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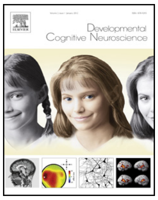

Developmental continuity in reward-related enhancement of cognitive control

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ABSTRACT

Adolescents engage in more risky behavior than children or adults. The most prominent hypothesis for this phenomenon is that brain systems governing reward sensitivity and brain systems governing self-regulation mature at different rates. Those systems governing reward sensitivity mature in advance of those governing self-control. This hypothesis has substantial empirical support, however, the evidence supporting this theory has been exclusively derived from contexts where self-control systems are required to regulate reward sensitivity in order to promote adaptive behavior. In adults, reward promotes a shift to a proactive control strategy and better cognitive control performance. It is unclear whether children and adolescents will respond to reward in the same way. Using fMRI methodology, we explored whether children and adolescents would demonstrate a shift to proactive control in the context of reward. We tested 22 children, 20 adolescents, and 23 adults. In contrast to our hypothesis, children, adolescents, and adults all demonstrated a shift to proactive cognitive control in the context of reward. In light of the results, current neurobiological theories of adolescent behavior need to be refined to reflect that in certain contexts there is continuity in the manner reward and cognitive control systems interact across development.

1. Introduction

Adolescents engage in more risky behaviors than children or adults (Steinberg, 2010). For example, seventy-two percent of adolescent mortality is the result of preventable causes, such as accidents, suicide, and homicide (Eaton et al., 2008). Because these risk-taking behaviors are a public health concern, identification of the neurodevelopmental changes underlying them may lead to new insights for effective preventative interventions.

One hypothesis about why adolescents engage in risky behavior is that youth experience a mismatch in the maturation rate of relevant brain systems. Consistent with this view, there is evidence that brain systems involved in reward sensitivity – which might draw adolescence towards certain features in the environment – mature in advance of brain systems involved in cognitive control – which might help adolescents regulate their behavior. This maturational asynchrony may contribute to risk-taking because adolescents may be overly compelled by some features of the environment without the appropriate checks-and-balances afforded by control or regulatory circuitry (Somerville et al., 2010; Steinberg, 2010). However, we know relatively little about the ways that these reward and control systems might interact. This is because most of the existing research in this area has been focused upon situations in which cognitive control systems must regulate or constrain reward sensitivity systems. In contrast, less

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is understood about situations where reward sensitivity promotes cognitive control.

The present experiment was designed to begin to address this issue.

One test of how the cognitive control system regulates the reward system is the Iowa Gambling Task (Bechara et al., 1994). In this paradigm, participants must learn to avoid a deck of cards with high potential reward because it is also associated with high potential loss. To do this, the participant must exert cognitive control to suppress the impulse, driven by reward motivation, to choose the high-risk deck. Avoiding these high-risk situations allows participants to ultimately earn the most money over the course of the experiment, which in the context of this paradigm is adaptive behavioral performance. Unlike adults, in this context, adolescents typically choose the high reward/high risk deck more frequently than adults (Cauffman et al., 2010). Developmental changes in performance on the Iowa Gambling Task have also recently been examined using fMRI, and it has been found the prefrontal cortex (PFC), a central node of the cognitive control network, is increasingly engaged with age (Christakou et al., 2013). These findings suggest that inhibition of reward sensitivity through cognitive control is a mechanism underlying adaptive behavior. Yet there are also situations where adaptive behavior requires the opposite pattern, where it is reward systems that serve to promote cognitive control. As a case in point, individuals often perform better across a variety of challenging tasks when offered rewards (Geier et al., 2010; Jimura et al., 2010; Locke and Braver, 2008). Indeed, there is evidence that reward leads to improvements in cognitive control performance through a shift in cognitive control strategy (Braver, 2012). In sum, there appear to be many ways in which reward and cognitive control systems become integrated over development. Understanding imbalances in the interaction of these systems may shed light on some of the maladaptive behaviors, such as risk-taking, often observed in adolescents.

1.1. Reward, cognitive control, and development

A great deal has been learned about the neural mechanisms that support cognitive control in adults. Cognitive control is facilitated by a distributed network of brain regions, localized mainly in lateral prefrontal, parietal, and anterior cingulate cortices (Owen et al., 2005; Wager and Smith, 2003). Current theories suggest that cognitive flexibility is enabled by dual-modes of cognitive control (Braver and Barch, 2002). Adults are able to activate either proactive or reactive modes of cognitive control. In the proactive mode, information that is important to an individual's objective is maintained in the time period before self-control is required. For example, awareness that one needs to drive home at the end of the evening would lead an individual to anticipate being offered the next alcoholic drink and prepare a response to decline it. Reactive cognitive control reflects operations invoked subsequent to a stimulus. In keeping with the example above, after being offered another alcoholic drink, an individual would consider his/her situation and responsibility and then decline the offer. In the laboratory setting the AX-Continuous Performance Task (AX-CPT) has frequently been used to study proactive and reactive control. In this task participants are presented with a letter that serves as the cue (A or B) followed by a letter that serves as the probe (X or Y). Participants are instructed to press a button under his/her index finger when the letter "A" is followed by the letter "X", and to press the button under his/her index finger for all letter combinations. When participants engage in proactive strategy they primarily attend to the cue and in contrast if they employ a reactive strategy they primarily attend to the probe (Braver et al., 2009). Using this task, it has been demonstrated that reward motivation such as financial reward for good performance, leads adults to engage a proactive strategy of cognitive control which is also associated with better behavioral performance (Jimura et al., 2010; Locke and Braver, 2008).

One way that researchers have measured whether individuals implement proactive or reactive cognitive control strategies is through mixed block/event-related designs in functional magnetic resonance imaging (fMRI) (Visscher et al., 2003). With this type of design, the participant is presented with a series of trials separated by large periods of rest. This allows investigators to determine whether brain regions remain active across the group of trials (sustained activation) or whether the brain regions are engaged and disengaged with the presentation and termination of each individual trial (transient activation). Sustained brain activation is hypothesized to index proactive cognitive control as the brain regions are engaged across a block of trials independent of the stimulus presentation (Jimura et al., 2010). Additionally, sustained activation of the fronto-parietal network is associated with behavioral indices of proactive cognitive control (Locke and Braver, 2008; Jimura et al., 2010), and the fronto-parietal network has been consistently implicated in cognitive control (Owen, 2005; Dosenbach et al., 2008).

There are age-related changes in cognitive control and reward sensitivity across adolescence (Luna et al., 2010), though findings about the neural correlates of these changes are unclear. In terms of the cognitive control system, and whether there is greater or lesser activity in these regions across development, it appears to depend in part on the task and analysis. It has been demonstrated on a task of inhibitory control that trial-related activity decreases with age, while sustained activity increases with age (Velanova et al., 2009). Still other studies suggest different brain regions are engaged across development (Bunge et al., 2002). Despite the inconsistency in directionality, it does appear that cognitive control circuitry is engaged differentially across development, and that maturation of this circuitry is related to behavioral differences (Crone and Dahl, 2012).

A number of studies have found adolescents, relative to adults, show heightened neural responses to reward (Christakou et al., 2011; Ernst et al., 2005; Galvan et al., 2006; Geier et al., 2010; Padmanabhan et al., 2011; Smith et al., 2011). Some studies have found an underactivation of reward circuitry in adolescents relative to adults (Bjork et al., 2004; Bjork et al., 2011), however they seem to be the exception. Generally, it is accepted that adolescents exhibit