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Research Report

Developmental differences in sustained and transient activity underlying working memory

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ABSTRACT

The amount of information one can maintain in working memory (WM) increases between childhood and adulthood (Gathercole, 1994, 1999; Klingberg, 1998; Luciana, 1998; Luciana and Nelson, 1998). In addition to cognitive changes that occur early in life, childhood and adolescence are periods marked by significant neuroanatomical changes that are thought to underlie cognitive maturation. This study used a mixed state-item design and a parametric "*n*-back" task to explore the relationship between WM load and neural activity changes with age. Thirty-five participants from two age groups (9 to 13 and 18 to 23 years) were recruited. Our behavioral results indicated that children performed significantly worse than adults at loads of 2-back, but not 0- and 1-back. Our imaging results indicated that during performance of the 2-back task, children showed evidence for increased transient, but decreased sustained activity, in comparison to adults. These results suggest that for the 2-back condition, children had more difficulty maintaining task relevant information across trials and seemed to engage in a more reactive strategy wherein they reactivated context information on a trial-by-trial basis rather than maintaining over a delay. These results have important implications for understanding the development of specific processes within the WM system.

1. Introduction

A number of studies have shown that working memory performance (WM) improves during childhood (Gathercole, 1994, 1999; Klingberg, 1998; Luciana, 1998; Luciana and Nelson, 1998). In addition, studies that have assessed the relationship between brain-activity and age-related changes in WM from childhood to adulthood have shown that children activate many of the same regions as adults during WM tasks. However, these studies have also shown differences in the level of WM related activity between adults and children, with somewhat variable results across studies. It is possible that some of the variable results across studies reflect differences in the types of tasks used, and the degree to which such tasks tap different components of working memory (e.g., sustained activity that may reflect the maintenance of information versus item related activity that may reflect updating, manipulation, etc.) or use different memory loads. Thus, to better understand how WM related brain activity changes with increasing age, the present study used: 1) a state-item design that allowed us to differentiate between neural correlates of sustained and transient processes associated

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with WM; and 2) multiple memory loads to examine how age-related brain activity varied as a function of load.

Behavioral studies examining age related change in WM have fairly consistently shown that working memory capacity increases with age. For example, studies using variants of an Sternberg item recognition task, a task that clearly taps the ability to maintain items in WM, have shown that children perform less accurately than adolescents and/or adults at high load levels (de Belleroche and Neal, 1982; De Luca et al., 2003; Luciana, 1998; O'Hare et al., 2008; Thomason et al., 2009; Tsujimoto et al., 2004). Similar results have also been found using WM tasks that tap updating and temporal coding in WM, as well as the maintenance of information. For example, several studies have examined performance on the *n*-back task (Kwon et al., 2002; Vuontela et al., 2003), in which participants must look for items that match a stimulus present n-trials back (e.g., 1, 2 or 3 trials back). This task necessitates the updating of the contents of the memory set on each trial, and also requires individuals to code the order of items within memory. These studies have also consistently found reduced performance in children as compared to adults.

A growing number of studies have also examined the neurobiological mechanisms that may support age related changes in WM function. Although children attain adult-like levels of total cerebral volume by approximately 5 years (Giedd et al., 1996; Kretschmann et al., 1986; Reiss et al., 1996), gray and white matter in the brain continue to develop through adolescence, with maturational trajectories that differ across regions of the brain. White matter density increases linearly with age from childhood to adulthood (Giedd et al., 1999; Nagy et al., 2004; Schmithorst et al., 2002; Snook et al., 2005). In contrast, gray matter density is thought to increase and then decrease during pre- and post-adolescence, respectively (Giedd et al., 1999, 1996; Gogtay et al., 2004; Sowell et al., 1999a,b). Interestingly, maturation of regions thought to subserve WM (i.e., prefrontal, superior parietal, and temporal cortices) occurs last (Gogtay et al., 2004; Sowell et al., 2004, 2002). Further, a number of studies have shown that maturation of these regions is positively correlated with performance on cognitive tasks (Nagy et al., 2004; Sowell et al., 2004, 2001).

A number of studies have also used functional neuroimaging to compare developmental changes in the neural correlates of WM (Casey et al., 1995; Ciesielski et al., 2006; Crone et al., 2006; Klingberg et al., 2002; Kwon et al., 2002; Nelson et al., 2000; Olesen et al., 2003; Schweinsburg et al., 2005; Thomas et al., 1999; Tsujimoto et al., 2004). Many of these studies have found that children activate a number of the same regions as adults during WM tasks. However, there are mixed results with regard to the direction of age related changes in functional brain activation during WM tasks. For example, some studies report positive correlations between prefrontal brain activity and age (Casey et al., 1995; Ciesielski et al., 2006; Klingberg et al., 2002; Kwon et al., 2002; Schweinsburg et al., 2005), such that activity is greater in adults than children. In contrast, other studies report negative correlations (Klingberg et al., 2002; Schweinsburg et al., 2005; Tsujimoto et al., 2004), such that activity is greater in children than adults.

One possible explanation for this discrepancy across studies is that the majority have used blocked fMRI designs. Blocked fMRI designs confound activity related to processes associated with each individual trial within a task block with processes that are sustained across trials (Visscher et al., 2003). In the context of a WM task, the use of such a blocked design can confound activity related to sustaining information in WM memory across trials with activity related to processing each individual trial (response selection, updating, temporal coding). It is possible that developmental changes in WM are more associated with one component than another (e.g., maintenance of information versus updating/temporal coding), or that the *pattern* of age-related change in brain activity associated with one component versus the other might differ (e.g., increased or decreased activity associated with sustained or item related processes). Thus, using a block design may produce variable results across studies if tasks differ in the degree to which they emphasize WM processes such as maintenance of information versus updating/temporal coding. In order to separately examine these different components of brain activity with fMRI, one needs to use a state-item design that allows for separate estimates of sustained versus item-related functional brain activity. Using such a design, if we find age differences in sustained activity, it may suggest that children have relative difficulty actively maintaining item and order information. In contrast, if we find age-related differences in transient or item-related activity, it would suggest that children have difficulty with more item-specific processes, such as updating, temporal coding, or response selection.

Another possible explanation for the discrepancy in the direction of age-related differences in functional brain activation across WM studies is that age differences in the magnitude of activation could reflect age differences in neural efficiency. The hyperactivation in children compared with adults found in some studies may be the consequence of children having to recruit additional cognitive resources to accomplish the same task demands as adults. This phenomenon may be particularly apparent at lower loads that are still within the WM abilities of children. In contrast, hypoactivation in children may represent decreased neural activity when their WM abilities are exceeded at higher load levels. Such hypotheses related to changes in neural efficiency associated with WM have been suggested to account for functional brain activation changes in older adults, but may be equally applicable to development at the beginning of the life span (Reuter-Lorenz et al., 1999). Of those studies reporting increased activity in regions for children versus adults, few have compared activation levels in children and adults at multiple load levels. To our knowledge, only a handful of studies have looked at the relationship of WM capacity and load level in children with functional imaging (Klingberg et al., 2002; O'Hare et al., 2008; Thomason et al., 2009). Of these studies, two (Thomason et al., 2009) looked specifically at age related differences in activation across multiple load levels. Thomason et al. (2009) examined activation differences between children (ages 7 to 12) and adults across multiple loads (spans of 2, 4, or 6 in a parametric Sternberg paradigm) and found greater increases in activity within a number of regions in adults versus children. O'Hare et al. (2008) examined activation differences between children (ages 7 to 10), adolescents (ages 11 to 15) and young adults (ages 20 to 28) across multiple loads (spans of 1, 3, and 6 in a parametric Sternberg paradigm) and found that linear load-dependent activity was significantly increased in adolescents and young adults relative to children in left superior parietal lobe (BA7) as well as in right superior and inferior