.3.1 Temperament, cognitive control, and psychopathology

This chapter has so far reviewed the typical development of cognitive control that is observed, on average, across children. However, a substantial and growing literature has characterized individual differences in the development of cognitive control (e.g., Gehring et al., 2000; Henderson, 2010; Lewis et al., 2006; McDermott et al., 2009; Stieben et al., 2007; White et al., 2011). Critically, such individual differences have been linked to early differences in a child's temperament, as well as normative variation in later social outcomes and even psychopathology. For example, behavioral and physiological measures of cognitive control have been linked to negative mood induction conditions (Lewis et al., 2006, 2007) and to heightened levels of trait anxiety and internalizing symptoms (e.g., Gehring et al., 2000; Stieben et al., 2007). Here, we review literature on such relations, before turning to much broader differences across cultures.

A child's temperament refers to persistent individual differences that are thought to have a basis in biology. Relations between temperament and cognitive control are natural, as one influential model of temperament by Rothbart and colleagues (Rothbart, 1981; Rothbart and Bates, 2006) explicitly includes "regulation," referring to a child's ability to self-soothe and control their own behavior (Rothbart, 1981; Rothbart and Bates, 2006), as one of the dimensions of temperament. Critically, a growing corpus of studies has investigated how behavioral inhibition (BI) either relates to cognitive control directly or interacts with cognitive control to predict later outcomes in socioemotional development and psychopathology. We now turn to a review of relations between BI and cognitive control, as well as relations with other forms of temperament.

A number of studies from different laboratories have found that specific cognitive control functions moderate the developmental trajectory of BI in children (Henderson, 2010; Thorell et al., 2004; White et al., 2011). For example, Thorell et al. (2004) examined how BI and inhibitory control assessed at 5 years of age were associated with socioemotional functioning at 9 years of age. The results indicated that behaviorally inhibited children with high levels of inhibitory control were reported as being more socially anxious than behaviorally inhibited children with low levels of inhibitory control. Similarly, Fox and Henderson (2000) found that behaviorally inhibited 4-year-olds with high inhibitory control were less socially competent and more socially withdrawn than behaviorally inhibited children with low inhibitory control. Other neurophysiological evidence for the moderating role cognitive control has been found for the association between shyness and social-emotional maladjustment (Henderson, 2010). In 9- to 13-year-old children, Henderson (2010) found that shyness was associated with poor social outcomes primarily among children with greater neural activity associated with cognitive control, as measured by the N2 ERP component. Lahat et al., (2014b) found that among children with a large N2, BI was positively related to withdrawal and negatively related to assertiveness during social exclusion. Taken together, these results point to the role of conflict in shy children's social adjustment (Henderson, 2010; Lahat et al., 2014a,b). In a study using dense-array ERPs and source analyses, Lamm et al. (2012) showed that, during an inhibitory control task, children high in temperamental fearfulness showed modeled source activation in areas suggestive of ventrolateral PFC across both emotional and nonemotional conditions of the task. However, children low in temperamental fearfulness only showed this pattern of activation during the emotional condition. Results from this study suggest that while children low in temperamental fearfulness recruited increased inhibitory control only during the emotional conditions, or those conditions in which more cognitive control recourses were likely needed, children with high fearful temperaments sustain this increased level of inhibitory control across both neutral and emotional contexts (Lamm et al., 2012). These findings suggest that temperamentally fearful individuals show increased vigilance not only in emotional situations but also in nonemotional ones. Thus, these fearful individuals may refrain even from social situations that do not induce negative emotions.

Findings regarding the role of inhibitory control for temperamental BI or shyness are the opposite of results regarding another form of control instantiation: attention shifting (Eisenberg et al., 1998). For example, Eisenberg et al. (1998) found that children low on attention shifting and high on parental reports of negative emotions, such as fear, sadness, and anxiety, were rated by their parents and teachers as shyer 2 years later. Investigating this difference further, White et al. (2011) examined how attention shifting and inhibitory control, which were tested at 48 months of age, moderated the association between BI assessed at 24 months of age and anxiety problems in the preschool years. The results indicated that high levels of inhibitory control increased the risk for anxiety disorders among behaviorally inhibited children, whereas high levels of attention shifting decreased the risk for anxiety problems in these children. In a different study, Lahat et al. (2012) examined how these two forms of control instantiation—attention shifting and inhibitory control—moderated the relation between exuberant temperament in infancy and propensity for risk taking in childhood. Temperamental exuberance has been defined by positive reactivity to novelty, approach behavior, and sociability (Putnam and Stifter, 2005). Children with an exuberant temperament are also characterized by impulsivity, sensitivity to reward, fearlessness, and risk taking (Fox

et al., 2001; Polak-Toste and Gunnar, 2006; Rothbart and Bates, 2006). Control instantiation was assessed at 48 months of age. Risk taking propensity was measured when children were 60 months of age. The results indicated that exuberance was positively associated with risk taking propensity among children relatively low in attention shifting but unrelated for children high in attention shifting. Inhibitory control did not significantly moderate the link between exuberance and risk taking. Taken together, the findings from these sets of studies on temperament and different types of control instantiation demonstrate that attention shifting and inhibitory control have differential influences on levels of risk or adaptation. Furthermore, these two studies (Lahat et al., 2012; White et al., 2011) suggest that high levels of attention shifting may serve as a protective factor in the link between temperament and negative outcomes. This conclusion may have important implications for prevention and intervention efforts in the form of training to improve attention-shifting skills.

While the aforementioned findings provide evidence for the potential negative risks of excessive inhibitory control ability for children high in BI, it is important to note that the majority of such findings are primarily based on behavioral measures, which are confounded with monitoring. Similarly, neurophysiological research that leverages the N2 as an index of “inhibitory control” is not without limitation, as it remains debated as to whether the N2 ERP component more closely maps onto monitoring or control, with evidence suggesting a closer relation to monitoring (Donkers and van Boxtel, 2004). Thus, it is possible that many of the purported links between overactive inhibitory controls might more closely reflect increased monitoring. Indeed, as we will now review, individual differences in monitoring consistently relate to temperament and moderate risk for negative social outcomes or psychopathology.

The first study to provide evidence that BI directly relates to monitoring came from a study by McDermott et al. (2009). These authors studied adolescents with a mean age of 15 years who were part of a larger longitudinal study and were assessed during infancy and early childhood for BI. Using the ERN as an index of monitoring, it was found that adolescents with high childhood BI exhibited increased error monitoring relative to those low in childhood BI. Moreover, magnitude of the ERN moderated relations between BI and clinical anxiety, such that a higher risk for anxiety disorders was present for children assessed as high in BI and also exhibiting a larger ERN (McDermott et al., 2009). In a separate cohort of children, this basic set of relations was replicated at an earlier age, assessing BI in toddlerhood, the ERN at age 7 years and anxiety outcomes at age 9 years (Lahat et al., 2014a). Also in this second cohort of children, the ERN was found to relate to BI a third time when assessed at age 12 years, particularly when social context was taken into account (Buzzell et al., 2017c). In this third study, adolescents were required to perform a cognitive control task twice, once alone, and once while under social observation. The authors found that greater increases for the ERN, while under social observation, were predicted by early BI. Critically, longitudinal relations between early BI and social anxiety in adolescence were mediated by a combination of this increased ERN and also slowed behavioral responses after errors (Buzzell et al., 2017c). Thus, these more recent results point to the importance of social context when considering relations between temperament, cognitive control, and psychopathology.

The reviewed studies illustrate a consistent relation between the BI temperament and later individual differences in error monitoring. This pattern is consistent with similar relations that have been found for children characterized as high in fearfulness during early toddlerhood (2 years of age), who also exhibit larger ERNs later at 4.5 years of age (Brooker and Buss, 2014). However, one study has also shown that children with a temperament of negative emotionality that also have mothers with high anxiety actually demonstrate a smaller ERN (Torpey et al., 2013). Beyond error monitoring, children high in BI also demonstrate increased activation of the performance monitoring system in response to a variety of events. For example, children high in BI exhibit increased cingulate activation in response to stimulus conflict, likely reflecting conflict monitoring (Jarcho et al., 2013). Similarly, children high in BI demonstrate an enhanced N2 ERP, which can be interpreted as an index of conflict monitoring as well (Lahat et al., 2014b). Indeed, following source localization of the N2 in a go/no-go task, it was found that children high in BI exhibited greater cingulate activity for high conflict trials, consistent with increased conflict monitoring for these children (Lamm et al., 2014).

To summarize, substantial variation in cognitive control can be observed during childhood and adolescence, and such variation relates to temperament, social outcomes, and psychopathology. In general, it appears that certain temperaments, such as BI, are associated with increased monitoring for errors or conflict later in development. Moreover, at least for children high in BI, increased monitoring is actually a risk factor for anxiety. Similarly, it appears that enhanced inhibitory control is also a risk factor for children high in the BI temperament; however, more work using neural measures is needed to confirm this relation. Having reviewed individual variation in cognitive control, we now turn to more global variation by reviewing cross-cultural differences.

24.3.2 Cross-cultural differences in the development of cognitive control

Research on the development of cognitive control has mostly been conducted in Western cultures. However, an emerging body of cross-cultural studies suggests that Asian children may outperform Western children on measures of cognitive control (e.g., Lahat et al., 2010; Sabbagh et al., 2006). Research comparing children from Western and Asian cultures has

shown that Chinese children perform better on behavioral and neurophysiological measures of EFs than North American children (e.g., [Chen et al., 1998](#); [Ho, 1994](#); [Lahat et al., 2010](#); [Sabbagh et al., 2006](#); [Wu, 1996](#)). For example, [Sabbagh et al. \(2006\)](#) administered a battery of EF and theory of mind (ToM) tasks to preschoolers from China and the United States. ToM is the ability to attribute mental states—beliefs, intents, and desires—to oneself and others and to recognize that mental representations can differ across individuals ([Premack and Woodruff, 1978](#)). The Chinese preschoolers showed better performance than the US preschoolers on all measures of EF, but not on measures of ToM. However, individual differences in EF predicted ToM performance in both groups.

Chinese children's advanced performance on EF tasks may stem from the opportunities to exercise and practice these abilities that they encounter within their culture. For example, Chinese parents expect children to master impulse control at a much younger age than North American parents ([Chen et al., 1998](#); [Ho, 1994](#); [Wu, 1996](#)). Compared with Western parents, Chinese parents are more controlling and protective in child rearing. For example, they often encourage their young children to stay close to and to be dependent on them. Indeed, most Chinese infants and toddlers sleep in the same bed or in the same room as their parents ([Chen et al., 1998](#)). In addition, impulse control is more highly valued in Chinese daycare settings than in North American daycare settings ([Tobin et al., 1989](#)).

Another possibility for Chinese children's superior cognitive control was suggested by [Lahat et al. \(2010\)](#) in a study that focused on the N2 component of ERP. The study compared 5-year-old children from a Chinese-Canadian ethnic background with children from a European-Canadian background on a go/no-go task. No behavioral differences between the two cultural groups were observed, but robust N2 amplitude differences were found. Chinese-Canadian children showed larger (i.e., more negative) N2 amplitudes than European-Canadian children on the right side of the scalp on no-go trials as well as on the left side of the scalp on go trials. Source analyses of the N2 showed greater modeled source activation for Chinese-Canadian children in dorsomedial, ventromedial, and (bilateral) ventrolateral PFC. These findings reveal that Chinese-Canadian children show greater hemispheric differentiation than European-Canadian children, perhaps relating to more advanced cognitive control.

In sum, individual differences in cognitive control have also been observed in cross-cultural variations. Specifically, an emerging body of research comparing children from Asian and Western cultures has shown behavioral (e.g., [Sabbagh et al., 2006](#)) as well as neurophysiological ([Lahat et al., 2010](#)) evidence, suggesting advanced cognitive control abilities among children from a Chinese cultural background compared with children from a Western cultural background. Although the reasons for these differences are not clear yet, it is possible that differences in socialization between the two cultures play a major role.

24.4 Chapter summary and future directions

In this chapter, cognitive control, its development, and relations to social behavior were reviewed. The chapter described how cognitive control is composed of two primary subdivisions, monitoring, and control instantiation. Toward this end, a focus was placed on reviewing error monitoring and inhibitory control in particular. As described earlier, these functions have been found to develop with the maturation of the PFC, and patterns of activation generally increase with age ([Zelazo et al., 2008](#)).

Based on behavioral and neural measures, error monitoring is shown to emerge early in childhood and exhibit sustained development through adolescence (e.g., [Backen Jones et al., 2003](#); [Bullock and Lutkenhaus, 1984](#); [Davies et al., 2004](#)). Error monitoring is shown to rely primarily on a central hub within the MFC that exhibits increasing activation across childhood and early adolescence ([Ladouceur et al., 2007](#)). However, continued development through adolescence and into adulthood appears to derive from more nuanced development within ventral–frontal structures linked to salience and emotional processing ([Buzzell et al., 2017b](#)). Studies examining the neural correlates of inhibitory control development have shown that PFC activation not only increases with age but also becomes more focalized (e.g., [Bunge et al., 2002](#); [Durstun et al., 2006](#); [Luna et al., 2001](#)). As discussed, with development, brain regions not associated with task performance decrease in activation, whereas regions relevant to task performance increase in activation.

In this chapter, the role of cognitive control in the development of decision-making and motivation was also reviewed. Studies have shown that the development of decision-making takes an inverted U-shaped form, with steady improvements during childhood (e.g., [Kerr and Zelazo, 2004](#)) and a propensity for risk taking during adolescence due to a mismatch between the developmental trajectories of motivation and cognitive control ([Somerville and Casey, 2010](#)). fMRI studies with adolescents (e.g., [Geier et al., 2010](#)) have shown increased activation in brain regions associated with cognitive control during anticipation of reward. Moreover, early adolescence appears to be marked by heightened sensitivity to social influences on cognitive control, with social observation yielding increases in error monitoring sensitivity ([Barker et al., 2015](#); [Buzzell et al., 2017c](#)), as well as heightened sensitivity to social rejection during this developmental window ([Gunther Moor et al., 2010](#)).

Inhibitory control and error monitoring have been found to show associations with individual differences and their social–emotional outcomes (e.g., Fox and Henderson, 2000; Lamm et al., 2012; McDermott et al., 2009; White et al., 2011). This body of research has shown that children with a fearful temperament who are also high in inhibitory control or error monitoring are at risk of developing negative social–emotional outcomes, such as social withdrawal and anxiety disorders. However, evidence for individual differences associated with cognitive control comes mostly from behavioral and electrophysiological studies, and more work is needed.

Individual differences relating to cultural variation have also been found, particularly when comparing Chinese children with children from Western cultures. These studies provide behavioral (Sabbagh et al., 2006) as well as neurophysiological (Lahat et al., 2010) evidence for advanced performance on cognitive control tasks among Chinese children. It is possible that socialization processes that differ across the two cultures contribute to these differences in cognitive control. However, given that the cross-cultural neurophysiological work has been conducted with Asian children who grew up in North America, future research should compare Western children with Asian children who are raised in Asia.

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