



Functional developmental similarities and differences in the neural correlates of verbal and nonverbal working memory tasks

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Abstract

Relatively little is known about the functional development of verbal and nonverbal working memory during adolescence. Behavioral studies have demonstrated that WM capacity increases with age, yet relatively few studies have assessed the relationship between brain-activity and age-related changes in WM capacity, especially as it differs across multiple domains. The present study used an n-back task and functional magnetic resonance imaging to assess age-related differences in the neural correlates of word and face working memory tasks. Seventy-eight individuals between the ages of 14 and 27 underwent scans while performing word and face “n-back” working memory tasks. We found very little evidence for age-related differences in accuracy and reaction time. We did find similarities and differences between adolescents and adults in the neural correlates of word and face working memory tasks, even in the absence of performance differences. More specifically, we found similar age-related differences in left superior parietal cortex for both word and face stimuli. We also found that age-related differences in a number of other regions (including left inferior frontal lobe, left supramarginal gyrus, left rolandic sulcus, right cerebellum and left fusiform gyrus) differed according to stimulus type. Our results provide further evidence for continued functional development through adolescence and into adulthood.

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Childhood and adolescence are periods marked by significant neuroanatomical change. White matter density increases linearly with age from childhood to adulthood (Giedd et al., 1999; Nagy, Westerberg, & Klingberg, 2004; Schmithorst, Wilke, Dardzinski, & Holland, 2002; Snook, Paulson, Roy, Phillips, & Beaulieu, 2005), while grey matter growth is thought to resemble an inverted “u-shaped” curve, characterized by increases in grey matter density prior to puberty followed by decreases in grey matter density during post-adolescence (Giedd et al., 1999, 1996; Gogtay et al., 2004; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999). Interestingly, there are regional differences in the timing and pattern of brain maturation. For example, the primary sensorimotor cortices mature earlier than higher order association areas such as the superior temporal gyrus, posterior parietal cortex, and prefrontal cortex (Gogtay et al., 2004). As is reported by Gogtay et al. (2004), the dor-

solateral prefrontal cortex (DLPFC), parts of the parietal lobe and lateral temporal lobes, which are involved with executive functions, are amongst the last to mature. More specifically, research suggests that maximal grey matter density loss in frontal cortex occurs between adolescence and adulthood with little further maturational change occurring in parietal, temporal, and occipital cortices during this age period (Sowell, Thompson, Holmes, Jernigan, et al., 1999). The period of maximal grey matter density loss in parietal cortex is also delayed, but precedes that of the frontal cortex and occurs between childhood and adolescence (Sowell, Thompson, Holmes, Jernigan, et al., 1999). White matter development resembles that of grey matter, such that myelination progresses from posterior/inferior to anterior/superior brain regions, with delayed myelination of parietal and frontal cortices (Yakovlev & Lecours, 1967).

As the brain continues to develop structurally, there are also refinements in various cognitive abilities, as the brain becomes more capable of performing complex cognitive functions. Of particular relevance to the present project is the working memory (WM) system, a set of cognitive processes that allow for the temporary maintenance and manipulation of

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information “on-line” (Baddeley, 1996). Baddeley’s prominent model of WM separates this cognitive construct into three components: the phonological loop, visuospatial sketchpad, and central executive (Baddeley & Hitch, 1974). The central executive is involved with functions such as the manipulation and updating of information and is thought to depend on the dorsolateral prefrontal and superior parietal cortices (for review, see Baddeley, 2003). Further, these central executive functions are thought to be primarily amodal (i.e., engaged across multiple WM domains) (Braver et al., 2001; D’Esposito et al., 1998; Nystrom et al., 2000; Owen, 1997; Ravizza, Delgado, Chein, Becker, & Fiez, 2004), while the phonological loop and visuospatial sketchpad maintain domain specific information and are thought to be supported by dissociable brain systems. For example, the phonological loop has been associated with the function of left inferior frontal cortex, left ventral parietal cortex and temporoparietal cortex (Smith, Jonides, & Koeppe, 1996). In contrast, the visuospatial sketchpad has been associated with the function of right occipital cortex, right ventrolateral frontal cortex, and right posterior parietal cortex, although there is some evidence for recruitment of regions in left hemisphere for more demanding tasks (Smith et al., 1996).

Recent literature on cognitive development suggests that the WM system (central executive functions, in particular) continues to develop through adolescence and early adulthood (Gathercole, Pickering, Ambridge, & Wearing, 2004; Luciana, Conklin, Hooper, & Yarger, 2005; Luna, Garver, Urban, Larzar, & Sweeney, 2004). For example, separate domain specific buffers as well as the central executive component of WM seem to be present by age 6 (Gathercole et al., 2004), but all three components continue to develop through childhood and adolescence (Gathercole et al., 2004; Hale, Bonik, & Fry, 1997). Studies examining the development of WM across childhood and adolescence suggest that the development of this cognitive system coincides with the timing of neuroanatomical maturation in dorsal frontal and parietal cortices, with the development of the executive control component of WM continuing throughout childhood and adolescence (Anderson, Anderson, Northam, Jacobs, & Catroppa, 2001; Brocki & Bohlin, 2004; Gathercole et al., 2004; Levin, Eisenberg, & Benton, 1991; Luciana & Nelson, 1998). Given that the central executive components of WM are utilized for both verbal and nonverbal materials, one would expect similar developmental changes across WM domains in functions and brain regions associated with these amodal components of WM.

Structural and functional changes in brain regions involved with WM (i.e., parietal and frontal regions) occur later than a number of other brain regions and seem to coincide with development of WM functions (Gogtay et al., 2004; Sowell, Thompson, Holmes, Batth, et al., 1999; Sowell, Thompson, Holmes, Jernigan, et al., 1999), thus providing suggestive evidence for a relationship between brain maturation and WM development. Several studies have examined this relationship using neuroimaging techniques and have suggested continued maturation of brain regions into the 2nd and 3rd decades of life. However, functional neuroimaging studies exploring cognitive development have focused on a much younger age range

and have suggested that children engage in different strategies to compensate for inefficiencies in brain processing. While studies on younger children have provided important information regarding early cognitive and neural development, a potential interpretive issue in these studies is that differences in brain activation may reflect performance differences as there are still significant and often large differences in WM capacity between young children and adults. Studying adolescents who are more cognitively developed, but whose brains are presumably still not functionally mature, allows us to look for developmental differences in activated networks, with little or no performance differences. For example, if performance differences are not present between groups, functional imaging enables us to explore whether adolescents perform the task in the same way that adults do or rather whether adolescents use some sort of compensatory mechanism or alternate strategy that enables them to fulfill task demands in the same way that older individuals do.

Functional differences in brain activity between groups in the absence of performance differences could imply that groups are engaging in different strategies to fulfill task demands for verbal and nonverbal stimuli types. Behavioral work on strategy changes with development have focused primarily on younger children and have shown that while children younger than 7 appear to rely on visual features of visually presented stimuli, children 8 and older appear to rely more heavily on phonological cues and rehearsal (Hitch & Halliday, 1983; Hitch, Woodin, & Baker, 1989). Palmer (2000) suggested that this evolution in strategy use might be more complex than a simple shift from strategies that are visually based to those that are more phonological in nature. In a series of experiments, she showed that younger children rely primarily on visual strategies but that by the ages of 6 and 7 children engage in a dual-coding strategy whereby visual presentations activate both visual and phonological representations (Palmer, 2000). She also suggested that adult-like strategy use is characterized by the automatic phonological recoding of visual information. Given that there are structural and functional maturational changes continuing through adolescence, it is possible that the recoding of information is still not fully automatized in adolescents and they may engage in different strategies to compensate for inefficiencies in brain processing. Several studies looking at visuospatial working memory across development have found greater brain activity in adults compared to children within regions implicated in verbal rehearsal (Kwon, Reiss, & Menon, 2002; Scherf, Sweeney, & Luna, 2006), which provides further support for the hypothesis that adults are better able to recode visual information into phonological form. On the other hand, it is also possible that by mid to late adolescence, material specific effects do not significantly differ from that of adults and that associated functional brain activity will not differ between groups.

To date, the majority of the studies examining WM during development have used nonverbal visuospatial stimuli, and have found that children activate a network of regions that are similar to those activated by adults during performance of WM tasks (Casey et al., 1995; Nelson et al., 2000; Thomas et al., 1999). At the same time, these studies also report a pos-

itive association with age in regions typically associated with WM (Klingberg, Forssberg, & Westerberg, 2002; Kwon et al., 2002; Schweinsburg, Nagel, & Tapert, 2005). Collectively, the visuospatial WM neuroimaging literature suggests that children engage many of the same regions that adults do when performing WM tasks, but that children show greater activation than adults in superior parietal and frontal cortices that are associated with higher order executive functions. Importantly, very little is known about age-related changes in brain activity associated with verbal and nonverbal object domains of working memory. To our knowledge, only one functional neuroimaging study has assessed verbal working memory in children (ages 9–11; Casey et al., 1995), and reported WM related activation in superior, middle, and inferior frontal cortex as well as anterior cingulate and orbital gyrus. Of these five regions, significant age-related increases in activity (across the 9–11 age range) were found in inferior frontal gyrus and middle frontal gyrus, although this finding was speculative due to their small sample size ($N=6$). As is stated by the authors, these regions are consistent with those activated by adults during performance of an identical task. However, data from adults was not collected in the study, and thus comparisons were made between data from children in their study and data from adults in a separate study.

While all of these studies have provided important information about the neural correlates of WM development, it remains unclear as to whether age-related differences in a network of regions thought to subserve WM vary across object and verbal domains of WM during adolescence. The literature reviewed above indicates that children show reduced activation in DLPFC in both verbal and visuospatial working memory, which is consistent with the putative role of DLPFC in amodal central executive processes. There is also evidence that children showed reduced activation of dorsal parietal cortex in spatial WM, but activation in this region has not been examined in verbal or object WM in children or adolescence. As such, the dearth of research on developmental changes in verbal and nonverbal object WM make it difficult to determine whether there are material specific effects on the development of cortical regions supporting WM and whether functional differences in later maturing regions (i.e., superior parietal cortex and DLPFC) are still present during mid to late adolescence.

The goal of the present study was to examine age-related differences (between adolescence and adulthood) in the neural correlates of word and face working memory tasks. More specifically, we were particularly interested in exploring developmental differences in activated networks in an adolescent group that is

presumably more cognitively mature. Differences in functional activation, in the absence of performance differences could suggest that the adolescent group is using different strategies to fulfill task demands. To explore this question of interest, we administered word and face versions of the 2-back WM task to adolescents and young adults ranging in age from 14 to 27. We expected to see age-related effects in DLPFC and superior posterior parietal activity during both word and face WM.

1. Methods

1.1. Participants

Seventy-eight participants were recruited through the clinical core of the Conte Center for the Neuroscience of Mental Disorders (CCNMD) at Washington University in St. Louis as a healthy control comparison group for a study of schizophrenia. Exclusion criteria included any of the following: (a) meeting *DSM-IV* criteria for substance abuse or dependence within the past 6 months; (b) presence of any lifetime history of Axis I psychotic disorder (including Bipolar Disorder), but not other Axis I disorders; (c) head injury (past or present) with documented neurological sequelae or resulting in loss of consciousness; (d) meeting *DSM-IV* criteria for mental retardation (mild or greater in severity); (e) meeting *DSM-IV* criteria for substance abuse (severe) or dependence (any type) at any time within the past 3 months. Demographic information is displayed in Table 1. Participants ranged in age from 14 to 27 years old (mean age = 21.2 years, $S.D.=3.54$) and included 47 females and 31 males. As described in more detail below, our analyses involved identifying brain regions showing age-related differences in activation using two age groups (adolescents and young adults). These groups consisted of the 15 youngest (range = 14–17 years, mean age = 16.1 years, $F:M=8:7$) and 15 oldest (range = 24–27 years, mean age = 25.7, $F:M=9:6$) participants. The groups did not differ significantly on handedness [$F(1, 30)=0.52, p=.82$], gender [$\chi^2=.14, p=.71$], or parental education [$F(1, 30)=0.30, p=.59$]. Mean vocabulary scores (scaled) were significantly lower in the adolescent age group [$F(1, 30)=6.0, p=.02$] (see Table 1). Diagnoses for all participants were determined using the Structured Clinical Interview for *DSM-IV* (SCID-IV; (Spitzer, Williams, Gibbon, & First, 1990), and were assessed using the Scales for the Assessment of Negative and Positive Symptoms (SANS/SAPS (Andreasen, 1983a,b). The clinical assessments were conducted by a master's-level research assistant who had completed SCID-IV training and participated in regular diagnostic and clinical rating training sessions as part of the CCNMD. A consensus meeting between the SCID-IV interviewer and the expert clinician determined the participant's final diagnosis. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971).

1.2. Tasks and materials

Participants performed a “2-back” version of the “n-back” task while being scanned. Participants also performed episodic encoding tasks in the same session, the data from which are the focus of a different report (McAuley, Brahmhatt, & Barch, 2007). The episodic tasks were performed after the WM task and there was no overlap in stimuli used that would have confounded the results of the WM portion of the study. During the WM task, stimuli (words or

Table 1
 Demographic data for groups

Characteristic	Young (ages 14–17)		Old (ages 24–27)		Significance	
	M	S.D.	M	S.D.	F/χ^2	Sig.
Age (years)	16.1	1.2	25.7	1.0		
Gender (% male)	47		40		.14	.71
Parent's ed. (years)	15.9	1.9	15.5	2.1	.30	.59
Handedness (% right)	86.7		86.7		.52	.82
Vocabulary scores (scaled)	10.9	2.7	13.3	2.6	6.0	.02



Fig. 1. Example of word and face stimuli used in the present study.

faces) appeared one at a time on the screen and participants were told to push one button (target) any time they saw a stimulus that was the same as the stimulus they saw two trials back. If the stimulus was not the same as the one presented two trials back, they were told to push another button (nontarget). Stimuli for the word tasks were concrete visually presented words, 3–10 letters in length, presented in 48 point Geneva font (Fig. 1). The words came from one of two lists that were matched on frequency, length, and concreteness. Stimuli for the face tasks were non-famous faces (Barch, Csermansky, Conturo, Snyder, & Ollinger, 2002; Braver et al., 2001; Kelley et al., 1998; Logan, Sanders, Snyder, Morris, & Buckner, 2002). These faces were in color and had an equal number of male and female faces (see Fig. 1 for examples of stimuli).

Participants performed each WM task in a run lasting 4.25 min. Each run included four task blocks of 16 trials each and three fixation blocks of 10 trials each interleaved in alternating order with the task blocks. In addition, there were four fixation trials at the beginning of each run that were discarded in the analysis of the data (used to allow MR signal to reach steady state) and four additional fixations at the end. Task blocks lasted 40 s and fixation blocks lasted 25 s. Each of the items in a task block was presented for 2 s followed by a 500 ms interstimulus interval. During fixation blocks, a cross hair appeared continuously and participants were told to fixate. Visual stimuli were generated by an Apple PowerMac and PsyScope (Cohen, MacWhinney, Flatt, & Provost, 1993) and projected to participants with a Sharp LCD projector onto a screen positioned at the head end of the bore. Participants viewed the screen through a mirror attached to the top of the MR head coil. A fiber-optic key press interfaced with the PsyScope Button box was used to record participant's behavioral performance. The order in which participants performed the word versus face version of the n-back task was counterbalanced.

1.3. Procedure

1.3.1. Scanning

Scanning was performed on the 1.5T S VISION system at the Research Imaging Center of the Mallinckrodt Institute of Radiology at Washington University Medical School. Functional images were collected using an asymmetric spin-echo echo-planar sequence sensitive to blood oxygenation level-dependent (BOLD) contrast (T2*) (TR = 2500 ms, TE = 50 ms, FOV = 24 cm, flip = 90°). During each functional run, 102 sets of oblique axial images were acquired parallel to the anterior–posterior commissure plane (3.75 mm × 3.75 mm in plane resolution). Nineteen 7 mm thick slices were acquired in each image. Structural images were acquired using a coronal MP-RAGE 3D T1-weighted sequence (TR = 9.7 ms, TE = 4 ms, flip = 10°; voxel size = 1 mm × 1 mm × 1.2 mm). These

structural images were used for between subject registration and anatomic localization.

Preprocessing of the fMRI data included: (1) compensation for slice-dependent time shifts; (2) elimination of odd/even slice intensity differences due to interpolated acquisition; (3) realignment of data acquired in each subject within and across runs to compensate for rigid body motion (Ojemann et al., 1997); (4) intensity normalization to a whole brain mode value of 1000; (5) spatial smoothing with an 8-mm FWHM Gaussian kernel. Functional data were transformed into stereotaxic atlas space (Talairach & Tournoux, 1988) by computing a sequence of affine transforms and resampled to 3 mm cubic voxels. Methods for movement correction and cross subject registration are analogous to the linear methods used in AIR (Woods, Grafton, Holmes, Cherry, & Mazziotta, 1998).

1.3.2. Statistical analysis

1.3.2.1. Functional magnetic resonance imaging data (fMRI). For each participant, we estimated the magnitude of task-related activation in each voxel with a general linear model (GLM) using a box-car function convolved with a canonical hemodynamic response, with separate estimates for each material type (e.g., WM-words, WM-faces). These estimates were then entered into appropriately designed ANOVAs and *t*-tests (described below) that treated subjects as a random factor. A region of interest-based approach was used to identify brain regions showing developmental changes associated with the various components of the working memory system, using regions identified with the following three functions in the literature: (1) visuospatial sketchpad; (2) phonological loop; (3) executive functions. The first step for this approach was to create region files for each working memory domain using boundaries from previous literature (see Table 2). We made regions composed of spheres with a 15 mm diameter. For the visuospatial sketchpad component, we included seven regions that were found to be significantly more active for face working memory than a sensorimotor control task in a study by Courtney, Ungerleider, Keil, and Haxby (1996). Eleven regions were included in the phonological loop component of the analysis and boundaries for these regions were based on the review paper by Vigneau et al. (2006). This review included studies of reading tasks, only some of which required working memory. For the executive function component, we included 14 regions that were based on coordinates described in a review paper by Wager and Smith (2003). This review included studies reporting whole brain comparisons of WM tasks in comparison with a control task with similar perceptual and motor requirements.

1.3.2.2. Within group analyses. We conducted a repeated measures ANOVA with task (task vs. fixation) and condition (word vs. face) as within subject factors for each group independently. We were particularly interested in identifying regions that showed one of the following effects in one or both group: (1) a main effect of task; (2) a task by condition interaction. The results of these within group analyses (particularly the analysis within the adult group independently from the adolescent group) served to validate our choice of ROIs.

1.3.2.3. Between group analyses. We also conducted a repeated measures ANOVA with task (task vs. fixation) and condition (word vs. face) as within subject factors and age group as a between subject factor. We were particularly interested in identifying regions that showed one of the following effects: (1) a main effect of task, with no further interaction with age (i.e., similar task-related activation in the young and older age groups and in word and face conditions); (2) a task by condition interaction, with no further interaction with age (i.e., similar task-related activation in the young and older age groups that differed for word and face conditions); (3) a task by age interaction (age group differences in task-related activation for both word and face conditions); (4) a task by condition by age interaction (age group differences in task-related activation that varied as a function of word or face conditions). To interpret the task by condition by age interactions, we conducted repeated measure ANOVAs with task and condition as within group factors for adults and adolescents separately using all regions that showed a task by condition by age interaction.

A potential interpretive issue in this study is that both vocabulary scores on the WASI and performance accuracy for faces were significantly lower in the adolescent versus adult participants. As such, it is possible that group differences

Table 2
 Regions of interest

Regions of interest	Brodmann's area	Coordinates		
Visuospatial scratchpad				
Left fusiform gyrus	19	-35	-78	-6
Left inferior frontal	44	-40	+8	+28
Anterior cingulate	32	0	+20	+36
Right orbital or inferior frontal	11/47	+22	+40	-4
Right fusiform gyrus	19	+28	-78	-12
Midline cerebellum		+2	-42	-16
Right middle frontal	45/46	+32	+36	+20
Phonological loop				
Left rolandic sulcus	4	-47	-6	+44
Left precentral gyrus	6	-48	+2	+26
Left inferior frontal gyrus	47	-44	+23	+15
Left rolandic operculum	13	-48	+8	+3
Left inferior frontal gyrus	47	-33	+37	-6
Left supramarginal gyrus	40	-42	-52	+37
Left superior temporal gyrus	22	-50	-38	+12
Left planum temporale	42	-60	-27	+9
Left superior anterior temporal gyrus	21	-56	-12	-3
Left inferior posterior temporal gyrus	37	-50	-60	-7
Left middle temporal gyrus	20	-51	-35	-11
Executive function				
Left VLPFC	10	-36	+31	+13
Left DLPFC	9	-44	+6	+32
Left inferior parietal lobe	40	-38	-50	+42
Right DLPFC	9	+40	+34	+29
Right cerebellum		+30	-61	-27
Left fusiform gyrus	37	-43	-55	-21
Right superior parietal lobe	7	+32	-60	+44
Right inferior frontal gyrus	47	+34	+31	-8
Left superior parietal lobe	7	-12	-71	+47
Medial presupplementary motor area	6/32	+0	+10	+50
Right lingual gyrus	18	+2	-85	+9
Right precentral gyrus	6	+28	-2	+57
Left thalamus		-8	-12	+11
Right middle frontal gyrus	6/9	+43	+2	+31
Left premotor cortex	6	-28	-2	+57

in brain activity may be related to differences in intelligence or performance rather than age. To address this question, we first reanalyzed the data using a subset of individuals (12 adolescents, 13 adults) that were matched on scaled vocabulary scores to determine which of the regions that showed a significant group effect survived after differences in vocabulary scores were taken into account. Next, we reanalyzed the data using a subset of individuals (13 adolescents, 15 adults), that were matched on performance accuracy for both word and face stimuli. More specifically, in these matched groups, performance accuracy did not significantly differ between adolescents and adults for word or face stimuli (although both groups were still more accurate on words than faces as a whole). While we were unable to match the adolescent and adult groups

such that there were no significant group differences between total word and face accuracy, we did reanalyze the data using a subset of adults (14 adults) who showed no significant performance differences between total word and total face accuracy.

1.3.2.4. Behavioral data. We examined the difference in task-related accuracy and reaction times between the two age groups. The behavioral data (accuracy and RTs to correct target and nontarget trials) were analyzed using repeated measures ANOVAs with group as a between subject factor and condition (word, face) and trial type (target, nontarget) as within subject factors.

2. Results

2.1. Behavioral data

The repeated measures ANOVA for accuracy indicated a significant main effect of trial type (target vs. nontargets; $F(1, 28) = 5.6, p = .025, \eta^2 = .166$) and condition (words vs. faces; $F(1, 28) = 32.7, p = .000, \eta^2 = .539$), such that both age groups had significantly more errors for targets than nontargets (93rd and 96th percentiles, respectively) and faces than words (94th and 98th percentiles, respectively). There was also a condition by trial type interaction ($F(1, 28) = 4.3, p = .049, \eta^2 = .132$), such that both groups made significantly more errors for target than nontarget trials for the face condition (92nd and 98th percentiles, respectively; $F(1, 29) = 7.8, p = .00, \eta^2 = .212$). Performance between target and nontarget trials for the word condition did not significantly differ (97th and 98th percentiles, respectively; $F(1, 29) = 1.36, p = .25, \eta^2 = .045$). There was no significant main effect of group ($F(1, 28) = 1.4, p = .146, \eta^2 = .079$) nor significant interactions between group and any of these factors (all p 's $> .209$). When we analyzed data for the word and face conditions separately, we found that performance for word stimuli still did not significantly differ between groups ($F(1, 28) = .10, p = .75$). We did, however, find a very slight, but significant group difference in performance for face stimuli ($F(1, 28) = 5.2, p = .03$) although both the younger and older groups performed very well (at 94th and 96th percentiles, respectively; see Table 3). For reaction time, there was a significant main effect of condition ($F(1, 28) = 16.3, p = .000, \eta^2 = .368$), such that both age groups had longer reaction times for face versus word stimuli (see Table 3). There were no significant main effects of trial type ($F(1, 28) = 1.04, p = .317, \eta^2 = .036$) or group ($F(1, 28) = .177, p = .677, \eta^2 = .006$) nor any significant interactions between condition and group ($F(1, 28) = .46, p = .503, \eta^2 = .016$), trial type by group ($F(1, 28) = .614, p = .440, \eta^2 = .021$), and condition, trial type, and group ($F(1, 28) = 3.2, p = .085, \eta^2 = .102$).

Table 3
 Behavioral data for groups

Characteristic	Young (ages 14–17)		Old (ages 24–27)		Significance	
	M	S.D.	M	S.D.	F/χ^2	Sig.
Word accuracy (% correct)	.98	.03	.98	.02	.10	.75
Word reaction time (ms)	868	156	810	194	.84	.37
Face accuracy (% correct)	.94	.03	.96	.03	5.2	.03
Face reaction time (ms)	934	154	923	205	.03	.87

Table 4
 Within group analyses

Regions of interest	Adults			Adolescents		
	Task	Task × condition	Task × condition pattern	Task	Task × condition	Task × condition pattern
Visuospatial scratchpad						
Left fusiform gyrus	2.1**	.17		1.6**	.69	
Left inferior frontal cortex	2.7**	.56		1.9**	1.2**	w > f
Anterior cingulate	.86*	.90*	f > w	.85*	.10	
Right fusiform gyrus	2.2**	1.0*	f > w	2.2**	.50	
Midline cerebellum	.80*	.12		.59	.28	
Phonological loop						
Left rolandic sulcus	2.6**	.25		1.6**	1.9**	w > f
Left precentral gyrus	1.9**	.60		2.2**	1.1**	w > f
Left inferior frontal gyrus	.15	.09		.21	1.0*	w > f
Left rolandic operculum	2.1**	.27		1.6**	.89*	
Left supramarginal gyrus	1.8**	.08		2.2**	1.4**	w > f
Left superior temporal gyrus	.43	.24		.80*	.63	
Left planum temporal	1.8**	.63		.65	.64	
Left superior anterior temporal gyrus	1.1**	.63		.93*	.27	w > f
Left inferior posterior temporal gyrus	.89*	.08		.29	.34	
Executive function						
Left VLPFC	.54	.26		.88*	.60	
Left DLPFC	1.7**	.39		2.7**	1.0*	w > f
Left inferior parietal lobe	3.9**	.11		2.5**	1.2**	w > f
Right DLPFC	1.7**	.44		1.1**	.63	
Right cerebellum	3.5**	1.5**	f > w	1.7**	.41	
Left fusiform gyrus	1.9**	1.0*	f > w	1.6**	.71	
Right superior parietal lobe	3.2**	1.0*	f > w	1.9**	.44	
Left superior parietal lobe	1.4**	.28		.10	.41	
Medial presupplementary motor area	2.7**	.54		2.3**	.54	
Right lingual gyrus	.32	.57		.36	1.6**	w > f
Right precentral gyrus	2.3**	.51		.12	.71	
Left thalamus	1.9**	.35		1.5**	.44	
Right middle frontal gyrus	2.5**	1.6**	f > w	1.1**	.05	
Left premotor cortex	1.6**	.06		.83*	.57	

Values represent effect sizes (Cohen's *d*). Task × condition patterns indicate the pattern of activity for face (f) stimuli vs. words (w). ***p* < .01, **p* < .05.

2.2. Functional magnetic resonance imaging data (fMRI)

2.2.1. Within group analyses

2.2.1.1. Adults. As shown in Table 4, for the visuospatial scratchpad regions, adults showed a main effect of task within a number of regions including bilateral fusiform gyrus, left inferior frontal cortex, anterior cingulate, and midline cerebellum. They also showed a task by condition interaction within anterior cingulate and right fusiform gyrus, such that the difference in activity between task and fixation was greater for faces than words. For the phonological loop regions, adults showed a main effect of task in a number of regions including left rolandic sulcus, left precentral gyrus, left rolandic operculum, left supramarginal gyrus, left inferior posterior temporal gyrus, left superior anterior temporal gyrus, and left planum temporal, but did not show any task by condition interactions in these regions. Lastly, for executive function regions, the adults showed a main effect of task in numerous regions, including bilateral DLPFC, left inferior parietal lobe, right cerebellum, left fusiform gyrus, right superior parietal lobe, left superior parietal lobe, left premotor cortex, medial presupplementary motor area, right precentral gyrus, left thalamus, and right middle frontal

gyrus. They also showed a task by condition interaction in left fusiform gyrus, right cerebellum, right superior parietal lobe, and right middle frontal gyrus. In all of these regions, the difference in activity between task and fixation was greater for faces than words.

2.2.1.2. Adolescents. Next we conducted within group analyses for each of the three working memory domains within the adolescent group. For the visuospatial regions, the adolescents showed a main effect of task in a number of regions, including bilateral fusiform gyrus, left inferior frontal cortex, and anterior cingulate. All but one region (midline cerebellum) showing significantly greater activity for task than fixation in adults showed the same pattern in adolescents. Adolescents also showed a task by condition interaction in left inferior frontal cortex, such that the difference in activity between task and fixation was greater for words than faces. For the phonological loop regions, the adolescents showed a main effect of task in numerous regions, including left rolandic sulcus, left precentral gyrus, left rolandic operculum, left supramarginal gyrus, left superior temporal gyrus, and left superior anterior temporal gyrus. Of note, all but two regions (left inferior posterior tempo-

ral gyrus and left planum temporal) showing a main effect of task in adults showed the same effect in adolescents. Additionally, adolescents showed a significant task by condition interaction within left supramarginal gyrus, left inferior frontal gyrus, left rolandic sulcus, left precentral gyrus, and left rolandic operculum, such that the difference in activity between task and fixation was greater for words in all regions. This interaction was not present within the adult group. Lastly, for executive function regions, the adolescents showed a main effect of task in numerous regions, including bilateral DLPFC, left VLPFC, left inferior parietal lobe, left fusiform gyrus, medial presupplementary motor area, left thalamus, left premotor cortex, right cerebellum, right superior parietal lobe, and right middle frontal gyrus. All but two regions (right precentral gyrus and left superior parietal lobe) showing significantly greater activity for task than fixation in adults showed the same pattern in adolescents. The adolescents also showed a task by condition interaction in left inferior parietal lobe, left DLPFC, and right lingual gyrus, where they showed greater task-related activity for word stimuli than faces.

2.3. Between group analyses

2.3.1. Regions showing task and task by condition effects

Our first goal was to identify regions within visuospatial, phonological, and executive domains where activity did *not* significantly differ between age groups (see methods for details of the analysis).

2.3.1.1. Visuospatial sketchpad. As shown in **Table 5**, in the between group analyses, six regions (bilateral fusiform gyrus, left inferior frontal cortex, anterior cingulate, midline cerebellum, and right middle frontal cortex) showed a main effect of task. There was one region (right fusiform gyrus) showing a task by condition interaction with greater task-related activity for faces than words.

2.3.1.2. Phonological loop. There were a number of regions (including left supramarginal gyrus, left rolandic sulcus, left precentral gyrus, left rolandic operculum, and regions within left temporal cortex) that showed a main effect of task. There

Table 5
 Between group analyses

Regions of interest	Task	Task × condition	Task × age group	Task × age group × condition		
				Adults	Adolescents	
Visuospatial scratchpad						
Left fusiform gyrus	2.5**	.68	.10	.51		
Left inferior frontal	2.5**	.65	.12	1.3**	w = f	w > f
Anterior cingulate	1.2**	.38	.21	.55		
Right fusiform gyrus	3.0**	.81* f > w	.11	.13		
Midline cerebellum	.96*	.17	.03	.30		
Right middle frontal	.88*	.26	.21	.82*	w = f	w = f
Phonological loop						
Left rolandic sulcus	2.9**	1.7** w > f	.42	1.5**	w = f	w > f
Left precentral gyrus	2.9**	1.3** w > f	.10	.57		
Left inferior frontal gyrus	.26	.95* w > f	.40	.87*	w = f	w > f
Left rolandic operculum	2.5**	.60	.06	.90*	w = f	w > f
Left supramarginal gyrus	2.8**	.96* w > f	.03	1.1**	w = f	w > f
Left superior temporal gyrus	1.4**	.51	.34	.34		
Left planum temporal	.86*	.66	.20	.38		
Left superior anterior temporal gyrus	1.4**	.08	.13	.55		
Left inferior posterior temporal gyrus	.83*	.33	.41	.24		
Executive function						
Left VLPFC	1.0*	.27	.25	.38		
Left DLPFC	2.9**	.95* w > f	.06	.33		
Left inferior parietal lobe	4.4**	1.0* w > f	.55	.86*	w = f	w > f
Right DLPFC	2.0**	.14	.57	.76*	w = f	w = f
Right cerebellum	3.4**	.65	.77*	1.3**	w < f	w = f
Left fusiform gyrus	2.3**	.35	.54	1.0*	w < f	w = f
Right superior parietal lobe	3.4**	.09	.20	.86*	w < f	w = f
Left superior parietal lobe	.84*	.50	.97*	.24	Adol < Adult	
Medial presupplementary motor area	3.5**	.15	.33	.75		
Right lingual gyrus	.48	1.5** w > f	.07	.56		
Right precentral gyrus	2.1**	.42	.78*	.91*	w = f	w = f
Left thalamus	2.4**	.20	.05	.56		
Right middle frontal gyrus	2.4**	.84* f > w	.77*	.74	Adol < Adult	
Left premotor cortex	.89*	.71	.68	.67		

Values represent effect sizes (Cohen's *d*). Task × condition patterns indicate the pattern of activity for face (f) stimuli versus words (w). Bolded results represent regions showing task by age group and task by condition effects that remained after vocabulary and performance differences were accounted for. ***p* < .01, **p* < .05.

were four regions (left supramarginal gyrus, left inferior frontal gyrus, left rolandic sulcus, and left precentral gyrus) that showed a task by condition interaction with greater task-related activity for words than faces.

2.3.1.3. Executive function. There were numerous regions (including bilateral DLPFC, left superior parietal lobe, right precentral gyrus, left VLPFC, left inferior parietal lobe, left fusiform gyrus, medial presupplementary motor area, left thalamus, left premotor cortex, right precentral gyrus, right cerebellum, right superior parietal lobe, and right middle frontal gyrus) that showed a main effect of task (see Table 5). There were four regions (left inferior parietal lobe, left DLPFC, right lingual gyrus, and right middle frontal gyrus) that showed a task by condition interaction. Task-related activity within left inferior parietal lobe, left DLPFC, and right lingual gyrus was greater for words than faces while task-related activity within right middle frontal gyrus was greater for faces than words.

2.3.2. Regions showing effects of age

Our second goal was to identify regions within visuospatial, phonological and executive domains where activity *did* significantly differ between age groups.

As stated earlier, a potential interpretive issue in this study is that both vocabulary scores on the WASI and performance accuracy for faces were significantly lower in the adolescent versus adult participants. Thus, below we report regions showing a significant effect before and after differences in vocabulary scores and performance accuracy were accounted for. Further, when we reanalyzed the data using a subset of adults (14 adults) who showed no significant performance differences between total word and total face accuracy, we found that all but one region (left thalamus) continued to show a task by condition effect in adults even when performance accuracy for the two conditions had been matched.

2.3.2.1. Visuospatial sketchpad. There were no regions that showed a task by age group interaction. There were two regions (left inferior frontal cortex and right middle frontal cortex) that showed a task by condition by age group interaction. However, when age differences in vocabulary scores and performance were taken into account, only the left inferior frontal cortex continued to show a task by condition by age group interaction. Post hoc tests were conducted to examine task by condition effects in adult and adolescent groups separately. In the adolescent group, task-related activity within left inferior frontal cortex was significantly greater for words than faces while task-related activity in the adult group did not significantly differ between word and face conditions (see Fig. 2a).

2.3.2.2. Phonological loop. There were no regions that showed a task by age group interaction. There were four regions (left supramarginal gyrus, left inferior frontal gyrus, left rolandic sulcus, and left rolandic operculum) that showed a task by condition by age group interaction. However, when age differences in vocabulary scores and performance were taken into account,

only two regions (left supramarginal gyrus and left rolandic sulcus) continued to show a task by condition by age group interaction. Post hoc tests conducted to examine task by condition effects in adolescent and adult groups separately, indicated that in the adolescent group, task-related activity within left supramarginal gyrus was significantly greater for words than faces while task-related activity in the adult group did not significantly differ between word and face conditions (see Fig. 2b). Task-related activity within left rolandic sulcus was also significantly greater for words than faces in the adolescent group, but did not significantly differ between word and face conditions for adults (see Fig. 2c).

2.3.2.3. Executive function. There were four regions (left superior parietal lobe, right cerebellum, right precentral gyrus, and right middle frontal gyrus) that showed a task by age group interaction such that the adolescents showed significantly less task-related activity than the adult group for both word and face stimuli. However, when age differences in vocabulary scores and performance were taken into account, only one region (left superior parietal lobe) continued to show a task by age group interaction. There were six regions within left inferior parietal lobe, left fusiform gyrus, right precentral gyrus, right cerebellum, right superior parietal lobe, and right DLPFC which showed a task by condition by age group interaction. However, when age differences in vocabulary scores and performance were taken into account, only two regions (right cerebellum and left fusiform gyrus) continued to show a task by condition by age group interaction. Post hoc tests conducted to examine task by condition effects in adolescent and adult groups separately, indicated that in the adolescent group, task-related activity within right cerebellum did not significantly differ between word and face conditions while task-related activity in the adult group was significantly greater for faces than words (see Fig. 2d). Task-related activity within left fusiform gyrus was also significantly greater for faces than words in the adult group, but did not significantly differ between word and face conditions for adolescents (see Fig. 2e).

3. Discussion

The goal of the present study was to examine age-related differences in the neural correlates of word and face working memory tasks. We were particularly interested in exploring developmental differences in activated networks in an adolescent rather than child group because adolescents were more likely to have performance levels that were similar to that of our adult group. Differences in functional activation, in the absence of performance differences, could suggest that the adolescent group is using different strategies to fulfill task demands. Analysis of accuracy data demonstrated a very small, but significant group difference for faces, but not words. There was no evidence for significant differences in reaction time between the adolescents and young adults. The neuroimaging results also indicated that adolescents and young adults demonstrated many similarities in the patterns of brain activation associated with both word and face conditions. However, the imaging data also revealed some

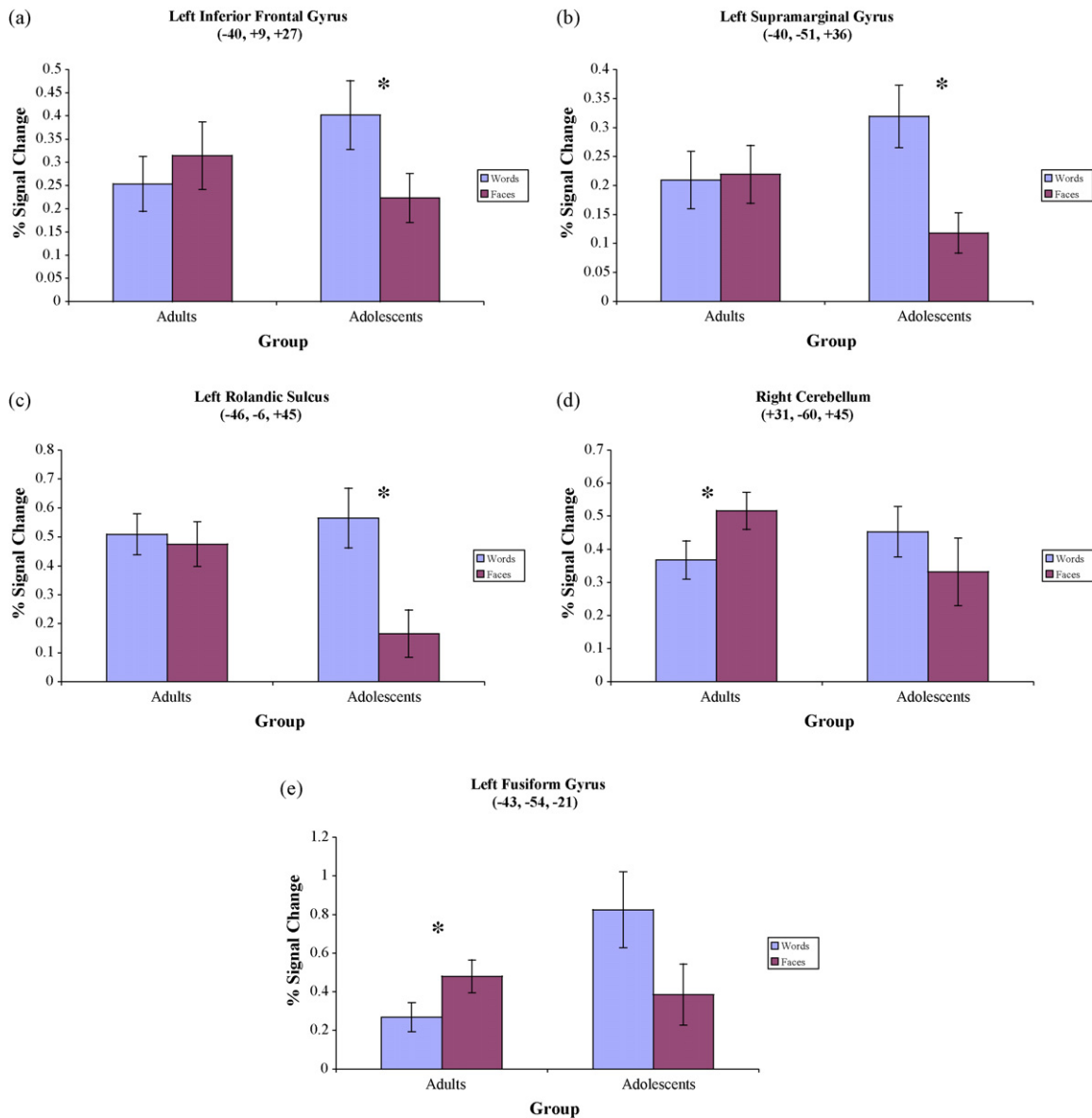


Fig. 2. Mean percent signal change for each age group (adults, adolescents) in each condition (word, face). Significant differences between word and face conditions are noted with asterisks. Standard errors are displayed.

group differences in the pattern of brain activity associated with performance of this task.

Before we began exploring age-related differences in activation, we conducted an analysis within the adult group independently from the adolescent group to validate our choice of ROIs. Results from this analysis showed task-related activation in many regions consistent with those reported in previous studies that have used the n-back task to examine WM-related function. Many of the regions we found active for both word and face conditions were the same as those found in a recent meta-analysis of n-back working memory studies by Owen, McMillan, Laird, and Bullmaore (2005), including inferior and superior parietal cortex, bilateral dorsolateral prefrontal cortex, left rolandic sulcus, left precentral gyrus, left rolandic operculum, left supramarginal gyrus, premotor cortex, and midline cerebellum. Consistent with findings from a study by Nystrom

et al. (2000) who contrasted neural correlates for letters versus objects (visual shapes), we found increased activity in anterior cingulate, right superior parietal lobe, and right middle frontal gyrus for face compared to word stimuli. Findings of increased activity for faces versus words in regions of right frontal and parietal cortices have also been reported by other studies examining material specific activation for word and face stimuli (Barch, Sheline, Csernansky, & Snyder, 2003; Braver et al., 2001). We also found increased activity for face compared to word stimuli in bilateral fusiform gyrus and right cerebellum. However, unlike Barch et al. (2003) and Braver et al. (2001), both of which used a verbal and face object working memory paradigm, we did not find evidence for greater activity in left ventrolateral prefrontal cortex, left inferior frontal cortex, nor left inferior parietal cortex for words versus faces in our adult group. The current results are similar to those of Nystrom et al. (2000), who also failed to

find clear material specific activation for verbal compared to nonverbal material. As noted by Nystrom, such results suggest that participants may sometimes use similar strategies to complete tasks with different stimulus types or they may combine strategies for all stimulus types.

We also found that adolescents and adults both showed task-related activity that did not differ by group in many regions including bilateral fusiform gyrus, anterior cingulate, left precentral gyrus, left superior anterior temporal gyrus, left DLPFC, premotor cortex, and left thalamus. These findings of adult-like activity in a number of regions are consistent with previous studies reporting that children activate many of the same regions as adults do during performance of a WM task. While studies with younger children have reported a further increase in activity in such regions as a function of increasing age (Klingberg et al., 2002; Kwon et al., 2002; Schweinsburg et al., 2005), our results suggest that there is little further change in some regions once participants have reached adolescence. The most unexpected finding was of no significant age differences in activity in DLPFC, a region thought to support various aspects of executive control. More specifically, both adults and adolescents showed strong bilateral task-related activity in DLPFC. In left DLPFC, there was neither a significant task by group nor task by group by condition interaction. In right DLPFC, we found a significant task by group by condition interaction, however, this significant effect was no longer present once group differences in performance and vocabulary scores were accounted for. The few studies that have included adolescents (Kwon et al., 2002; Klingberg et al., 2002) have reported age-related increases in DLPFC activity, although both of these studies included a much broader age range that extended from childhood into adulthood, and did not separately examine adolescents. One recent study by Crone, Wendelken, Donohue, van Leijenhorst, and Bunge (2006) examined brain activation in three age groups (ages 8–12 years, 13–17 years, and 18–25 years) during performance of an object working memory task. They reported that adults and adolescents recruited DLPFC for manipulation relative to maintenance trials, while children failed to recruit these regions during the delay period. Our results are consistent with the findings of Crone et al, in that the adolescents showed similar DLPFC activity to adults. One possible interpretation for these findings is that DLPFC may be functionally mature by late adolescence. However, discrepant findings between structural and functional studies could also reflect differential sensitivity of the two methods to age-related changes. Additionally, while we did not find developmental differences in the magnitude of DLPFC activation, it is possible that developmental differences in the extent of activation could exist (Scherf et al., 2006). Future studies looking at a broader age range (childhood to adulthood, including adolescence), multiple domains of working memory, different analysis approaches, and both structural and functional assessments are necessary to better understand the developmental trajectory of the DLPFC.

There was also one region that showed a significant task by age group interaction and five regions that showed a significant task by group by condition interaction once differences in performance and vocabulary were accounted for. There was one executive function region (left superior parietal lobe) in which

adults showed significantly greater activity than adolescents for both word and face stimuli. In a meta-analysis of neuroimaging working memory studies, Wager and Smith (2003) found the superior parietal cortex (BA7) to be the only region showing significant effects across various executive processes (i.e., updating, order memory, and manipulation). Crone and colleagues also found that adolescents and adults, but not children, recruited superior parietal cortex more strongly for manipulation trials than maintenance trials. However, it was not clear whether significant differences in the magnitude of activation was present between adolescent and adult groups in the Crone et al study. Our data suggests that, by adolescence, the superior parietal cortex is engaged in higher order executive processes, although not to the same extent as it is in adulthood, suggesting that this region may not yet be functionally mature by adolescence. As such, our findings suggest that the field needs to pay greater attention to the role of parietal cortex development in the maturation of WM and other executive functions.

We also found a number of regions that showed age-related changes that differed as a function of stimulus type and remained even when age differences in vocabulary scores and performance were taken into account. There was one visuospatial scratchpad region (left inferior frontal cortex) in which the adolescent group showed significantly greater activity for words than faces. In contrast, task-related activity in this region in the adult group did not significantly differ between word and face conditions. There were two phonological loop regions (left supramarginal gyrus and left rolandic sulcus) that showed a significant task by condition by age group effect. Within both left supramarginal gyrus and left rolandic sulcus, task-related activity in the adolescent group was significantly greater for word than face stimuli, while activity in these regions did not significantly differ between word and face conditions for adults. Lastly, within right cerebellum and left fusiform gyrus (two executive function regions), adults had significantly less task-related activity for words versus faces, while task-related activity in adolescents did not significantly differ between word and face conditions. The neuroimaging literature suggests that left supramarginal gyrus (Awh et al., 1996; Clark et al., 1996; Jonides et al., 1997; Smith et al., 1996) and left rolandic sulcus (Vigneau et al., 2006) are involved with verbal working memory and language processing, respectively. In our study, amongst the phonological loop regions, we found that adolescents, but not adults, showed significantly greater activity for words than faces within left supramarginal gyrus and left rolandic sulcus. We also found this same pattern of increased task-related activity for words than faces in adolescents, but not adults, within one visuospatial sketchpad region (left inferior frontal gyrus). While this region was found to be significantly more active for face working memory than a sensorimotor control task in the study by Courtney et al. (1996), this region has also been implicated in the phonological rehearsal of verbal information (Awh et al., 1996; Jonides, Smith, Marshuetz, Koeppel, & Reuter-Lorenz, 1998; Rama, Sala, Gillen, Pekar, & Courtney, 2001). Further, when we performed an additional analysis averaging across the three regions showing a significant stimulus effect in adolescents, we found that activity was significantly greater

in adults than in adolescents for face stimuli ($p < .01$). Thus, collectively, these results may suggest that adults, compared to adolescents, may be more heavily recruiting verbal strategies for the face WM task. However, this conclusion is very speculative and future studies examining neural correlates using tests of strategy use are necessary to examine this hypothesis.

There were several limitations in the current study. First, the present study did not include multiple load levels. As such, we could not rule out the possibility that differences between our two working memory conditions reflected differences in low-level processing of words and faces, and not specifically “working memory” activity. Future studies that use a parametric manipulation of load would help to address this issue. A second limitation in the current study was that both the adult and adolescent groups in our sample had greater overall performance accuracy for faces than words. Unfortunately, we were unable to match the adolescent and adult groups such that there were no significant group differences between total word and face accuracy, thus our stimulus type results could have been confounded by difficulty differences. We did reanalyze the data using a subset of adults (14 adults) who showed no significant performance differences between total word and total face accuracy and found that all but one region (left thalamus) continued to show a task by condition effect in adults even when performance accuracy for the two conditions had been matched. In addition, one of the main findings of this paper was that of decreased activity in left superior parietal lobe for adolescents versus adults. This finding was present across both word and face conditions regardless of task difficulty level.

To summarize, the present study showed both similarities and differences in the neural correlates of word and face working memory tasks in adolescents compared to adults. While many regions reached adult-like maturation by adolescence, there were still a number of age-related differences in other regions, including superior parietal cortex. The present study provides further evidence for protracted development of brain regions such as superior parietal cortex, which is thought to be critical for a number of high-level cognitive functions. Further, our results provided some evidence consistent with the hypothesis that adults may rely more heavily on verbal strategies for both verbal and nonverbal stimulus types than adolescents. However, in order to better understand the relationship between structural and functional maturation, it is necessary to examine a broader age range that begins in early childhood, extends through adulthood, and includes the adolescent age range.

References

Anderson, V. A., Anderson, P., Northam, E., Jacobs, R., & Catroppa, C. (2001). Development of executive functions through late childhood and adolescence in an Australian sample. *Developmental Neuropsychology*, *20*(1), 385–406.

Andreasen, N. C. (1983a). *The scale for the assessment of positive symptoms (SAPS)*. Iowa City: University of Iowa.

Andreasen, N. C. (1983b). *The scale for the assessment of negative symptoms (SANS)*. Iowa City: University of Iowa.

Awh, E., Jonides, J., Smith, E. E., Schumacher, E. H., Koeppe, R., & Katz, S. (1996). Dissociation of storage and rehearsal in verbal working memory: Evidence from PET. *Psychological Science*, *7*, 25–31.

Baddeley, A. (1996). Exploring the central executive. *Quarterly Journal of Experimental Psychology*, *49*(1), 5–28.

Baddeley, A. D. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience*, *4*(10), 829–839.

Baddeley, A. D., & Hitch, G. J. (1974). Working memory. In G. Bower (Ed.), *The psychology of learning and motivation* (pp. 47–89). New York: Academic Press.

Barch, D. M., Csernansky, J., Conturo, T., Snyder, A. Z., & Ollinger, J. (2002). Working and long-term memory deficits in schizophrenia. Is there a common underlying prefrontal mechanism? *Journal of Abnormal Psychology*, *111*, 478–494.

Barch, D. M., Sheline, Y. I., Csernansky, J. G., & Snyder, A. Z. (2003). Working memory and prefrontal cortex dysfunction: Specificity to schizophrenia as compared to major depression. *Biological Psychiatry*, *53*, 376–384.

Braver, T. S., Barch, D. M., Kelley, W. M., Buckner, R. L., Cohen, N. J., Meizin, F. M., et al. (2001). Direct comparison of prefrontal cortex regions engaged by working and long-term memory tasks. *NeuroImage*, *14*, 48–59.

Brocki, K. C., & Bohlin, G. (2004). Executive functions in children aged 6 to 13: A dimensional and developmental study. *Developmental Neuropsychology*, *26*(2), 571–593.

Casey, B. J., Cohen, J. D., Jezzard, P., Turner, R., Noll, D. C., Trainor, R. J., et al. (1995). Activation of prefrontal cortex in children during a nonspatial working memory task with functional MRI. *NeuroImage*, *2*, 221–229.

Clark, C. R., Egan, G. F., McFarlane, C. A., Morris, P., Weber, D., Sonkilla, C., et al. (1996). Updating working memory for words: A PET activation study. *Human Brain Mapping*, *9*, 42–54.

Cohen, J. D., MacWhinney, B., Flatt, M. R., & Provost, J. (1993). PsyScope: A new graphic interactive environment for designing psychology experiments. *Behavioral Research Methods, Instruments & Computers*, *25*(2), 257–271.

Courtney, S. M., Ungerleider, L. G., Keil, K., & Haxby, J. V. (1996). Object and spatial visual working memory activate separate neural systems in human cortex. *Cerebral Cortex*, *6*, 39–49.

Crone, E. A., Wendelken, C., Donohue, S., van Leijenhorst, L., & Bunge, S. A. (2006). Neurocognitive development of the ability to manipulate information in working memory. *Proceedings of the National Academy of Sciences*, *103*(24), 9315–9320.

D’Esposito, M., Aguirre, G. K., Zarahn, E., Ballard, D., Shin, R. K., & Lease, J. (1998). Functional MRI studies of spatial and nonspatial working memory. *Cognitive Brain Research*, *7*, 1–13.

Gathercole, S. E., Pickering, S. J., Ambridge, B., & Wearing, H. (2004). The structure of working memory from 4 to 15 years of age. *Developmental Psychology*, *40*(2), 177–190.

Giedd, J., Blumenthal, J., Jeffries, N. O., Castellanos, F. X., Liu, H., Zijdenbos, A., et al. (1999). Brain development during childhood and adolescence: A longitudinal MRI study. *Nature Neuroscience*, *2*, 861–863.

Giedd, J., Snell, J. W., Lange, N., Rajapakse, J., Casey, B. J., Kaysen, D., et al. (1996). Quantitative MRI of human brain development: Ages 4–18. *Cerebral Cortex*, *6*(4), 551–560.

Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., et al. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences*, *101*(21), 8174–8179.

Hale, S., Bonik, M. D., & Fry, A. F. (1997). Verbal and spatial working memory in school-age children: Developmental differences in susceptibility to interference. *Developmental Psychology*, *33*(2), 364–371.

Hitch, G. J., & Halliday, M. S. (1983). Working memory in children. *Philosophical Transactions of the Royal Society of London Series B*, *302*, 325–340.

Hitch, G. J., Woodin, M. E., & Baker, S. (1989). Visual and phonological components of working memory in children. *Memory and Cognition*, *17*, 175–185.

Jonides, J., Schumacher, E. H., Smith, E. E., Lauber, E. J., Awh, E., Minoshima, S., et al. (1997). Verbal working memory load affects regional brain activation as measured by PET. *Journal of Cognitive Neuroscience*, *9*, 462–475.

Jonides, J., Smith, E., Marshuetz, C., Koeppe, R., & Reuter-Lorenz, P. A. (1998). Inhibition in verbal working memory revealed by brain activation. *Proceedings of the National Academy of Sciences USA*, *95*, 8410–8413.

Kelley, W. M., Miezin, F. M., McDermott, K. B., Buckner, R. L., Raichle, M. E., Cohen, N. J., et al. (1998). Hemispheric specialization in human dorsal

- frontal cortex and medial temporal lobe for verbal and non-verbal memory encoding. *Neuron*, 20, 927–936.
- Klingberg, T., Forssberg, H., & Westerberg, H. (2002). Increased brain activity in frontal and parietal cortex underlies the development of visuospatial working memory capacity during childhood. *Journal of Cognitive Neuroscience*, 14(1), 1–10.
- Kwon, H., Reiss, A. L., & Menon, V. (2002). Neural basis of protracted developmental changes in visuo-spatial working memory. *PNAS*, 99(20), 13336–133341.
- Levin, H. S., Eisenberg, H. M., & Benton, A. L. (Eds.). (1991). *Frontal lobe function and dysfunction*. New York: Oxford University Press.
- Logan, J. M., Sanders, A. L., Snyder, A. Z., Morris, J. C., & Buckner, R. L. (2002). Under-recruitment and nonselective recruitment: Dissociable neural mechanisms associated with aging. *Neuron*, 33, 827–840.
- Luciana, M., Conklin, H. M., Hooper, C. J., & Yarger, R. S. (2005). The development of nonverbal working memory and executive control processes in adolescents. *Child Development*, 76(3), 697–712.
- Luciana, M., & Nelson, C. A. (1998). The functional emergence of prefrontally-guided working memory systems in four-to-eight-year-old children. *Neuropsychologia*, 36, 273–293.
- Luna, B., Garver, K. E., Urban, T. A., Larzar, N. A., & Sweeney, J. A. (2004). Maturation of cognitive processes from late childhood to adulthood. *Child Development*, 75(5), 1357–1372.
- McAuley, T., Brahmhatt, S. B., & Barch, D. M. (2007). Performance on an episodic encoding task yields further insight into functional brain development. *NeuroImage*, 34(2), 815–826.
- Nagy, Z., Westerberg, H., & Klingberg, T. (2004). Maturation of white matter is associated with the development of cognitive functions during childhood. *Journal of Cognitive Neuroscience*, 16(7), 1227–1233.
- Nelson, C. A., Monk, C. S., Lin, J., Carver, L. J., Thomas, K. M., & Truwit, C. L. (2000). Functional neuroanatomy of spatial working memory in children. *Developmental Psychology*, 36(1), 109–116.
- Nystrom, L. E., Braver, T. S., Sabb, F. W., Delgado, M. R., Noll, D. C., & Cohen, J. D. (2000). Working memory for letters, shapes, and locations: fMRI evidence against stimulus-based regional organization of human prefrontal cortex. *NeuroImage*, 11, 424–446.
- Ojemann, J., Akbudak, E., Snyder, A., McKinstry, R., Raichle, M., & Conturo, T. (1997). Anatomic localization and quantitative analysis of gradient refocused echo-planar fMRI susceptibility artifacts. *NeuroImage*, 6, 156–167.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113.
- Owen, A. M. (1997). The functional organization of working memory processes within human lateral frontal cortex: The contribution of functional neuroimaging. *European Journal of Neuroscience*, 9, 1329–1339.
- Owen, A. M., McMillan, K. M., Laird, A. R., & Bullmaore, E. (2005). N-back working memory paradigm: A meta-analysis of normative functional neuroimaging studies. *Human Brain Mapping*, 25(1), 46–59.
- Palmer, S. (2000). Working memory: A developmental study of phonological recoding. *Memory*, 8(3), 179–193.
- Rama, P., Sala, J. B., Gillen, J. S., Pekar, J. J., & Courtney, S. M. (2001). Dissociation of the neural systems for working memory maintenance of verbal and nonspatial visual information. *Cognitive, Affective and Behavioral Neuroscience*, 1(2), 161–171.
- Ravizza, S. M., Delgado, M. R., Chein, J. M., Becker, J. T., & Fiez, J. A. (2004). Functional dissociations within the inferior parietal cortex in verbal working memory. *NeuroImage*, 22(2), 562–573.
- Scherf, K. S., Sweeney, J. A., & Luna, B. (2006). Brain basis of developmental change in visuospatial working memory. *Journal of Cognitive Neuroscience*, 18(7), 1045–1058.
- Schmithorst, V. J., Wilke, M., Dardzinski, B. J., & Holland, S. K. (2002). Correlation of white matter diffusivity and anisotropy with age during childhood and adolescence: A cross-sectional diffusion-tensor MR imaging study. *Radiology*, 222(1), 212–218.
- Schweinsburg, A. D., Nagel, B. J., & Tapert, S. E. (2005). fMRI reveals alteration of spatial working memory networks across adolescence. *Journal of the International Neuropsychological Society*, 11(5), 631–644.
- Smith, E. E., Jonides, J., & Koeppe, R. A. (1996). Dissociating verbal and spatial working memory using PET. *Cerebral Cortex*, 6, 11–20.
- Snook, L., Paulson, L. A., Roy, D., Phillips, L., & Beaulieu, C. (2005). Diffusion tensor imaging of neurodevelopment in children and young adults. *NeuroImage*, 26(4), 1164–1173.
- Sowell, E. R., Thompson, P. M., Holmes, C. J., Batth, R., Jernigan, T. L., & Toga, A. W. (1999). Localizing age-related changes in brain structure between childhood and adolescence using statistical parametric mapping. *NeuroImage*, 9(6), 587–597.
- Sowell, E. R., Thompson, P. M., Holmes, C. J., Jernigan, T. L., & Toga, A. W. (1999). In vivo evidence for post-adolescent brain maturation in frontal and striatal regions. *Nature Neuroscience*, 2(10), 859–861.
- Spitzer, R. L., Williams, J. B., Gibbon, M., & First, M. B. (1990). *Structured clinical interview for DSM-III-R—patient edition (SCID-P, version 1.0)*. Washington, D.C: American Psychiatric Press.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.
- Thomas, K. A., King, S. W., Franzen, P. L., Welsh, T. F., Berkowitz, A. L., Noll, D. C., et al. (1999). A developmental functional MRI study of spatial working memory. *NeuroImage*, 10, 327–338.
- Vigneau, M., Beaucousin, V., Herve, P. Y., Duffau, H., Crivello, O., Houde, O., et al. (2006). Meta-analysing left hemisphere language areas: Phonology, semantics, and sentence processing. *NeuroImage*, (30), 1414–1432.
- Wager, T. D., & Smith, E. E. (2003). Neuroimaging studies of working memory: A meta-analysis. *Cognitive, Affective and Behavioral Neuroscience*, 3(4), 255–274.
- Woods, R. P., Grafton, S. T., Holmes, C. J., Cherry, S. R., & Mazziotta, J. C. (1998). Automated image registration. I. General methods and intrasubject, intramodality validation. *Journal of Computer Assisted Tomography*, 22(1), 139–152.
- Yakovlev, P. I., & Lecours, A. R. (1967). *The myelogenetic cycles of regional maturation of the brain. Regional development of the brain in early life*. M. A. Oxford (UK): Blackwell Scientific., pp. 3–70.