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Gender differences in working memory networks: A BrainMap meta-analysis

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ABSTRACT

Gender differences in psychological processes have been of great interest in a variety of fields. While the majority of research in this area has focused on specific differences in relation to test performance, this study sought to determine the underlying neurofunctional differences observed during working memory, a pivotal cognitive process shown to be predictive of academic achievement and intelligence. Using the BrainMap database, we performed a meta-analysis and applied activation likelihood estimation to our search set. Our results demonstrate consistent working memory networks across genders, but also provide evidence for gender-specific networks whereby females consistently activate more limbic (e.g., amygdala and hippocampus) and prefrontal structures (e.g., right inferior frontal gyrus), and males activate a distributed network inclusive of more parietal regions. These data provide a framework for future investigation using functional or effective connectivity methods to elucidate the underpinnings of gender differences in neural network recruitment during working memory tasks.

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1. Introduction

For over a century, unequal abilities between men and women, particularly within the intellectual domain, have been both intriguing and elusive. While evidence for gender differences in psychological processes have been noted across a diverse range of cognitive domains (Bradley, Codispoti, Sabatinelli, & Lang, 2001; Gur et al., 2000; Koch et al., 2007; Lynn & Irwing, 2002; Ragland, Coleman, Gur, Glahn, & Gur, 2000; Shaywitz et al., 1995; Volf & Razumnikova, 1999), mixed results (Stevens, 2011) have stunted progression toward an understanding of the potential basis for these differences from a strictly neurological perspective. While the majority of research in this area has focused on specific behavioral performance differences in relation to test performance, this study sought to determine the neurofunctional differences observed during working memory, a pivotal cognitive process shown to be

predictive of academic achievement and intelligence (Conway, Kane, & Engle, 2003).

Examining working memory as a whole, the observed neural activation patterns observed in functional neuroimaging studies consistently demonstrate prefrontal, temporal, and parietal involvement (Baddeley & Logie, 1999; Baddeley, 1981, 1997, 2000; D'Esposito et al., 1998a; D'Esposito, Ballard, Aguirre, & Zarahn, 1998b; D'Esposito, Postle, & Rypma, 2000; Haier, Jung, Yeo, Head, & Alkire, 2005; Na et al., 2000; Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000; Repovs & Baddeley, 2006), posited to reflect the components of Baddeley and colleagues (2011) revised model of working memory. However, it is widely accepted that working memory operates differently when presented with verbal compared to spatial information (Reuter-Lorenz et al., 2000; Smith, Jonides, & Koeppe, 1996). Verbal working memory preferentially engages the left hemisphere, specifically the inferior parietal lobe, lateral frontal lobe, the supramarginal gyrus (BA 10), premotor areas, and Broca's area (Jonides et al., 1998; Schumacher et al., 1996; Smith et al., 1996; Smith, Jonides, Marshuetz, & Koeppe, 1998). Spatial working memory has been associated with a more dispersed activation pattern across the hemispheres, consisting of the inferior frontal lobe, posterior parietal lobe, right occipital gyrus, right premotor area, right dorsolateral prefrontal cortex, and the

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extrastriate cortex in the occipital lobe (D'Esposito et al., 1998a; Jonides et al., 1993; van Asselen et al., 2006). It has long been acknowledged that working memory plays a key role in manipulating incoming information entering the cognitive system, whether the information is verbal or spatial in nature, interacting dynamically with attention and long-term memory. For this reason, working memory is an integral part of general cognitive processing with significant trickle-down effects on other critical processes. Therefore, observing gender differences among working memory networks could have robust effects in other areas of cognitive functioning.

Interestingly, when working memory is deconstructed into spatial and verbal components, evidence suggests that behavioral disparities emerge between genders (Halpern et al., 2007). Research has shown that from a behavioral performance perspective, males demonstrate greater mathematical (Lynn & Irwing, 2008), spatial (Kaufman, 2007; Lejbak, Crossley, & Vrbancic, 2011; Masters & Sanders, 1993; Nordvik & Amponsah, 1998), and object working memory (Lejbak et al., 2011) compared to females, and females display greater verbal (including episodic memory (Lewin, Wolgers, & Herlitz, 2001)) and writing skills than males (Bae, Choy, Geddes, Sable, & Snyder, 2000; Hedges & Nowell, 1995). The discrepancy in male and female spatial ability appears to begin as early as preschool and then becomes even more significant as males and females enter adulthood (Levine, Huttenlocher, Taylor, & Langrock, 1999), whereas the female superiority in verbal facets tends to appear slightly later, peaking in early adulthood (Willingham & Cole, 1997). Some researchers suggest that the male advantage in spatial ability helps set them above their female counterparts in mathematics, especially in areas like geometry, which involve the visualization of items in space (Casey, Nuttall, Pezaris, & Benbow, 1995).

Despite evidence that gender differences exist in working memory, there is an equally strong case for a lack of performance differences. In recent years, as functional neuroimaging has become more commonplace, studies that do not find explicit behavioral differences have the opportunity to view more intrinsic neurofunctional patterns. Multiple studies have found that there are no significant performance differences between the genders during verbal working memory tasks, but there is evidence for neurofunctional differences (Kaufman, 2007; Lejbak et al., 2011; Speck et al., 2000), suggesting that the behavioral differences may still exist, but the studies could be underpowered, or males and females could be using different psychological strategies. Specifically, Speck and colleagues (Speck et al., 2000) observed differences in the functional networks utilized to complete a verbal working memory task, with males accessing more right hemispheric regions such as the lateral prefrontal cortex, posterior cingulate and caudate, while females utilized the left hemisphere more prominently. Females have also shown greater activation in the middle, inferior, and orbital prefrontal regions, despite similar performance to male subjects in other studies (Goldstein et al., 2005). Taken collectively, neuroimaging data support the notion that certain brain regions can function differently in males and females to produce the same behavioral responses, which appears to be the case with working memory (Goldstein et al., 2005). These results suggest that using functional neuroimaging may allow researchers to develop more accurate models of gender differences within specific cognitive domains that would allow for theories of neuroanatomical and neurofunctional differences to be tested empirically (for review, please see Halpern et al., 2007).

From a neuroimaging perspective, recent research has shown that there are gender differences in functional connectivity during resting state (Filippi et al., 2013). Specifically, Filippi and colleagues (2013) found that women had greater intrinsic functional connectivity inclusive of the cingulate, dorsolateral prefrontal cortex,

and the inferior frontal gyrus, while men demonstrated increased functional connectivity in parietal regions, characteristics that the authors attribute to potential strategy differentiation. These observed differences could help explain the disparity in performance between the genders on various cognitive tasks, as well as bringing into question the possibility of inherent neural network differences. The present study focuses on the later implication of the resting state data with regard to working memory, to see if such differences exist during working memory performance. Furthermore, because of the diversity of paradigms used to examine working memory, we chose to pursue a meta-analysis that overcomes task-dependent activation differences, allowing for a more accurate depiction of gender differences within the construct of working memory. Therefore, the present study investigated the neural underpinnings of gender differences in working memory by capitalizing on the structure of the BrainMap database (Fox et al., 2005; Fox & Lancaster, 2002; Laird, Lancaster, & Fox, 2005b), a functional neuroimaging database that archives functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies with a meticulous coding scheme (Laird et al., 2009). Using meta-analysis to develop models of functional connectivity and subsequently probing differences in connectivity networks has been demonstrated to be both robust and effective (Robinson, Laird, Glahn, Lovallo, & Fox, 2010).

2. Methods

In order to ascertain the neural underpinning of working memory for males and females, the BrainMap database was queried using Sleuth version 2.2 (Fox et al., 2005; Laird et al., 2005b, 2009). In short, Sleuth is a free, publicly available search tool that allows users to search the BrainMap database among any of the meta-data categories contained within the database. We entered the following search criteria: (1) studies coded within the behavioral domain of cognition and paradigm class of working memory (e.g., Experiments → Behavioral Domain → Cognition → Memory – Working), (2) studies reporting activations only (e.g., Experiments → Activation → Activations Only), (3) studies using normal, healthy subjects (e.g., Experiments → Context → Normal Mapping), and (4) studies using only males or only females (e.g., two separate searches, one for each gender, were performed, Subjects → Gender → Females (or Males) Only). Resultant whole-brain coordinates of activation during working memory tasks were then downloaded (males: 44 papers, 2316 locations, 141 experiments, 127 conditions, 701 subjects; females: 15 papers, 402 locations, 36 experiments, 49 conditions, 200 subjects; to download the complete workspace files for the male and female searches, please visit http://aucanlab.com/?page_id=128). Coordinates that were not reported in Talairach space in their original publication were transformed into Talairach space by the GingerALE analysis program using the icbm2tal transform (Laird et al., 2010; Lancaster, Laird, Fox, Glahn, & Fox, 2005).

Activation likelihood estimation (ALE) meta-analysis (Eickhoff et al., 2009; Laird et al., 2005a; Turkeltaub, Eden, Jones, & Zeffiro, 2002) was performed on the sets of coordinates identified as activated during working memory tasks to identify regions of convergence within each search (i.e., males and females were run separately). ALE capitalizes on the nature of voxel-wise studies that are commonly reported in a standard stereotaxic space (x, y, z) by pooling 3D coordinates from like studies, and providing the probability of an event occurring at each brain voxel. The algorithm treats each coordinate of activation as a spatial probability, and ALE maps are subsequently calculated by computing the convergence of activation probabilities for every voxel. Permutation testing is then applied. Specifically, an ALE null-distribution is created by randomly assigning the same number of foci from the original analysis throughout the brain, and calculating ALE maps iteratively after every reassignment. The original ALE scores are then compared to the random null distribution to assign *p*-values (Laird et al., 2005a; Turkeltaub et al., 2002). A revised ALE algorithm was proposed and subsequently implemented in the statistical toolbox GingerALE version 2.3 (Eickhoff et al., 2009). The new algorithm is statistically more robust as it treats the data using a random-effects approach, and models the uncertainty associated with a given coordinate. Furthermore, the analysis is anatomically constrained to exclude deep white matter, with the reasoning that 'true' activations originate in the gray matter, thus if we do not constrain the analyses, there is a potential bias in the permutation testing that creates the null-distribution by which *p*-values are determined (Eickhoff et al., 2009). Our analysis used the revised algorithm proposed by Eickhoff and colleagues (2009). False discovery rate (FDR) is defined as having no more than 5% false positives (i.e., if you are using an FDR corrected *p*-value of 0.05). In an ALE meta-analysis, FDR is dependent on the number of permutations implemented (Laird et al., 2005a). ALE maps from the present study were thresholded conservatively at an FDR-corrected *p*-value of 0.05 with a cluster threshold of 100 mm³.

Table 1
 Gender differences in working memory across all working memory tasks.

Convergent brain regions											
Lobe	Region	BA	Females			Males			ALE		
			x	y	z	x	y	z			
Frontal	Right Middle Frontal Gyrus	6	26	2	52	28	-6	52	0.032	0.095	
		9	34	2	38	32	2	34	0.018	0.058	
	Left Middle Frontal Gyrus	6/9	28	28	30	32	30	32	0.018	0.067	
		6/9	-28	-4	50	-26	-8	54	0.030	0.083	
			-36	28	26	-40	26	26	0.026	0.043	
Limbic	Left Cingulate Gyrus	32	-4	10	42	-2	16	40	0.029	0.054	
Parietal	Right Precuneus	7	12	-64	48	16	-72	44	0.023	0.107	
		19	30	-60	40	30	-70	38	0.022	0.051	
	Left Superior Parietal Lobule	7	-28	-62	48	-30	-54	48	0.014	0.079	
	Left Inferior Parietal Lobe	40	-34	-50	36	-38	-52	38	0.028	0.072	
Sub-lobar	Right Claustrum		32	14	0	30	14	6	0.016	0.054	
Temporal	Left Middle Temporal Gyrus	39	-32	-60	30	-34	-68	30	0.017	0.047	
Female-specific network											
Anterior	Right Culmen				34		-56		-22	0.023	
					4		-36		-8	0.014	
Frontal	Left Precentral Gyrus		4		-44		-8		40	0.019	
	Left Frontal Gyrus		6		-6		6		54	0.030	
	Right Medial Frontal Gyrus		10		0		0		56	0.016	
	Left Precentral Gyrus				-40		2		28	0.015	
	Right Medial Frontal Gyrus		9		8		46		16	0.015	
	Right Inferior Frontal Gyrus		13		38		22		10	0.029	
	Left Inferior Frontal Gyrus		45		-50		28		6	0.020	
	Right Inferior Frontal Gyrus		46		52		28		12	0.024	
	Left Middle Frontal Gyrus				-42		14		20	0.023	
	Right Middle Frontal Gyrus				46		38		22	0.026	
	Right Inferior Frontal Gyrus			47		26		14		-12	0.017
Limbic	Right Anterior Cingulate		32		8		36		20	0.020	
	Left Amygdala				-22		-6		-10	0.031	
	Right Amygdala				22		-2		-12	0.023	
	Right Hippocampus				28		-14		-10	0.024	
Occipital	Right Cuneus		18		12		-78		28	0.018	
	Right Precuneus		31		20		-72		28	0.017	
Parietal	Left Postcentral Gyrus		2		-54		-18		28	0.018	
	Left Precuneus		7		-22		-66		36	0.022	
			31		-2		-50		30	0.017	
	Right Inferior Parietal Lobule		40		46		-54		40	0.023	
					34		-46		40	0.017	
Sub-lobar	Right Thalamus (Medial Dorsal Nucleus)				4		-16		4	0.031	
	Left Thalamus				-12		-18		6	0.018	
	Right Caudate Head				18		24		4	0.024	
	Left Claustrum				-30		14		8	0.016	
	Left Putamen (Lentiform Nucleus)				-18		12		8	0.016	
Temporal	Left Superior Temporal Gyrus		13		-42		-46		24	0.020	
	Left Middle Temporal Gyrus		39		-46		-68		26	0.037	
Male specific network											
Anterior	Right Cerebellum Nodule				10		-52		-28	0.060	
	Left Middle Frontal Gyrus	6			-48		0		38	0.072	
	Left Superior Frontal Gyrus				0		8		48	0.120	
	Left Medial Frontal Gyrus				-4		-20		56	0.031	
							-8		-10	0.042	
	Right Middle Frontal Gyrus	9			42		12		40	0.048	
	Left Inferior Frontal Gyrus	9			-50		10		30	0.063	
	Left Middle Frontal Gyrus				-44		14		26	0.043	
	Right Middle Frontal Gyrus	10			34		48		16	0.046	

Table 1 (Continued)
Male specific network

Midbrain	Left Brainstem (Red Nucleus)		0	–20	–4	0.040
Occipital	Right Cuneus	18	26	–76	20	0.065
	Left Cuneus		–18	–74	20	0.059
	Left Middle Occipital Gyrus	19	–28	–78	20	0.042
	Right Middle Occipital Gyrus	37	40	–64	10	0.031
	Right Precuneus	7	28	–56	52	0.045
	Left Precuneus		–14	–70	48	0.066
	Right Supramarginal Gyrus	40	40	–68	40	0.049
				–46	36	0.030
Posterior	Left Declive		–32	–66	–14	0.071
	Right Declive		26	–68	–16	0.065
	Left Cerebellar Tonsil		–32	–56	–32	0.041
			–40	–58	–34	0.031
	Left Declive		–2	–76	–10	0.054
	Right Declive		10	–68	–16	0.040
Sub-lobar	Left Insula	13	–34	16	10	0.050
	Right Thalamus		14	–20	16	0.067
	Left Thalamus (Ventral Lateral Nucleus)		–16	–16	14	0.059

3. Results

ALE results provide evidence for both common and gender-specific memory network utilization (please see Table 1). Common to both genders, bilateral middle frontal gyri (BA6/9), left cingulate gyrus (BA32), right precuneus (BA7/19), left inferior and superior parietal lobes (BA40,BA7, respectively), right claustrum, and left middle temporal gyrus (BA39) were found to be consistently activated during working memory performance. Gender specific networks also emerged. For females, we found that working memory tasks elicited consistent activity in regions of the limbic system such as the anterior cingulate (BA32), bilateral amygdala, and right hippocampus, in addition to an extensive prefrontal network inclusive of bilateral middle frontal gyri (BA46) and the right medial frontal gyrus (BA9). Males demonstrated a distributed gender-specific working memory network inclusive of the cerebellum, portions of the superior parietal lobe (BA7), the left insula (BA13), and bilateral thalamus (please see Figs. 1 and 2).

Post hoc *Decomposition of Working Memory*. Our initial findings revealed neural network recruitment differences in working memory, such that females demonstrated more limbic activation. Because of the disparate search set sizes, and to ensure our data were driven by cognitively coded papers, we did post hoc analyses examining the two most prevalent working memory tasks: the n-back and the delayed match to sample (DMTS) task. For these searches, we followed the above procedure, but in addition to the search criteria of ‘Experiments → Behavioral Domain → Cognition → Memory – Working’, we also included ‘Experiments → Paradigm Class → Delayed Match to Sample (or n-back)’. This allowed us to narrow our search to only those studies implementing n-back or DMTS tasks within the behavioral domain of ‘Cognition’. The DMTS and n-back search specific to females yielded 15 papers, 195 subjects, 45 experiments, 53 conditions, and 484 locations. The male workspace consisted of 30 papers, 397 subjects, 76 experiments, 89 conditions, and 757 locations. ALE was implemented as described above. Maps were thresholded at an FDR-corrected p -value of 0.05, with a cluster threshold of 100mm^3 . We also performed a quantitative contrast of the resultant ALE maps to objectively determine the differences between male and female networks in a statistically sound manner using the GingerALE program within the BrainMap environment. To do this, GingerALE performs a subtraction of one ALE image from the other. Similar to a traditional ALE analysis, GingerALE creates simulated data by pooling the coordinates from the original datasets and

randomly dividing them into two new groupings of the same size as the original datasets, then subtracting these new pairings (i.e., permutations are used to create a null distribution of which the real-data is then compared). The resultant images are converted to z-score maps.

Our results largely mirror the results obtained from including all working memory studies, with females demonstrating more activation throughout the limbic and prefrontal regions, including bilateral amygdalae and cingulate regions, and males activating more parietal areas, such as the inferior and superior parietal lobe and the precuneus (please see Tables 2–4). The quantitative assessment of gender differences on the resultant ALE maps from the post hoc analysis corroborated with evidence from visual assessment. Specifically, the females showed greater activation of limbic structures inclusive of the amygdalae, in addition to frontal regions such as the left medial and superior frontal gyri and the right middle and inferior gyri. Males demonstrated greater activation consistently in the left precuneus and superior parietal lobule, as well as the right insula (please see Table 5 and Fig. 3, Panel B).

4. Discussion

Despite over a century of scientific inquiry, little progress has been made in addressing the substrates of gender differences, specifically as they relate to working memory. Using a novel approach, we used the BrainMap database to probe neurofunctional differences in working memory. Our results provide evidence for differential network recruitment by males and females undergoing working memory tasks. The results are consistent with previous literature suggesting that males utilize more spatial processing related networks (i.e., parietal regions) than females, and females tend to recruit more prefrontal regions (Haier et al., 2005), suggesting that men and women may use different strategies to solve complex problems (Haier et al., 2005).

The congruent areas of activation are not surprising as they are the anatomical structures most associated with working memory processes. Across studies, there has been consistent activation patterns seen in the frontal, temporal, and parietal regions (Baddeley, 1981, 1997, 2000; Baddeley & Logie, 1999; D’Esposito et al., 1998a, 1998b, 2000; Na et al., 2000; Prabhakaran et al., 2000; Repovs & Baddeley, 2006). Baddeley and Hitch’s revised theory of working memory (2000) can be used to explain the observed activation patterns. In their theory, working memory was composed of four interconnecting systems: (1) the phonological loop, responsible

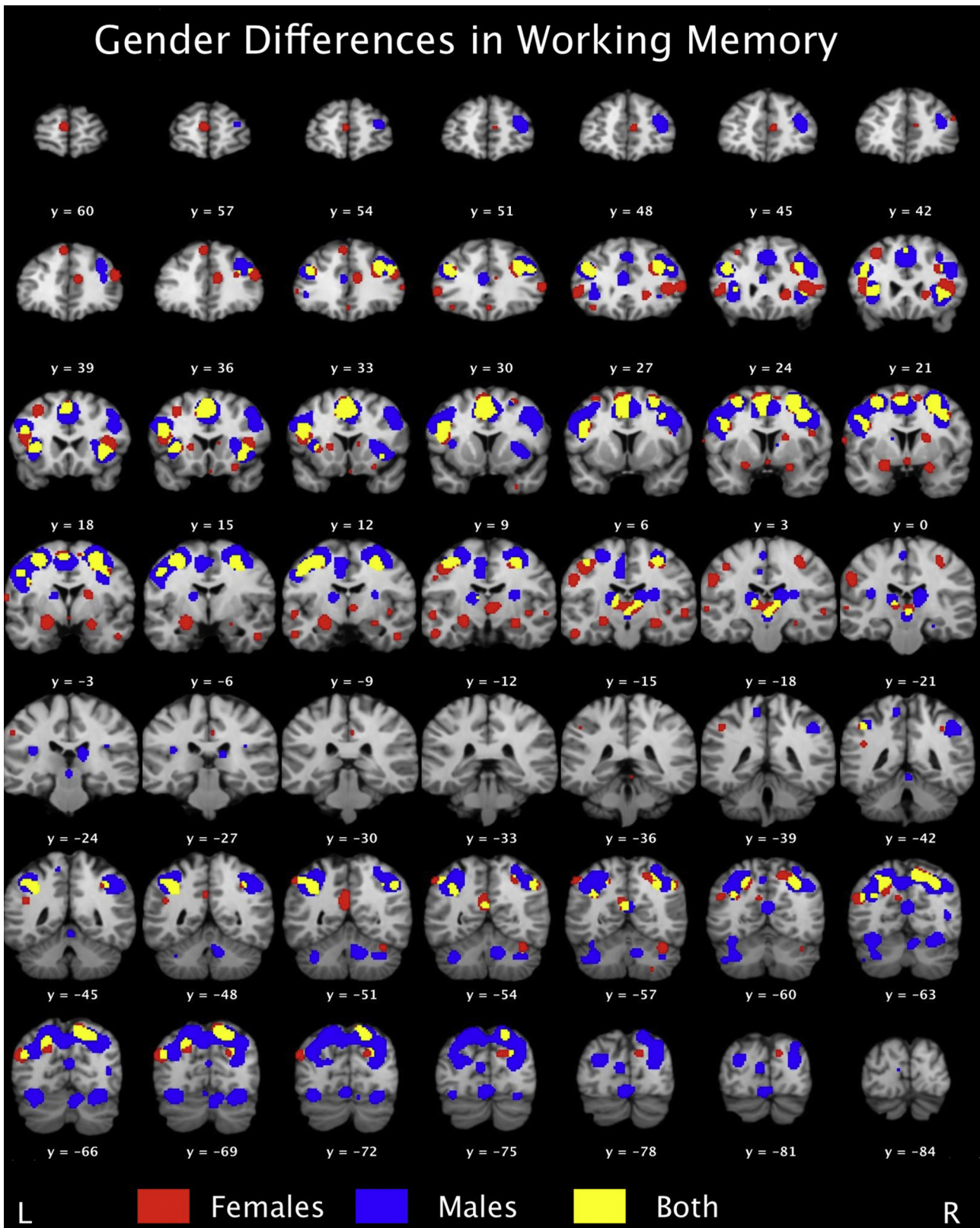


Fig. 1. Mosaic view of working memory networks in males (blue) and females (red). Brain regions recruited by both genders during working memory tasks are depicted by yellow. Maps were thresholded at $p < 0.05$, FDR-corrected. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

286 for the storage and maintenance of speech-based information,
 287 (2) the visuospatial sketchpad, which stores and maintains visual
 288 and spatial information, (3) the central executive, responsible
 289 for controlling and integrating the information from the prior

systems while also manipulating the information within working
 memory, and lastly, the most recently added component, (4) the
 episodic buffer, which assists with the binding of information to
 create episodes (Baddeley, 2000; Repovs & Baddeley, 2006). These

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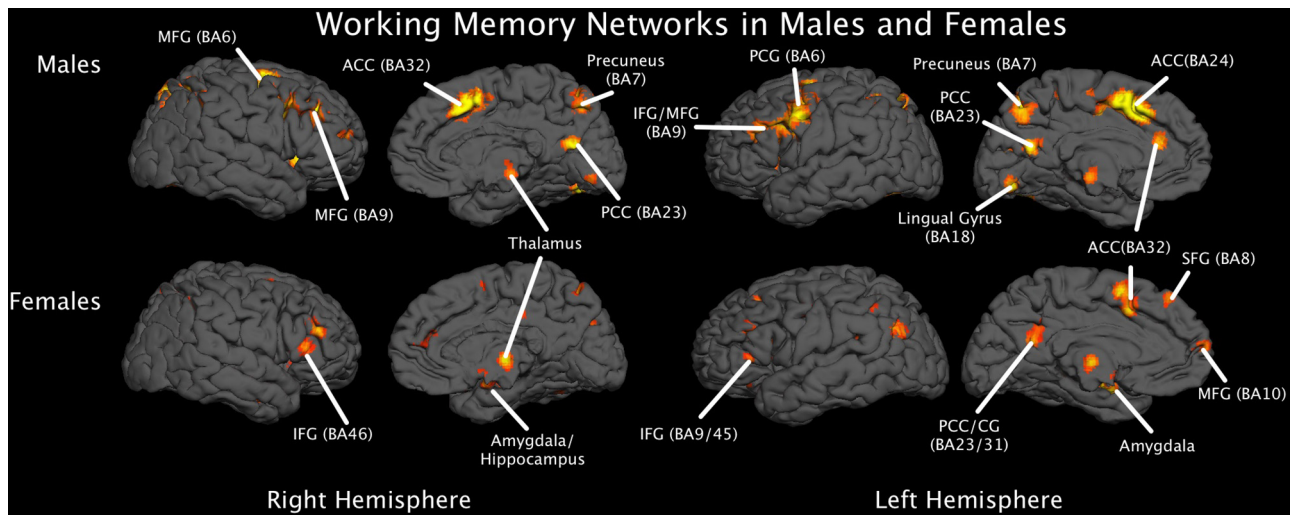


Fig. 2. 3D rendering of the working memory networks in males and females.

systems are not mutually exclusive, but rather are thought to have overlapping neural components inclusive of the regions we identified as convergent in our dataset. The prefrontal cortex has been found to reliably activate during working memory tasks, which can

be related back to the role of the central executive as well as the episodic buffer. Research has shown that the prefrontal cortex is critical in the maintenance and integration of verbal and spatial information (Prabhakaran et al., 2000), one of the primary roles of

Table 2
 Gender differences in DMTS and N-back working memory tasks.

Convergent brain regions				Females			Males			ALE	ALE
Lobe	Region	BA	x	y	z	x	y	z	Female	Male	
Anterior	Right Culmen		2	-50	-20	6	-42	-20	0.009	0.012	
Frontal	Left Middle Frontal Gyrus	6	-26	-4	50	-26	-8	56	0.022	0.051	
	Left Precentral Gyrus		-40	0	28	-44	0	30	0.035	0.051	
	Right Precentral Gyrus		42	2	28	32	0	34	0.010	0.049	
	Right Sub-Gyral		26	2	52	20	-6	56	0.029	0.047	
	Left Inferior Frontal Gyrus	9	-56	12	24	-52	10	30	0.011	0.034	
	Right Medial Frontal Gyrus		8	48	16	8	50	16	0.016	0.014	
	Right Middle Frontal Gyrus		28	34	24	32	30	32	0.013	0.039	
				48	16	34	48	16	36	0.009	0.021
	Left Middle Frontal Gyrus	10	-38	44	16	-42	50	4	0.012	0.013	
	Right Middle/Superior Frontal Gyrus		38	48	20	36	46	16	0.014	0.026	
			45	-50	28	-52	18	4	0.021	0.013	
	Left Extra-Nuclear/Inferior Frontal Gyrus	47	-30	18	-10	-32	20	-8	0.014	0.017	
Limbic	Left Cingulate Gyrus	31	0	-50	26	-2	-50	28	0.020	0.016	
		32	-4	10	42	-12	6	40	0.032	0.024	
Occipital	Left Lingual Gyrus	18	-20	-78	-8	-14	-82	-10	0.008	0.012	
	Right Cuneus		26	-68	18	26	-76	20	0.011	0.057	
Parietal	Left Postcentral Gyrus	3	-54	-18	26	-50	-18	38	0.015	0.011	
	Left Precuneus	7	-20	-64	38	-14	-70	48	0.020	0.041	
	Right Precuneus		12	-64	48	18	-70	46	0.019	0.064	
		19	30	-60	40	32	-66	38	0.022	0.025	
	Right Superior Parietal Lobule	7	38	-58	52	28	-58	54	0.009	0.032	
	Right Inferior Parietal Lobule	40	46	-54	40	44	-50	40	0.023	0.019	
Posterior	Left Cerebellar Tonsil		-36	-52	-44	-36	-56	-44	0.010	0.011	
	Right Cerebellar Tonsil		24	-58	-44	28	-58	-36	0.014	0.012	
	Right Declive		26	-70	-16	26	-68	-16	0.015	0.058	
Sub-lobar	Left Insula	13	-36	18	8	-34	16	10	0.024	0.025	
	Right Claustrum		32	14	0	32	12	4	0.019	0.029	
	Left Caudate Body		-6	0	10	-6	2	18	0.011	0.011	
Temporal	Left Superior Temporal Gyrus	22	-44	-34	-2	-46	-36	0	0.019	0.011	
	Left Fusiform Gyrus	37	-40	-54	-18	-42	-44	-12	0.027	0.010	
	Right Superior Temporal Gyrus	38	44	20	-18	42	20	-18	0.009	0.011	
	Left Middle Temporal Gyrus	39	-32	-60	30	-34	-68	30	0.014	0.018	

Table 3
Female-specific network in DMTS and N-back working memory tasks.

Lobe	Region	BA	x	y	z	ALE
Anterior	Right Pyramis		2	–64	–26	0.017
	Right Culmen		4	–42	–22	0.009
			10	–36	–20	0.009
			34	–56	–22	0.027
Frontal	Right Precentral Gyrus	4	32	–18	48	0.009
		6	24	–14	46	0.008
	Left Precentral Gyrus	6	–62	0	14	0.016
		6	–44	–8	40	0.021
	Left Middle Frontal Gyrus	6	–22	14	56	0.011
	Left Superior Frontal Gyrus	6	–6	6	54	0.039
	Right Medial Frontal Gyrus	6	10	0	56	0.010
	Right Middle Frontal Gyrus	6	16	14	58	0.011
		6	38	0	40	0.016
	Left Middle Frontal Gyrus	8	–34	16	42	0.013
	Left Medial Frontal Gyrus	8	–10	40	40	0.008
	Left Inferior Frontal Gyrus	9	–54	4	22	0.014
	Left Middle Frontal Gyrus	9	–52	14	32	0.010
		9	–36	28	26	0.026
	Left Medial Frontal Gyrus	9	–4	48	26	0.016
		10	–16	48	6	0.009
	Left Middle Frontal Gyrus	11	–20	48	–8	0.010
	Right Middle Frontal Gyrus	11	24	48	–10	0.009
	Right Inferior Frontal Gyrus	13	34	10	–12	0.015
	Right Medial Frontal Gyrus	25	2	14	–16	0.015
	Right Inferior Frontal Gyrus	44	42	16	10	0.013
	Left Inferior Frontal Gyrus	45	–42	16	16	0.021
	Right Middle Frontal Gyrus	46	46	38	22	0.026
	Right Inferior Frontal Gyrus	46	52	28	12	0.024
		47	26	14	–10	0.012
	Left Inferior Frontal Gyrus	47	–40	28	0	0.012
Limbic	Left Anterior Cingulate	25	0	0	–6	0.015
	Left Posterior Cingulate	31	–10	–54	18	0.012
	Right Cingulate Gyrus	31	4	–30	36	0.014
	Left Amygdala		–22	–6	–12	0.030
	Right Amygdala		22	–2	–12	0.025
	Right Hippocampus		28	–14	–12	0.025
Midbrain	Left Substantia Nigra		–8	–20	–8	0.016
Occipital	Left Cuneus	18	–8	–80	20	0.012
	Left Middle Temporal Gyrus	19	–40	–60	16	0.009
	Right Middle Occipital Gyrus	19	30	–80	22	0.012
	Left Precuneus	31	–8	–60	26	0.008
Parietal	Right Superior Parietal Lobule	7	36	–66	48	0.008
	Left Angular Gyrus	39	–46	–66	28	0.015
	Right Angular Gyrus	39	54	–64	32	0.010
	Left Inferior Parietal Lobule	40	–52	–54	44	0.017
	Left Inferior Parietal Lobule	40	–34	–50	36	0.026
	Right Inferior Parietal Lobule	40	34	–48	40	0.019
	Right Inferior Parietal Lobule	40	60	–32	30	0.009
Posterior	Right Declive		32	–64	–12	0.015
Sub-lobar	Left Insula	13	–42	–28	24	0.011
	Right Insula	13	36	20	18	0.009
		13	40	–12	–2	0.015
	Left Amygdala		–24	–10	–10	0.029
	Left Thalamus		–12	–18	6	0.024
	Right Thalamus (Medial Dorsal Nucleus)		4	–16	4	0.031
	Right Lateral Globus Pallidus		12	2	4	0.009
	Right Caudate Head		18	24	4	0.024
	Right Caudate Body		20	–2	20	0.008
	Right Lateral Globus Pallidus		22	–12	2	0.019
	Right Thalamus (Pulvinar)		26	–30	6	0.016
Temporal	Right Fusiform Gyrus	20	46	–6	–20	0.009
	Right Middle Temporal Gyrus	20	58	–42	–10	0.009
		21	56	–14	–6	0.013
	Left Middle Temporal Gyrus	21	–54	–12	–6	0.017
		22	–48	–46	2	0.014
	Left Superior Temporal Gyrus	38	–42	4	–8	0.008
		38	–38	8	–14	0.009
		38	–36	4	–14	0.009
	Right Angular Gyrus	39	46	–74	30	0.010

Table 4
Male-specific network in DMTS and N-back working memory tasks.

Lobe	Region	BA	x	y	z	ALE	
Anterior	Right Cerebellar Lingual		2	–42	–8	0.022	
	Right Nodule		10	–52	–28	0.051	
	Right Culmen		12	–60	–2	0.013	
Frontal	Left Middle Frontal Gyrus	6	–46	0	38	0.053	
	Left Medial Frontal Gyrus	6	–8	–10	48	0.015	
		6	–4	–20	56	0.027	
	Left Superior Frontal Gyrus	6	0	8	48	0.065	
	Right Middle Frontal Gyrus	6	28	–6	54	0.042	
	Left Superior Frontal Gyrus	10	–38	50	18	0.012	
	Left Precentral Gyrus	44	–52	6	10	0.010	
	Left Inferior Frontal Gyrus	46	–42	30	10	0.014	
	Left Middle Frontal Gyrus	46	–42	18	26	0.027	
	Left Inferior Frontal Gyrus	47	–48	18	–6	0.013	
Limbic	Left Posterior Cingulate	23	–4	–56	20	0.014	
		29	0	–42	22	0.018	
Midbrain	Left Red Nucleus		0	–20	–6	0.029	
Occipital	Left Cuneus	17	–6	–78	14	0.013	
	Right Lingual Gyrus	17	10	–88	–4	0.016	
	Left Cuneus	18	–18	–82	28	0.011	
	Left Middle Occipital Gyrus	19	–28	–78	18	0.023	
	Left Lingual Gyrus	19	–18	–60	–4	0.012	
	Right Middle Occipital Gyrus	19	38	–64	10	0.023	
	Left Inferior Temporal Gyrus	37	–44	–64	–2	0.011	
Parietal	Left Postcentral Gyrus	3	–40	–26	56	0.015	
	Left Superior Parietal Lobule	7	–30	–54	46	0.052	
	Right Precuneus	7	4	–52	60	0.011	
		7	6	–70	42	0.027	
		7	8	–50	44	0.015	
		7	28	–44	42	0.011	
	Left Precuneus	7	–4	–68	36	0.027	
		19	–10	–84	44	0.010	
	Left Inferior Parietal Lobule	40	–36	–52	36	0.034	
Posterior	Left Cerebellar Tonsil		–42	–58	–32	0.019	
	Left Declive		–34	–68	–14	0.052	
			–26	–84	–16	0.013	
			–12	–68	–18	0.025	
			–2	–76	–10	0.042	
	Right Uvula		6	–66	–34	0.015	
	Right Declive		10	–68	–16	0.040	
	Sub- lobar	Left Insula	13	–40	0	14	0.010
		Right Insula	13	36	–24	22	0.024
Left Caudate Body			–16	–2	16	0.014	
Left Thalamus (Ventral Lateral Nucleus)			–16	–16	12	0.048	
Right Caudate Body			8	4	10	0.020	
Right Thalamus (Lateral Dorsal Nucleus)			12	–20	16	0.052	
Left Cerebellum			–2	–82	–24	0.013	

the central executive and a feature of the episodic buffer. Solidifying this, research has demonstrated that tasks employing the episodic buffer reliably activate the right prefrontal cortex (Repovs & Baddeley, 2006). The activation seen in areas associated with language can be interpreted as a function of the phonological loop due to their importance in linguistic processing. Furthermore, activation observed in both the inferior and superior parietal cortices may be related to the visuospatial sketchpad due to their known pertinence in the integration of visual information and spatial cognition (please see Na et al., 2000 for a review).

Our data demonstrates consistency with the working memory literature, but also highlights differences that should be examined more thoroughly in future research. Differences in neurophysiology (i.e., cerebral glucose metabolism, cerebral blood flow) during rest have been observed between genders (Davidson, Schwartz, Pugash, & Bromfield, 1976; Gur et al., 1995; Ray, Morell, & Frediani, 1976). Given that our results are based on functional neuroimaging

results, which are tightly correlated with these physiological measurements, it is not surprising that differences in neural network recruitment exist during an active state as well. It is possible that the differences observed during rest 'prime' the brain to utilize certain networks preferentially. Given the strong limbic activation in the female dataset, it is also possible that females have more limbic contributions to working memory processing than males, a theory that should be investigated further using more advanced analysis techniques such as effective and functional connectivity.

Data from this study and previous research supports the notion that males and females rely on different brain networks to perform the same function, with the implications most notable in the academic realm. Halpern and colleagues (2007) suggest that we can use this knowledge to teach female and male students ways to solve problems that correspond to their most efficient cognitive process (i.e. verbal versus visuospatial solution strategies) to allow more flexibility in their problem solving and positively

Table 5
Gender differences in DMTS and N-back working memory tasks.

Females > Males							
Lobe	Region	BA	x	y	z	Z-Score	
Anterior Frontal	Right Culmen		30	–56	–24	3.01	
	Left Medial Frontal Gyrus	6	–13	10	53	3.35	
			–8	6	56	3.09	
	Left Superior Frontal Gyrus	45	–10	12	58	3.29	
			50	22	11.14	3.72	
	Right Inferior Frontal Gyrus	46	54	26	14	3.43	
			46	32	24	3.29	
			50	32	18	3.09	
	Limbic	Right Parahippocampal Gyrus	28	26	–20	–10	3.43
				34	20	–3.6	–9.2
Left Uncus			21	–12	–16	2.66	
			–22.6	–0.53	–13.57	3.89	
Left Amygdala			–16.67	–4	–18	3.43	
			–16	–8	–10	3.35	
Right Amygdala			25	–3	–11.5	2.85	
			19.5	–9.5	–12	2.83	
			18	–4	–16	2.82	
Right Hippocampus			32	–10	–14	2.70	
Sub-lobar	Left Insula	13	–42	–6	–6	3.09	
	Left Thalamus		–2	–11	2	2.97	
	Right Claustrum		36.86	–12.86	–0.29	3.72	
	Right Lateral Globus Pallidus		25.6	–14	–4.8	3.24	
	Right Medial Globus Pallidus		18.67	–4.67	–8	2.79	
	Right Putamen		30	–18	–8	3.54	
			29	–15	–6	3.35	
			28	–8	–8	3.19	
Temporal	Right Thalamus		6	–8	2	2.82	
	Left Sub-Gyral	21	–44	–6	–10	3.24	
	Left Superior Temporal Gyrus	22	–50.5	–8.75	–4.25	3.72	
Males > Females Frontal	Left Medial Frontal Gyrus	6	–12.8	–17.4	55.6	3.89	
			–4	–24	59	3.72	
			–4.8	–17.2	58.4	3.29	
			0	–14	56	2.85	
	Left Middle Frontal Gyrus		–19	–7	60	3.16	
	Left Precentral Gyrus		–28	–14	62	2.99	
	Right Sub-Gyral		24	–10	54	3.29	
	Parietal	Left Precuneus	7	–26	–56	54	3.04
		Left Superior Parietal Lobule		–30	–61	45	2.95
				–26	–62	54	2.93
Sub-lobar	Right Insula	13	36	–22	25	3.04	

336 impact performance overall. Furthermore, a trickle down effect of
 337 understanding the neural differences underlying working memory
 338 processes between genders may lead to advancements in unbiased
 339 test design, particularly with regard to popular standardized
 340 tests such as the GRE and SAT, which have been criticized for hav-
 341 ing gender-biased questions. Such considerations may alleviate the
 342 gender discrepancy observed in academics.

343 Working memory is utilized during many complex cognitive
 344 functions, and the knowledge of gender differences could bring
 345 into question preferential strategy use, and unlock methods that
 346 would eliminate the gender gap. Due to working memory's pivotal
 347 role across a diverse set of cognitive functions, there is a possibil-
 348 ity of neurofunctional differences during processing, and if this is
 349 the case, research addressing these differences will yield greater
 350 insight into gender specific cognitive function and expand the lit-
 351 erature on gender differences in these constructs. Furthermore,
 352 with the robust and sensitive cognitive neuroscience tools, we may
 353 delineate the neurophysiological basis of the differences.

354 Possible limitations on the present study are those that are
 355 shared among meta-analysis based methods. We were unable to
 356 control for specific attributes of the participants that could add pos-
 357 sible confounds to the overall data such as handedness and where

the female participants were in their menstrual cycle, both of which
 have been shown to impact imaging data. There were also more
 males than females in the studies included in our meta-analysis. In
 this study, we did not select working memory tasks based on their
 content either (i.e., verbal versus spatial). Research has shown that
 different working memory tasks utilize different brain networks, so
 depending on the tasks used in the experiments some differences
 could be related to proportions of specific tasks used (Na et al.,
 2000) in each workspace. We examined the behavioral domains
 and paradigms within each of our search sets (Fig. 3). As noted in
 the figure, only a very small percentage of data were coded as emotion,
 perception, interoception, or action (73% of the female dataset and
 76% of the male dataset were coded as cognition). The majority of
 both data sets were drawn from classic working memory paradigms
 (84% of paradigms in the female dataset and 56% in the male dataset
 were either delayed match to sample or n-back paradigms). In the
 deconstruction analysis that we carried out post hoc, we limited
 our search to only those tasks that were coded as n-back or DMTS,
 and coded under the behavioral domain of 'Cognition'. These addi-
 tional analyses did not change our initial findings, thus, we believe
 our sample is robust and likely offsets the possibility of the above
 confounds.

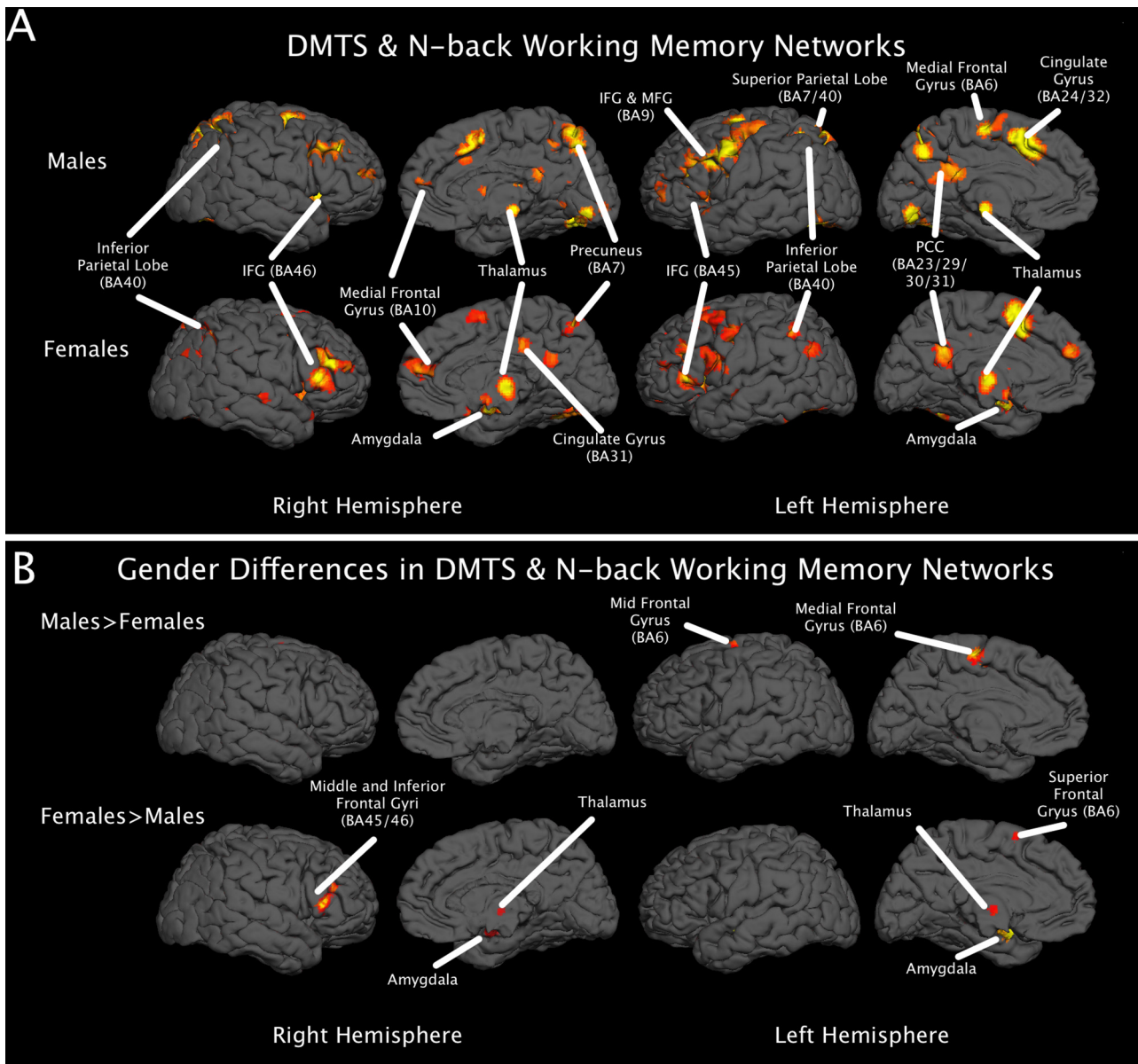


Fig. 3. (A) 3D rendering of networks involved in n-back and DMTS tasks, thresholded at $p < 0.05$, FDR-corrected. (B) 3D rendering from the contrast analysis of the resultant ALE maps from panel A, thresholded at $z > 2.3$.

Future studies should attempt to have an even gender distribution to control for any effects caused by the greater depth of the male workspace. As shown in Fig. 4, the male dataset also had a more diverse profile of working memory paradigms compared to the female workspace. However, we do note that our post hoc analysis that just examined n-back and DMTS cognitive tasks still demonstrated gender differences. Therefore, future studies should focus on increasing the number of verbal and spatial working memory papers to further deconstruct the observed differences. Additionally, future neuroimaging studies should use the models presented in this paper to look at functional and effective connectivity differences during working memory. Using this strategy, we may be able to probe the strategic differences and their effects on the neurofunctional networks subservient to working memory. These differences may exist even when activation patterns don't demonstrate differences between genders.

Although gender differences are socially and scientifically important to understand, few studies have addressed their potential neurophysiological basis. Addressing these issues could lead to

advances in our understanding of the underlying neural networks that may be responsible for gender differences in working memory, potentially leading to tailored developmental cognitive programs or novel strategy development that could reduce the gender gap that is thought to exist in some areas of cognition (Irwing & Lynn, 2002, 2005, 2006). It also provides a foundation to further investigate brain based gender differences and the implications they have for all areas of cognition (Davidson et al., 1976; Gur et al., 1995). To our knowledge, this is the first study addressing neural network differences in working memory using meta-analytic modeling, a powerful and robust technique that capitalizes on the advantages of archived functional neuroimaging studies (Laird et al., 2005c; Minzenberg, Laird, Thelen, Carter, & Glahn, 2009). Here, we have provided a preliminary model of neurofunctional gender-specific working memory networks. Further research directions could use this model to ascertain why and how males and females use different neural networks during working memory tasks, or could attempt to assess when these neurofunctional differences first appear in development as well as

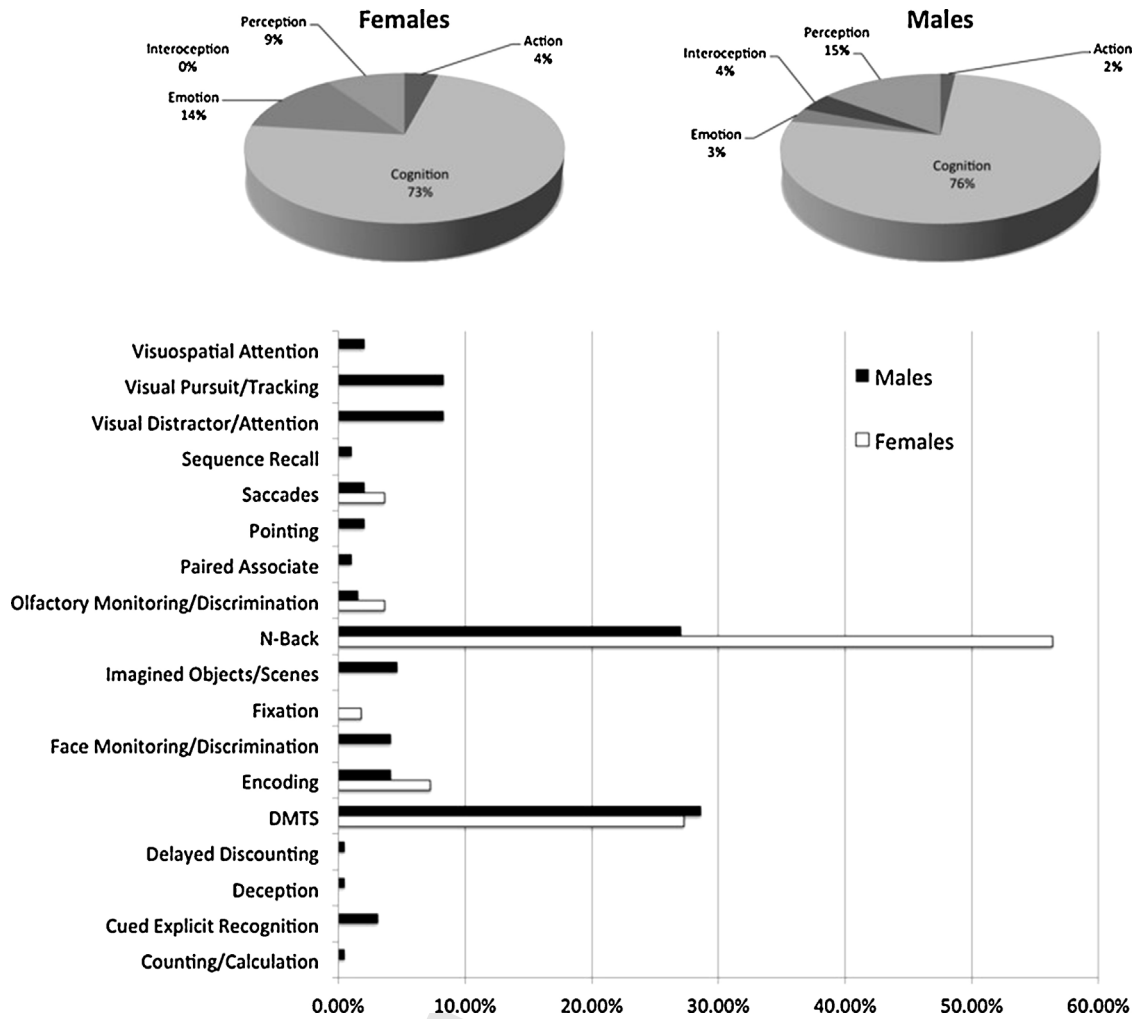


Fig. 4. Behavioral domain (top panels, shown in pie graph form) and paradigm breakdown (bottom panel) of the male and female workspaces. Because of the disparate workspace sizes, all values are shown as percentages within each gender-specific workspace, respectively.

the possible stimuli influencing the emergence of these observed difference.

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