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Effects of response preparation on developmental improvements in inhibitory control

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ABSTRACT

Studies in adults indicate that response preparation is crucial to inhibitory control, but it remains unclear whether preparation contributes to improvements in inhibitory control over the course of childhood and adolescence. In order to assess the role of response preparation in developmental improvements in inhibitory control, we parametrically manipulated the duration of the instruction period in an antisaccade (AS) task given to participants from ages 8 to 31 years. Regressions showing a protracted development of AS performance were consistent with existing research, and two novel findings emerged. First, all participants showed improved performance with increased preparation time, indicating that response preparation is crucial to inhibitory control at all stages of development. Preparatory processes did not deteriorate at even the longest preparatory period, indicating that the youngest participants were able to sustain preparation at even the longest interval. Second, developmental trajectories did not differ for different preparatory period lengths, highlighting that the processes supporting response preparation continue to mature in tandem with improvements in AS performance. Our findings suggest that developmental improvements are not simply due to an inhibitory system that is faster to engage but may also reflect qualitative changes in the processes engaged during the preparatory period.

1. Introduction

Inhibitory control is the ability to direct behavior through internally-represented goals and it is crucial for exerting top-down control of behavior. Various studies using different measures of inhibitory control have shown that performance improves through childhood into adolescence (Davidson, Amso, Anderson & Diamond, 2006; Dempster, 1992; Diamond & Taylor, 1996; Fuster, 2002; Luciana & Nelson, 1998; Ridderinkhof, Band & Logan, 1999; Ridderinkhof, van den Wildenberg, Segalowitz & Carter, 2004; Ridderinkhof & van der Molen, 1997; Williams, Ponesse, Schachar, Logan & Tannock, 1999), and its improvement enhances information-processing abilities that facilitate overall cognitive development (Dempster, 1992). However, what underlies developmental improvements in inhibitory control remains unclear. Single-cell monkey studies and human neuroimaging studies have shown that essential to inhibitory control is response preparation (Connolly, Goodale, Menon & Munoz, 2002; Curtis & D'Esposito, 2003; DeSouza, Menon & Everling, 2003; Ford, Goltz, Brown & Everling, 2005), the ability to engage inhibitory processes during the time of instruction prior to the period when a response is required. Response preparation, or engaging preparatory set, is a prospective function that involves choosing, planning, and readying a response prior to target appearance (Connolly et al., 2002; Fuster, 2002; LaBerge, Auclair & Sieroff, 2000). In the present study, we aimed to characterize the role of response preparation in age-related improvements in inhibitory control from childhood into adulthood by parametrically varying the length of the preparatory interval (also referred to as the instruction period). We chose a range of intervals that included prolonged time intervals so as to allow exploration of upper limits in the ability to sustain a preparatory state over development.

The antisaccade (AS) task (Hallett, 1978), which requires the suppression of a reflexive visually elicited eye movement and the generation of a voluntary response guided by an internal representation, is particularly well-suited for exploring the role of response preparation on developmental improvements of inhibitory control. Single-cell non-human primate studies and human neuroimaging studies of this task have carefully delineated the role of response preparation on the ability to inhibit a response (Amador, Schlag-Rey & Schlag, 2004; Connolly et al., 2002; Curtis & Connolly, 2008; Curtis & D'Esposito, 2003; DeSouza et al., 2003; Everling, Dorris, Klein & Munoz, 1999; Everling & Fischer, 1998; Everling & Munoz, 2000; Ford et al., 2005; Funahashi, Chafee & Goldman-Rakic, 1993; Schlag-Rey, Amador, Sanchez & Schlag, 1997). Given that the AS task is not easily amenable to strategy use and responses do not require transferring

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information across modalities (stimulus input and response output both occur in the visual domain), it is particularly well-suited to studies of developmental change.

Developmental improvements in AS performance have been well-characterized in healthy children and adolescents and consistently indicate a protracted pattern of maturation into adolescence (Fischer, Biscaldi & Gezeck, 1997; Fukushima, Hatta & Fukushima, 2000; Klein, 2001; Klein & Feige, 2005; Klein & Foerster, 2001; Klein, Foerster, Hartnegg & Fischer, 2005; Luna, Garver, Urban, Lazar & Sweeney, 2004; Munoz, Broughton, Goldring & Armstrong, 1998; Nieuwenhuis, Ridderinkhof, van der Molen & Kok, 1999; Romine & Reynolds, 2005). Specifically, from childhood to mid-adolescence, there is a significant decrease in rates of inhibitory errors, indicating improvements in the ability to consistently exert inhibitory control. Latencies to initiate correct antisaccades also show a significant decline over childhood and into adolescence, with adult levels being reached at approximately fifteen years of age. For both inhibitory parameters, developmental trajectories are characterized by a curve fit (Klein & Foerster, 2001; Luna et al., 2004), indicating that improvements in inhibitory abilities occur more rapidly in childhood and rates of change slow in the adolescent years.

Behavioral studies have manipulated the length of the preparatory period to examine the role of preparation in performance of adults. These studies indicate advantages of prolonged preparatory periods in supporting inhibitory control (Cepeda, Kramer & Gonzalez de Sather, 2001; Kramer, Hahn & Gopher, 1999; Meiran, 1996;2000; Rogers & Monsell, 1995) and AS performance in particular (Barton, Greenzang, Hefter, Edelman & Manoach, 2006; Connolly et al., 2002). In the AS task, the preparatory period is well-defined by the period of instruction when subjects see a cue instructing them to prepare to inhibit a response but are awaiting the unpredictable location where the visual target they must suppress will appear. During this period, participants must prepare by fixating on the instruction cue, maintaining the task instruction to inhibit a response, and pre-setting the oculomotor system to decrease the probability of making a reflexive saccade upon seeing the target in order to successfully execute an AS. Adult studies have established that longer preparatory times lead to fewer errors and shorter latencies to initiate a correct AS response (Barton et al., 2006; Connolly et al., 2002), and that preparation in adults can be sustained for long instruction periods spanning more than 7000 ms (Curtis & Connolly, 2008).

Successful inhibition on the AS task requires recruitment of a widely distributed brain circuitry that includes the frontal eye fields (FEF), supplementary eye fields (SEF), dorsolateral prefrontal cortex (DLPFC), posterior parietal cortex, anterior cingulate cortex, basal ganglia, dorsomedial thalamus, and superior colliculus (Burman & Bruce, 1997; Doricchi et al., 1997; Everling et al., 1999; Funahashi et al., 1993; Gottlieb & Goldberg, 1999; Luna et al., 2001; O'Driscoll et al., 1995; Schlag-Rey et al., 1997; Sweeney et al., 1996). Single-cell studies have shown that successful generation of antisaccades requires enhanced activity in cortical and subcortical regions that support oculomotor control including the DLPFC (Funahashi et al., 1993), lateral intraparietal area (Gottlieb & Goldberg, 1999), SEF (Amador et al., 2004; Schlag-Rey et al., 1997), FEF (Everling & Munoz, 2000), and superior colliculus (Everling et al., 1999; Everling & Fischer, 1998) during the instruction phase, prior to target appearance. Findings from neuroimaging studies suggest similar processes occur in humans, with studies indicating that frontal and parietal areas show greater activity during the instruction period but not the response generation period for correct trials (Brown, Vilis & Everling, 2007; Connolly et al., 2002; Curtis & D'Esposito, 2003; DeSouza et al., 2003; Ford et al., 2005). These preparatory modulations of the oculomotor control circuitry are also correlated with performance (Curtis & D'Esposito, 2003; Ford et al., 2005). Importantly, regions identified to support response preparation and AS performance in general are recruited by children, teens, and adults, but are activated at different magnitudes across development (Luna et al., 2001; Velanova, Wheeler & Luna, 2008). Limitations in AS performance in children and adolescents may be underlain by immaturities in the ability to rapidly process information in task-relevant regional circuitry that would undermine the ability to engage areas crucial to AS performance during the preparatory period. This suggests that, in light of their immaturities, children and adolescents may benefit from additional time to prepare an inhibitory response. This study sought to examine the role of preparation on AS performance over the course of development using a behavioral approach.

While this has not yet been investigated using the AS task, three studies have examined the role of preparation on inhibitory control over development. These studies found improved performance with increased preparation times in children using the stop-signal task (Carver, Livesey & Charles, 2001a,b) and the continuous performance task-AX (CPT-AX) (Okazaki et al., 2004), suggesting that increased preparation time does benefit performance in younger age groups. However, results regarding interactions of age group and preparation time were mixed. Two studies using short preparatory intervals (none longer than 900 ms) reported a synergistic interactions in samples of five to nine year old children (Carver et al., 2001a,b), suggesting that increases in preparation time actually *enhance* age-related differences in inhibitory control performance rather than allow younger participants to compensate for slow preparatory processes. Another study by (Okazaki et al., 2004) that included older children (ages nine to thirteen) and used longer time intervals (800 to 3000 ms) did not find an interaction of preparation time and age, suggesting that increased preparation does *not* affect age-related differences. Given the non-overlapping age ranges and preparatory periods across studies using two different tasks, it is not clear if these results are discrepant due to methodological variations or if they actually represent different effects of preparation at different periods in development.

We extend this research by considering age as a continuous variable as well as in defined age groups and by including a wider age range. This approach allowed us to characterize the shape of development and more precisely identify when adult levels of performance are reached. In addition, we also apply group comparisons when probing the nature of simple effects in order to compare our results with the existing literature and to maximize statistical power. The age range used is wider than in previously reported studies, making this the first study of the effects of preparation over development to include adolescents in addition to children and adults. Adolescents are relevant to this study because during this period inhibitory abilities continue to improve (Fischer et al., 1997; Fukushima et al., 2000; Klein, 2001; Klein & Foerster, 2001; Luna et al., 2004; Luna & Sweeney, 2004; Munoz et al., 1998; Nieuwenhuis et al., 1999; Romine & Reynolds, 2005) and psychopathologies characterized by impairments in inhibitory control typically emerge (Ettinger et al., 2004; Everling & Fischer, 1998; Hutton & Ettinger, 2006). Importantly, we were able to examine patterns of developmental improvement and their interactions with response preparation using a continuous age variable, which allowed us to use a regression framework to examine and model the nature of developmental change. As noted by Klein and colleagues (Klein & Feige, 2005; Klein, Foerster & Hartnegg, 2007), this is an important departure from previous developmental studies that have relied on group-based comparisons that require imposing artificial boundaries between age groups that may alter the nature of results or undermine our ability to understand when developmental changes occur. Still, to facilitate interpretation of our data in the context of the existing literature, we supplemented our analyses by also examining the effects of preparation time on performance at discrete stages of development (childhood, adolescence, and adulthood).

The AS task was chosen over other inhibitory control tasks because the role of response preparation has been well-delineated at multiple