

Effects of incentives, age, and behavior on brain activation during inhibitory control: A longitudinal fMRI study



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ABSTRACT

We investigated changes in brain function supporting inhibitory control under age-controlled incentivized conditions, separating age- and performance-related activation in an accelerated longitudinal design including 10- to 22-year-olds. Better inhibitory control correlated with striatal activation during neutral trials, while Age X Behavior interactions in the striatum indicated that in the absence of extrinsic incentives, younger subjects with greater reward circuitry activation successfully engage in greater inhibitory control. Age was negatively correlated with ventral amygdala activation during Loss trials, suggesting that amygdala function more strongly mediates bottom-up processing earlier in development when controlling the negative aspects of incentives to support inhibitory control. Together, these results indicate that with development, reward-modulated cognitive control may be supported by incentive processing transitions in the amygdala, and from facilitative to obstructive striatal function during inhibitory control.

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1. Introduction

Adolescence is recognized as a period of increased behavioral risk associated with greater mortality (Eaton et al., 2012). Although direct links between real-world risk-taking and brain maturation have yet to be established, research to date suggests that neural systems supporting cognitive control and incentive processing follow different developmental trajectories, which may lead to increased impulsivity in the face of rewarding situations (Casey et al., 2008; Galvan et al., 2006; Luna et al., 2014; Steinberg, 2005). Although initial neurodevelopmental studies have

been influential in guiding research toward the interaction of reward processing and cognitive control, there are three limitations in the existing literature. First, in tasks where performance increases with age (e.g., the antisaccade task; Luna et al., 2001), many prior studies have not compared neural activation patterns due to both task performance and age. That is to say, while developmental studies often control performance differences by using tasks that generate equal performance or through analytic models, in the present study we placed both behavior and age into the same model to account for shared vs. unique variance explained by each, allowing for the examination of their interaction. Second, most developmental studies have been cross-sectional in design, limiting implications toward developmental change (Singer and Willett, 2003). We address these limitations by focusing on how incentives, age, and performance, modulate brain activity during inhibitory control throughout middle childhood to young adulthood using an accelerated longitudinal design.

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Behavioral studies indicate peak sensitivity to reward during adolescence (Cauffman et al., 2010), yet neuroimaging results have been inconsistent. Functional magnetic resonance imaging (fMRI) studies have shown developmental peaks in striatal activation when processing rewards (Ernst et al., 2005; Galvan et al., 2006; Geier et al., 2010; Padmanabhan et al., 2011; Van Leijenhorst et al., 2010), as well as developmental troughs (Bjork et al., 2004, 2010; Lamm et al., 2014).

Relatively less is known about the development processes underlying loss compared to what is known of these processes for reward (Spear, 2011). In adults, behavioral economics studies indicate that losses are valued two-fold compared to gains (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992) suggesting a psychological difference between rewards and losses. Behaviorally, adolescents and adults tend to exhibit similar levels of loss-aversion, while neuronally adolescents recruit striatal and frontal regions to a greater degree than adults when making decisions involving losses (Barkley-Levenson et al., 2012; Weller et al., 2010). While the circuitry underlying the processing of losses and gains similarly include anterior cingulate, nucleus accumbens (NAcc), and amygdala, it is differentially engaged during these two types of tasks (Levin et al., 2012; Tom et al., 2007).

In concert with motivation, inhibitory control, which is a core component of executive function, continues to mature through adolescence (Bunge et al., 2002; Fischer et al., 1997; Luna et al., 2004; Munoz et al., 1998) supported by age-related changes in frontoparietal activation (Bunge et al., 2002; Ordaz et al., 2013). The antisaccade (AS) task probes the integrity of cortico-subcortical inhibitory control (Hallett, 1978) and elicits decreases in dorsolateral PFC activation from childhood to adolescence, when it reaches adult-like levels (Ordaz et al., 2013). The AS task elicits increases in dACC activation from childhood into adulthood, and correlates with performance (Ordaz et al., 2013). These results suggest that inhibitory control is largely available by adolescence but with continued specialization that may undermine cognitive control and influence decision-making.

The effect of incentives on cognitive control have shown that incentives enhance activation in task-relevant neural regions (Krawczyk and D'Esposito, 2011; Krawczyk et al., 2007; Locke and Braver, 2008; Yamamoto et al., 2013). In a rewarded AS task, behavioral performance was greater for reward than for non-reward trials, and rewards activated oculomotor circuitry supporting inhibitory control (Geier et al., 2010). Alternatively, others have found that when reward is contingent on suppressing an small immediate reward in favor of a larger delayed reward, regions supporting inhibitory control show relatively decreased activation (O'Connor et al., 2012). The authors suggest that successful inhibitory control over an immediate reward requires attentional disengagement. This would be similar to behavioral studies that have found success in delay of gratification to be facilitated by strategies that involve diverting attention from the immediate reward by engaging in other activities, such as making up unrelated games (Mischel et al., 1989).

To examine the developmental effects of potential rewards and losses on cognitive control, we performed an incentivized AS fMRI study using an accelerated longitudinal design. The study sample consisted of individuals ranging from 10- to 20-years of age, with each being sampled two or three times at approximately 15-month intervals. We selected 22 regions typically associated with reward processing and inhibitory control and thought to underlie incentive and cognitive processing, including those that have been found to change through development (e.g. striatum, orbitofrontal cortex, ventromedial prefrontal cortex). Based on past results (Ernst et al., 2005; Galvan et al., 2006; Van Leijenhorst et al., 2010) including our own (Geier et al., 2010; Padmanabhan et al., 2011), we make the following hypotheses. Activation in reward and cognitive control regions will show distinct age related effects across different incentives. During incentive trials, activity in ventral striatum will peak during adolescence while it will not change in neutral trials. Performance will improve with age, and with incentives, especially in younger subjects. As a second aim, we also sought to characterize the shape (linear vs. curvilinear) of developmental trajectories afforded by a longitudinal design.

2. Methods

2.1. Participants

The data for these analyses include 187 initial participants ranging in age from 10- to 20-years. Data was collected as part of an ongoing study and participants were enrolled from Pittsburgh and surrounding areas for behavioral testing and neuroimaging approximately every 15 months for two-and-a-half years. After accounting for motion, whole-brain coverage, behavioral measures, number of trials, and number of visits, the resulting data set included eighty-two subjects (41 females; Fig. 1) providing data across two ($N = 49$) or three ($N = 33$) visits. Participants were compensated \$75, plus up to an additional \$25 based on accumulation of points. Immediately prior to scanning, subjects were asked to rate how 'valuable' (7-point Likert

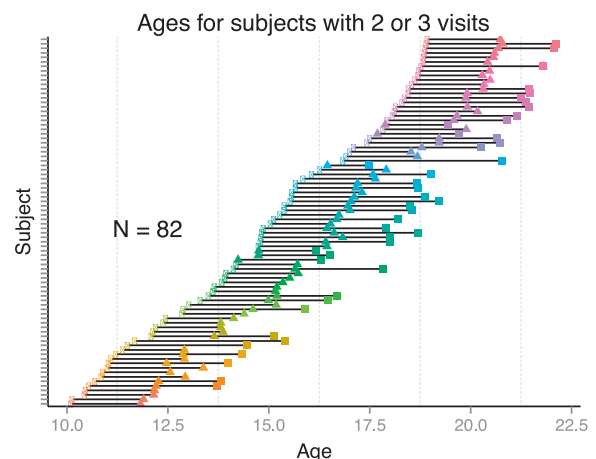


Fig. 1. Distribution of ages for subjects included in the current data set.

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