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Working memory filtering continues to develop into late adolescence



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ABSTRACT

While most measures of working memory (WM) performance have been shown to plateau by midadolescence and developmental changes in fronto-parietal regions supporting WM encoding and maintenance have been well characterized, little is known about developmental variation in WM filtering. We investigated the possibility that the neural underpinnings of filtering in WM reach maturity later in life than WM function without filtering. Using a cued WM filtering task (McNab and Klingberg, 2008), we investigated neural activity during WM filtering in a sample of 64 adults and adolescents. Regardless of age, increases in WM activity with load were concentrated in the expected fronto-parietal network. For adults, but not adolescents, recruitment of the basal ganglia during presentation of a filtering and related basal ganglia function may still be maturing throughout adolescence and into adulthood.

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1. Introduction

Working memory (WM) is the ability to maintain representations of recently experienced or recalled information over a short period of time (Curtis and D'Esposito, 2003). The capacity of working memory in humans is limited (Cowan, 2001; Miller, 1956), and individual differences in capacity are correlated with a variety of cognitive and social outcomes including school performance (Dumontheil and Klingberg, 2012; Finn et al., 2014; Gathercole et al., 2003). Working memory encoding and maintenance without distractors is reliant on the middle frontal gyrus (MFG) and superior parietal cortex, specifically, the intraparietal sulcus (IPS; Todd and Marois, 2004). Recent research has shown that WM filtering ability - the ability to filter extraneous or distracting information from WM during encoding - is strongly associated with overall WM capacity and accuracy (Vogel et al., 2005). Evidence from neuroimaging suggests that the basal ganglia (BG) play an important role in filtering out extraneous information (McNab and Klingberg, 2008). Although a variety of studies have tracked the development of WM and associated neural systems from childhood to early adulthood (Asato et al., 2010; Curtis and D'Esposito, 2003; Lenroot and Giedd, 2006; Sowell et al., 1999, 2004), developmental

* Corresponding author. Tel.: +1 734 276 0246. *E-mail address:* sheridan.margaret@unc.edu (M.A. Sheridan). variation in patterns of neural function that support WM filtering, specifically, remain largely unexplored.

Contemporary neurocognitive theories of WM function suggest that, during encoding and maintenance, activity in the MFG reflects a top-down control process that serves to maintain representations of visual stimuli which are processed in the IPS (Curtis and D'Esposito, 2003). Research on WM in humans and other primates has consistently shown activity in the MFG (Goldman-Rakic, 1996) and IPS (Hartley and Speer, 2000; Nelson et al., 2000; Thomas et al., 1999) during tasks where working memory load is manipulated. The MFG and IPS appear to make distinct contributions to WM. Activity in the MFG, but not IPS, is implicated in top-down control over representations in WM (Feredoes et al., 2011; Sakai et al., 2002). Activity in the IPS appears to reflect actual WM storage or maintenance; this idea is supported by several ERP studies which have found that contralateral delay signal over parietal scalp scales with WM load but plateaus when load exceeds the capacity of the subject (McCollough et al., 2007; Vogel and Machizawa, 2004; Vogel et al., 2005). Functional magnetic resonance imaging (fMRI) studies have localized this 'contralateral delay' signal to the IPS, such that blood oxygen level dependent (BOLD) signal in the IPS is associated with the number of items being maintained in WM (Todd and Marois, 2004; see also: Xu and Chun, 2006).

Recent research additionally suggests a crucial role for the BG in filtering information into WM. Evidence for this hypothesis comes from several sources. Computational models of WM that model the BG as responsible for selectively updating information in WM

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reproduce core human WM abilities including acquiring new filtering rules, selective rapid encoding of new information, and robust maintenance (Frank et al., 2001; Hazy et al., 2006). Importantly, general hypotheses about patterns of neural activity during WM tasks based on these models have been tested successfully in empirical studies (Braver and Bongiolatti, 2002; Frank, 2005; Frank et al., 2004; Koechlin et al., 2000, 2003; for review, see Hazy et al., 2006). However, none of these studies attempted to isolate the BG's role in filtering specifically, McNab and Klingberg (2008) addressed this problem directly with a novel task in which subjects were prepared for a delayed match to sample task via a cue, which indicated the presence or absence of distractors in the upcoming encoding period. Neural activity during cues which indicated the upcoming presence of distractors compared to cues which did not was thought to reflect activity in filtering-related structures absent confounding activity from encoding or maintenance processes (McNab and Klingberg, 2008; Sakai and Passingham, 2006). In this study the authors demonstrated that activity in the BG was increased for distractor cues relative to non-distractor cues in their adult sample. This increased filter preparatory activity in the BG was associated with reduced encoding of distractors as measured by reduced IPS activity during maintenance as well as better task performance. Additional studies of the BG's role in filtering have shown that individuals with lesions in the BG are more likely to attend to irrelevant information in WM tasks (Baier et al., 2010; Voytek and Knight, 2010).

1.1. Development of WM during childhood

The greatest increases in WM capacity occur before midadolescence, with gains continuing more gradually into young adulthood (Cowan et al., 2006; Gathercole, 1999; Kwon et al., 2002; Sander et al., 2011). The fronto-parietal WM network follows a similar developmental course, with frontal and parietal gray matter volume peaking between 10 and 14 years of age and decreasing into the twenties (Dempster, 1992; Lenroot and Giedd, 2006). These structural changes have been associated with changes in WM ability (Darki and Klingberg, 2014; Kharitonova et al., 2013). Additionally, WM related activity in the prefrontal and parietal cortices increases with increasing age during childhood and throughout adolescence (Casey et al., 1995; Klingberg et al., 2002; Kwon et al., 2002; Thomas et al., 1999; Thomason et al., 2008). As children develop they are better able to recruit brain regions associated with WM encoding and maintenance (e.g. MFG, IPS) and their performance on WM tasks improves in parallel to the structural and functional development of these structures.

Few studies have examined the development of WM filtering specifically. Spronk et al. (2012) found that 12-16 year olds show reduced WM filtering capability relative to adults. WM performance without filtering was also impaired in adolescents in this study, suggesting a possible confounding effect of simple WM performance. Other research has suggested that age-related discrepancies in filtering performance may occur only when WM capacity is taxed (Cowan et al., 2010). Alternately, the development of filtering ability may drive increases in WM capacity in middle childhood and early adolescence, as several authors have linked filtering ability and related brain activity to WM capacity in adults (McNab and Klingberg, 2008; Vogel et al., 2005). Simple WM encoding and maintenance performance appears to stabilize by late adolescence, but performance on more complex WM tasks, such as those involving distraction or manipulation of stimuli in memory, have shown performance gains during this period (Bunge and Wright, 2007; Crone et al., 2006; Schleepen and Jonkman, 2010). Relatedly, the BG appear to mature into young adulthood (Asato et al., 2010; Lenroot and Giedd, 2006; Østby et al., 2009; Sowell et al., 1999) suggesting that WM filtering may continue to develop

throughout adolescence even after simple maintenance and encoding processes have reached adult levels. Examination of filtering function in later adolescence may help disentangle changes in WM filtering function from developmental changes in WM encoding and maintenance.

No studies to date have examined the functional neurodevelopment of WM filtering in late adolescence. The present study addresses these gaps in the literature by adapting an established fMRI paradigm (McNab and Klingberg, 2008) for use in a sample of older adolescents, around 16 years in age on average, and adults. Given that WM maintenance is likely to be well developed by late adolescence, but WM filtering may continue to mature, we hypothesized that adolescents would perform worse on filter trials than adults and that they would recruit the BG less robustly than adults in response to cues indicating the presence of distractors.

2. Methods

2.1. Sample

A sample of 64 adolescents and adults aged 13–36 participated. Of these, three adolescents and one adult participant whose total accuracy were less than 2.5 SD below the mean (<39% correct) were excluded as behavioral outliers. Of the remaining participants, Forty-three were adolescents age 13–18 (M=16.74, SD=1.22, 70% female) and 17 were adults age 19–36 (M=24.44, SD=5.18, 53% female). Exclusion criteria included psychiatric medication use with the exception of stimulant medications for ADHD (discontinued 24 h before the scan), metal orthodontics unsuitable for MRI, claustrophobia incompatible with entering the MRI machine, active substance use disorder, major developmental or genetic disorders, and non-English speaking. All procedures were approved by the institutional review board for the protection of human subjects at Boston Children's Hospital.

47 subjects (43 adolescents and 4 adults) were recruited as part of a previous study. These participants took part in a two-session lab visit that included assessments of IQ using the 2-subtest short form of the Wechsler Abbreviated Scale of Intelligence (WASI), violence exposure, mental health, and emotional reactivity. Of these approximately 1/3 of the subjects reported experiencing some form of violence during childhood¹. Data from this study are described elsewhere (McLaughlin et al., 2015). The remaining 13 adults were recruited from the Boston and Cambridge area using flyers and word of mouth. These individuals participated in a one-session lab visit that included MRI and fMRI only. To estimate IQ in this group, we administered the matrix reasoning subscale of the WASI; *t*-scores on this subscale were used for all participants as an index of IQ.

Matrix reasoning data were missing for 13 subjects due to experimenter error. In the entire sample, matrix reasoning ability was significantly higher in adults (M = 59.8, SD = 6.81) than adolescents (M = 49.4, SD = 11.26, t(45) = 2.772, p = .008). When including this estimate of IQ as a covariate modified our results, we report this difference.

¹ Because some of the children in the previous study's sample had been exposed to violence (e.g., maltreatment, community violence) a composite violence exposure score was calculated based on measures of exposure to home and neighborhood violence using the Screen for Adolescent Violence Exposure (Hastings and Kelley, 1997) and the Childhood Trauma Questionnaire (Bernstein et al., 1997). Violence scores for the additional adult sample who were not part of the original study were imputed from the mean score of the control group from the original study which assumes that adults were not exposed to traumatic violence. We performed all analyses with and without this variable as a control and found that it did not account for any finding presented in this paper.

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