

The Effect of Individual Differences in Working Memory Capacity on Sentence Comprehension: An fMRI Study

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Abstract This study explores the interaction between working memory systems and language processing by examining how differences in working memory capacity (WMC) modulates neural activation levels and functional connectivity during sentence comprehension. The results indicate that two working memory systems may be involved in sentence comprehension, the verbal working memory system and the episodic buffer, but during different phases of the task. A sub-region of the left inferior frontal gyrus (BA 45) was correlated with WMC during the probe and not during sentence reading while the only region to reveal a correlation with WMC during sentence reading was the posterior cingulate/precuneus area, a region linked to event representation. In addition, functional connectivity analysis suggests that there were two distinct networks affected by WMC. The first was a semantic network that included the middle temporal cortex, an anterior region of the inferior frontal gyrus and the inferior parietal region. The second included the posterior cingulate and BA 45 of the inferior frontal gyrus. We propose here that high capacity readers may generate an event representation of the sentence during reading that aids in comprehension and that this event representation involves the processing of the posterior cingulate cortex.

Keywords Working memory · Individual differences · fMRI

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Introduction

One of the long running debates in the psycholinguistic literature relates to the relationship between language and working memory (WM, Fedorenko et al. 2006; Caplan and Waters 1999; King and Just 1991; Gordon et al. 2002; MacDonald and Christiansen 2002). There are numerous studies that show a link between working memory capacity (WMC) and language processing, particularly sentence comprehension (Caramazza et al. 1981; Friedrich et al. 1984; King and Just 1991; Lauro et al. 2010; Papagno et al. 2007). For example, in a meta-analysis Daneman and Merikle's (1996) found that individual differences in WMC significantly predicted reading comprehension, but only for complex span tasks like the reading span and not for storage-only span tasks like forward digit span. Additionally, operation span tasks with numerical stimuli also predict comprehension, not just verbal span tasks. This suggests that the verbal-processing component in these WM measures does not fully account for the working memory-comprehension association (Engle et al. 1992; Kane et al. 2004). The current study attempts to further explore this interaction between working memory and comprehension by examining the involvement of WM systems other than the verbal WM system during sentence comprehension.

Working memory (WM) is considered to be a multi-domain workspace composed of various storage and processing modules (Baddeley et al. 2010; Logie 2011). There are at least three domain specific modules: memory for verbal sequences; visuo-spatial/motor sequences; and episodic, integrated multidimensional representations. Much of the previous research examining the relationship between language and WM has focused on its relationship with the verbal WM system. However, it may very well be

that language interacts with the visuo-spatial and episodic buffers as well, likely via mental imagery.

This study proposes that the use of event representations in the service of sentence comprehension may vary as a function of WMC. Language is thought to activate internal representations of previously experienced events, or schematic abstractions (Lakoff 1987; Langacker 1987; Talmy 2000). The activation of these internal representations may then be used to create an event representation or situation model of the sentence which aids in comprehension. Bergen et al. (2007) have shown that mental imagery is triggered by both subject nouns and verbs in the service of sentence comprehension. Also, McRae et al. (2005) argue that accessing a verb activates information regarding the event it encodes including the entities that typically participate in the event. Both studies suggest that event information, or complex integrated multidimensional representations may be triggered via language. We argue here that the construction of this event representation requires WM resources and therefore, may vary as a function of WMC.

It may also be that these different WM modules are more or less involved in comprehension at different points during the task. The typical sentence comprehension task presents a sentence (what we refer to as the online phase) followed by a probe to test comprehension (off-line phase). The online sentence processing is viewed as the *interpretive processes* of “recognizing words and appreciating their meanings and syntactic features; constructing syntactic and prosodic representations; and assigning thematic roles, and other aspects of propositional and discourse-level semantics” (Caplan and Waters 1999, p. 78). On the other hand, off-line processing is thought of as the *post-interpretive processes* associated with the post hoc usage of extracted meanings to accomplish the task (e.g., responding to a comprehension probe; Caplan and Waters 1999). As such it is predicted that during sentence reading episodic memory systems are more involved in the activation of event knowledge and the integration of information into an event representation. Conversely, during the comprehension probe executive control processes required to extract the appropriate information from the WM representation generated during sentence processing are more involved.

Previous studies have used neuroimaging to explore the impact of individual differences in WM on language related activation (Fiebach et al. 2005; Prat et al. 2007). Generally, these studies have found that high capacity readers outperform low WMC readers in that they have faster reading and response times and are more accurate. High capacity readers also elicit less activation. For example, in a recent functional magnetic resonance imaging (fMRI) study Prat et al. (2007) explored the impact of WMC differences on neural network properties outlined by

Newman and Just (2005)—efficient use of neural resources, adaptability to changing demands, and the coordination or synchronization of nodes within cortical networks. It was found that high capacity readers demonstrated greater neural efficiency in that they elicited less activation in conjunction with better behavioral performance. They also showed better synchronization of the processing nodes within the language network as revealed by increased functional connectivity. This study reveals that WM has a significant impact on not only behavior but also the neural network that supports language. However, their analysis was limited to regions that have been previously identified as part of the language network rather than performing a whole brain analysis. Therefore, it was not possible to explore how other neuro-cognitive networks (e.g., WM networks) may be differentially interacting with the language network.

The primary goal of the current study was to explore the impact WMC has on sentence comprehension. To accomplish this goal we examined the interaction between WMC and activation during both sentence reading and when responding to a comprehension probe. In this way the differential impact of WM on these two processing phases could be determined. Additionally, functional connectivity analysis was performed to explore how WMC impacted the connectivity between language-related and WM related processing regions.

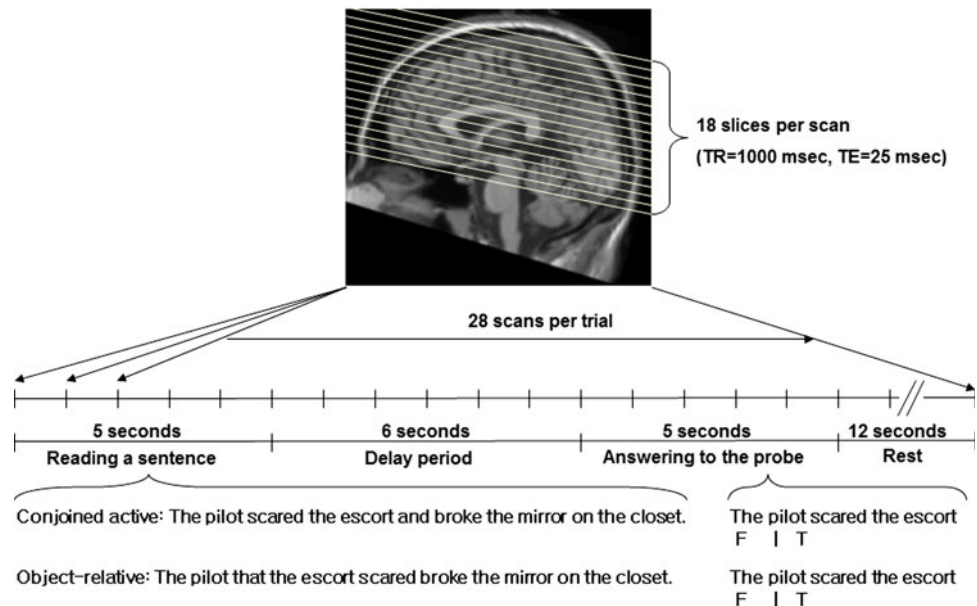
Methods

Participants

Fifty participants took part in this study. They were all Indiana University students without any history of neurological disorders (28 female, age = 22.5 ± 3.1). All participants gave signed informed consent which was approved by the Indiana University Institutional Review Board.

Experimental Procedure

This study combines data from three separate studies with overlapping stimuli (Lee and Newman 2010; Newman et al. 2009; Newman and Ikuta 2010); the non-overlapping stimuli were treated as fillers of no interest. Each study was composed of three sessions, training, imaging and debriefing sessions. During the training session, all participants were administered the Edinburgh handedness inventory and the Daneman and Carpenter (1980) Reading Span Test to obtain a measure of WM capacity. Participants were all right-handed and their reading span scores ranged from 2 to 5 (Mean = 3.4 ± 0.98). During the training session, participants were also introduced to the

Fig. 1 Experimental Design

sentence comprehension experiment that they would perform and completed 16 practice trials to familiarize them with the experimental procedure. Immediately after the fMRI scan, participants completed a debriefing questionnaire. The questionnaire was designed to determine how the participant performed the task as well as assess their perception of difficulty.

The fMRI experiments used a single trial event-related design in which each trial was treated as an event block (Kruggel and von Cramon 1999; Zarahn et al. 1997; Zarahn 2000; Fig. 1). A trial could be divided into two phases; a sentence reading phase and a responding to a comprehension probe phase. Participants were instructed to read each sentence thoroughly and respond as quickly and accurately as possible to probes that were presented 6 s later. Participants were told to place a greater weight on accuracy than speed of responding. Sentence materials were taken from Keller et al. (2001) which were derived originally from Just et al. (1996). The object-relative sentences were syntactically more complex (Caplan and Waters 1999; Just et al. 1996; Keller et al. 2001; Prat et al. 2007). Stimuli were equated across conditions for frequency, word length, sentence length and animacy.

Probes were constructed by asking if one of the nouns performed the act denoted by one of the two verbs. Thirty-three percent of the probes were false. Example stimuli include:

Conjoined active: The pilot scared the escort and broke the mirror on the closet.

The pilot scared the escort.

Object-relative: The pilot that the escort scared broke the mirror on the closet.

The pilot broke the mirror.

The duration of each trial was 16 s. A trial began with a sentence being presented in the middle of the screen for 5 s. After 5 s, an X was presented on the screen for 6 s during a delay to allow the hemodynamic response to approach baseline. By inserting the 6 s delay the online sentence reading phase and off-line comprehension phase could be distinguished. Finally, a comprehension probe was presented for 5 s with a cue (i.e. FIT). The cue indicated the appropriate response (a right index finger for true and the left index finger for false). After each trial, a 12 s ITI was added to allow the hemodynamic response to return to baseline.

Each experiment was composed of 4 runs. Each run contained 3, 28 s fixation periods located at the beginning, middle and end of each run. The baseline hemodynamic response was measured by averaging the signal during the 28 s fixation periods (fixation to a star sign, *). Stimuli were presented on the screen located behind the scanner and viewed by participants via a mirror attached on the head coil. Fiber optic button boxes in each hand were used to record behavioral responses. Incorrect responses were removed from the response time analysis and the fMRI data analysis.

fMRI Acquisition and Analysis

Functional MRI was conducted on a 3T Siemens TRIO scanner with an 8-channel radio frequency head coil located in the Imaging Research Facility at Indiana University. Functional images were obtained in eighteen oblique axial slices with 5 mm thickness and a 1 mm gap (TR = 1,000 ms, TE = 25 ms, flip angle = 60°, matrix size = 64 × 64, FOV = 240 × 240 mm²) by a gradient

echo planar imaging (EPI) sequence. Before statistical analysis, for all functional images, conventional preprocessing procedures such as slice timing correction, head motion correction by realignment and spatial normalization were conducted using SPM8 software (Wellcome Department of Imaging Neuroscience; <http://www.fil.ion.ucl.ac.uk/spm>). In the spatial normalization step, all functional images were warped to the Montreal Neurological Institute (MNI) EPI template and resampled to $2 \times 2 \times 2 \text{ mm}^3$ voxels. A conventional statistical inference was performed on the normalized functional images from each individual by using the general linear model and Gaussian random field theory (Friston et al. 1995). A canonical hemodynamic response function (HRF) with trial onsets and durations for each phase (including the delay period) was used to generate a statistical parametric map.

Multiple regression analysis was performed using SPM8 for the sentence and probe phases and object-relative and conjoined active conditions separately as well as for the object-relative minus conjoined active contrast. Reading span was entered as a covariate. This allowed for the examination of regions whose activation was correlated with reading span as well as the exploration of the activation for a given contrast when reading span was covaried out. In addition, a standard one sample *t* test was performed without entering reading span as a covariate. A threshold of $p < 0.001$, uncorrected was used. The extent threshold of 92 voxels was determined using Monte Carlo simulations via AlphaSim (a part of the Afni software package).

Functional Connectivity Analysis

The functional connectivity between the regions found to be impacted by WM capacity WMC during sentence comprehension was analyzed. The regions included the two regions within the left IFG (MNI: $-42, 20, 30$, BA44/45 and $-28, 42, 6$, BA45/46), the posterior temporal cortex ($-44, -44, -2$), the inferior parietal cortex ($-36, -52, 48$) and the posterior cingulate ($-8, -44, 6$). These coordinates reflect the centroids of significant activation from the fMRI syntactic complexity contrasts or the correlation analyses with individual reading span scores carried out in SPM8. The ROIs were chosen to be spheres with a 5 mm radius. The center of the sphere was the peak activation voxel. Five participants were excluded from this analysis due not having a complete dataset (one run was removed due to excess motion).

An analysis similar to psychophysiological interactions analysis (PPI) was performed. Instead of examining whether the correlation in activity between two brain areas is different in different psychological contexts (which is what PPI does) we explored whether that activity is different across individuals with different WM capacities. For each

participant, the voxel timecourses in the ROIs were regressed against the time series for the motion correction parameters and global signal of the whole brain. Partial correlation analysis (regressing out time series from the other ROIs) was performed on each pair of regions using mean signal intensity¹. Z-scores were then computed from the Pearson product-moment correlation coefficients for each ROI pair for each participant using Fisher *r*-to-*Z* transformation. The correlation between individual reading span scores and pairwise regional connectivity was then assessed using linear regression analysis.

Results

Behavioral Results

Fifty participants' fMRI and behavioral data are included in this study. The reaction time (RT) and error rate for object-relative (OR) and conjoined active (CA) sentences were compared using a paired sample *t* test. The results revealed that the object relatives elicited more errors (OR: $M = 15 \pm 11 \%$; CA: $M = 7 \pm 8 \%$; $t = 7.2$, $p < 0.0001$) and a slower RT (OR: $M = 2405 \pm 445 \text{ ms}$; CA: $M = 2053 \pm 401 \text{ ms}$; $t = 10.8$, $p < 0.0001$). RT and error rate were also correlated with WM capacity. For CA sentences, only RT was correlated with WMC [error: $r = 0.26$; $F(1,49) = 3.08$, $p = 0.06$; RT: $r = 0.38$; $F(1,49) = 8.07$; $p < 0.01$]. For OR sentences both RT and error were significantly correlated with WMC [error: $r = 0.45$; $F(1,49) = 12.1$, $p < 0.005$; RT: $r = 0.33$; $F(1,49) = 5.95$; $p < 0.05$].

fMRI Sentence Phase

Syntactic Complexity effect

During the sentence phase object-relative sentences elicited increased activation in the caudate body bilaterally (MNI: $6, 16, 14/-8, 20, 12$; $z = 4.67/4.16$; $k = 189/202$) and the left caudate tail (MNI: $-24, -38, 10$; $z = 3.82$; $k = 189$). The comparison between object-relative and conjoined active sentences was also performed while regressing out WM capacity. The same regions were found when WMC was regressed out (the caudate nucleus).

Additionally, we explored the correlation between WM and the activation related to the syntactic complexity effect, no regions were found to be significantly correlated.

¹ To explore possible within-network effects among selected ROIs, the same analysis was also performed using full correlation for either the mean or the first component of ICA in the signals from individual ROIs.

Correlation with Object-Relative Sentences

Working memory capacity was also correlated with each sentence type separately. For the object-relative condition, the traditional WM-related regions were not found to be correlated with WMC as measured by the reading span task. One region did reveal a significant negative correlation, the posterior cingulate/precuneus region (PCC/MNI coordinates: $-8, -44, 6$; $k = 108$; $z = 3.55$), see Fig. 2.

To confirm this correlation a two-sample t test was performed by dividing the participants into two groups: a low capacity group ($\text{span} \leq 3$, $n = 27$) and a high capacity group ($\text{span} > 3$, $n = 23$). The low capacity readers revealed greater activation in the same PCC region which extended into the right hemisphere (MNI coordinates: $-8, -44, 6$; $k = 976$; $z = 3.93$) and the medial prefrontal cortex (MNI coordinates: $2, 62, 32$; $k = 209$; $z = 3.6$).

Correlation with Conjoined Active Sentences

No region reached threshold for the conjoined active condition. However, when the cluster threshold was relaxed a similar PCC region as observed for OR sentences was observed for this condition.

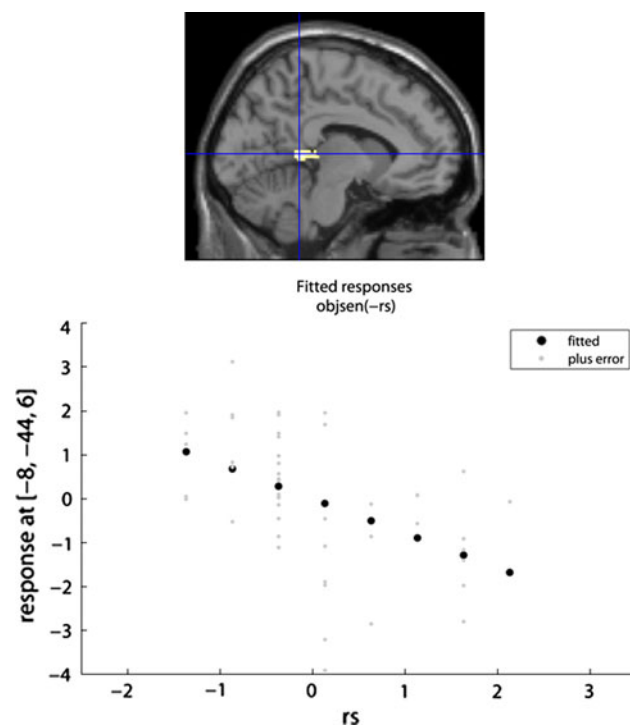


Fig. 2 Depicts the activation within the posterior cingulate cortex that was correlated with WMC during the sentence phase of object-relative: sentence

fMRI Probe Phase

Syntactic Complexity effect

Object-relative and conjoined active sentences were compared when WMC was regressed out and when it was not. Significant overlap in the pattern of activation as well as notable differences were observed for these two analyses (see Table 1; Fig. 3). Syntactic complexity effects were observed in the caudate, the middle frontal gyrus that extended inferiorly, medial prefrontal cortex, the precuneus and the inferior parietal cortex. When WM was regressed out, activation was also observed in middle temporal cortex and the posterior lobe of the cerebellum.

Additionally, we explored the correlation between WM and the activation related to the syntactic complexity effect, no regions were found to be significantly correlated.

Correlation with Object-relative Sentences

When examining each condition separately, the object-relative sentences revealed a significant negative correlation with WM capacity in the superior IFG (BA 45, MNI coordinates: $-50, 26, 26$ $k = 92$; $z = 3.65$) see Fig. 4.

Correlation with Conjoined Active Sentences

For the conjoined active condition, significant negative correlations were observed in the SMA (MNI: $-14, 6, 62$ $k = 98$, $z = 3.75$); PCC/precuneus (MNI: $-16, -52, 12$ $k = 191$, $z = 3.54$); putamen (MNI: $-26, -2, -20$; $k = 244$; $z = 3.85$); and the right caudate tail (MNI: $26, -24, 16$; $k = 199$, $z = 3.68$) regions, the left IFG activation failed to pass the extent threshold (IFG/MNI $-50, 26, 22$ $k = 87$; $z = 3.52$).

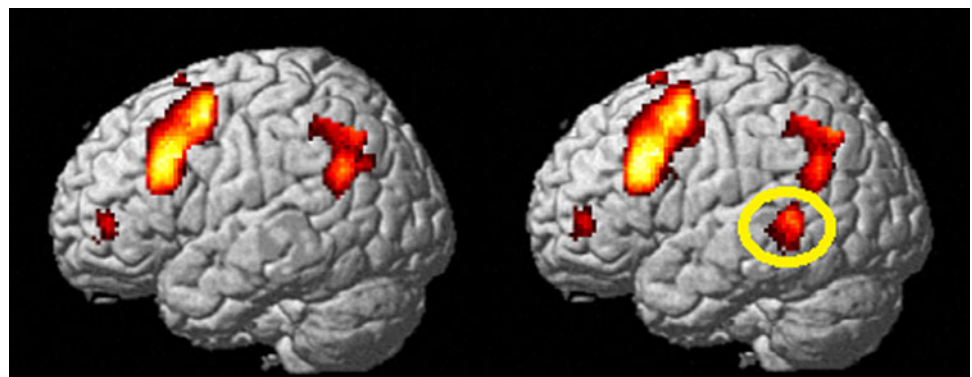
Functional Connectivity

We examined whether functional connectivity was modulated by WMC. After global signal regression using partial correlation based on the mean signal, BA45/44-PCC and IPL-PCC connectivity were found to be significantly modulated by WMC [$r = 0.36$, $F(1, 44) = 6.407$, $p < 0.015$ and $r = -0.30$, $F(1, 44) = 4.228$, $p < 0.046$, respectively]. In addition, the connectivity between the more anterior IFG region, BA45/46, and the temporal ROI [$r = 0.305$, $F(1, 44) = 4.419$, $p < 0.041$] as well as between the inferior parietal and temporal ROI [$r = 0.34$, $F(1, 44) = 4.369$, $p < 0.044$] were found to be modulated by WMC after global signal regression and full correlation analysis, using ICA and mean signal, respectively.

Table 1 Syntactic complexity effect during the probe

Region	BA	k	z	x	y	z
OR minus CA without regressing WMC						
Middle Frontal Gyrus (left)	4/6/44	2,181	5.71	-42	20	30
Inferior Parietal Cortex (left)	40/39/7	933	4.44	-36	-50	50
Inferior Frontal Gyrus (left)	45/46	121	4.09	-28	42	6
Caudate Body (left)		501	5.35	-12	-6	22
Caudate Body (right)		124	4.3	12	-4	20
Caudate Body		151	4.14	-24	-46	12
OR minus CA regressing WMC						
Middle Frontal Gyrus (left)	9/6/44	2,800	5.95	-42	20	30
Inferior Parietal Cortex (left)	40/39/7	1,018	4.78	-36	-52	48
Inferior Frontal Gyrus (left)	45/46	146	4.19	-28	42	6
Superior Frontal Gyrus (left)	6	118	3.79	-2	14	68
Posterior Temporal Cortex (left)	22/37	413	4.83	-44	-44	-2
Caudate Body (left)		551	5.23	-12	-6	22
Caudate Tail (left)		256	4.36	-24	-44	12
Caudate Body (right)		137	4.24	12	-4	20

Fig. 3 The figure shows the syntactic complexity (object-relative minus conjoined active). The *left* figure shows the activation when WMC is not regressed out and the *right* is when it is regressed. The *left temporal activation* is present only when WMC is controlled



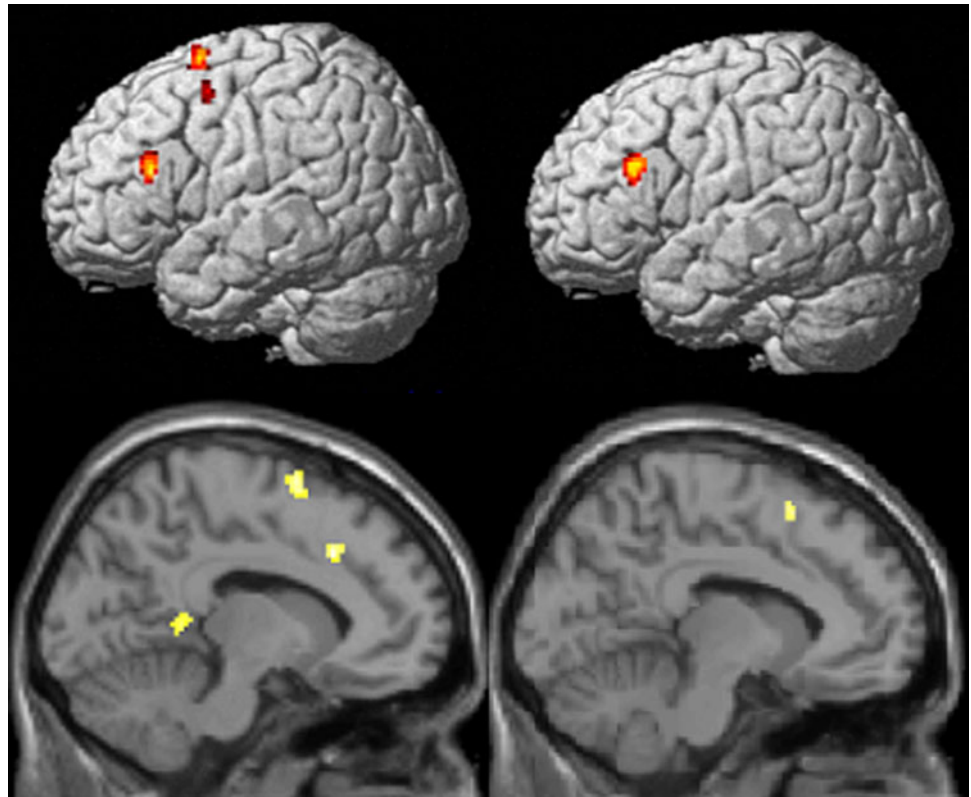
Discussion

There is a rich literature that has explored the relationship between WM and sentence comprehension. The results presented demonstrate that WMC modulates neural activation during both the sentence reading and the probe phases, however, the cortical region impacted varied as a function of processing phase. Activity of a non-traditional language region, the PCC cortex, was found to be correlated with WM capacity during sentence reading (particularly for the object-relative sentences). Conversely, the inferior frontal gyrus was correlated with WMC during the probe phase. It was also found that functional connectivity was modulated by WMC. Specifically, the connectivity between the PCC and the IFG region mentioned above as well as the temporal cortex and a more anterior region of the IFG were found to be positively correlated with WMC. These results suggest a strong, but intricate relationship between WM and sentence comprehension.

Posterior Cingulate

The PCC region was found here to be correlated with WMC for both object-relative and conjoined active conditions, although during different processing phases. The region has been found to be involved in a number of memory processes (Burianova et al. 2010) including semantic, episodic and visuo-spatial memory (Aggleton and Pearce 2001; Binder et al. 2009; Binder and Desai 2011; Vincent et al. 2006; Epstein et al. 2007). For example, in a review of 120 neuroimaging studies of semantic processing Binder et al. (2009) performed an activation likelihood estimation technique and found that the PCC was strongly related to semantic processing along with the lateral parietal, inferior frontal, lateral temporal, and middle frontal regions. The PCC is most interesting here. Yarkoni et al. (2008) also found activation of a similar region of the PCC during the comprehension of story narratives. There it was suggested that readers create

Fig. 4 The figure depicts probe phase activation that is correlated with WMC during conjoined active (*left, top and bottom*) and object-relative sentences (*right, top and bottom*)



a situation model that aids in comprehension and retention of the text. A situation model (or event representation) is a mental representation of the situation described in text which includes the readers' knowledge of events, characters, goals, etc.; information pulled from long-term memory stores. We argue that it is akin to mental imagery during comprehension, as mentioned in the introduction. The hypothesis that the PCC is involved in the creation of an event representation fits all of the memory functions that have been attributed to the region including semantic, the temporary storage of integrated information related to episodic memory and information related to typical events including the characters that participate in those events.

The PCC is also thought to be part of the default-mode network (Raichle et al. 2001) and has often been found to show decreased activation relative to baseline. In fact, Yarkoni et al. (2008) found increased "deactivation" (negative activation) in the PCC related to the development of a situation model/event representation. We found a similar pattern here in that the PCC activation was negatively correlated with reading span such that the activation was more *negative* the higher the reading span score (see Fig. 2). One possible explanation for these results is that high WMC readers are more likely than low capacity readers to generate an event representation during sentence reading because they have the resources available to do so. Because this event representation facilitates sentence

comprehension and retention, high capacity readers may be expected to have better behavioral performance.

Inferior Frontal Gyrus

One region of the left IFG (BA 45/44 at the inferior frontal sulcus) revealed a correlation with WMC, but only during the probe. While this region has been found to be involved in language processing previously, it has also been linked to WM processes. For example, Nee et al. (2012) performed an activation likelihood estimation analysis of 36 neuroimaging studies of executive WM processes. They found that a similar region appears to be involved in post-retrieval selection (i.e., selecting from competing information being held in memory). This region's correlation with WMC during the probe phase, therefore, is likely related to post-retrieval selection and not language specific processes. The correlation observed is such that the higher the WMC the less activation elicited. This fits our hypothesis presented earlier. The high capacity readers developed an event representation to ease comprehension and retention processes; therefore, post-retrieval selection is also eased.

It is important to note that the left IFG is composed of multiple sub-regions that have been linked to different language processes (e.g., Price 2010). For example, BA 44 has been linked to syntactic/hierarchical processing while BA

45/47 has been linked to semantic processing (Friederici 2012; Newman et al. 2009; Price 2010). However, the left IFG has also been linked to a number of general cognitive processes, particularly those linked to executive functions like WM, interference and inhibitory processes (Bunge et al., 2003; Derrfuss et al. 2004; Wagner and Smith 2003). What we suggest here is that at least part of the left IFG is not performing language specific processes but is instead involved in cognitive processing that greatly impacts comprehension, particularly for low WMC participants. It is important to note that this region does not overlap with those that have been linked to language (e.g., BA 44 and BA45/47).

The Role of Episodic Memory During Comprehension

According to the definition, the episodic buffer is a “limited capacity temporary store that forms an interface between a range of systems all having different basic memory codes” (Baddeley et al. 2010, p. 229). Interestingly, Baddeley and colleagues argue that the episodic buffer is a passive store and is not responsible for the binding of multidimensional information, but that the bound chunks, or in this case the bound event representation, is created within another system. We propose here that the PCC/precuneus region is associated with the episodic buffer and that during sentence comprehension participants generate a multidimensional representation of the sentence that is held there.

The functional connectivity results may support our hypothesis. Two networks were observed. The first involves the MTG, anterior IFG, and IPL—the connectivity between MTG and the anterior IFG and MTG and IPL was correlated with WMC. This finding indicates that communication between these regions increased with WMC. These are regions that have long been linked to language comprehension processes, semantic processing in particular (e.g., Binder et al. 2009). Therefore, the high capacity readers showed increased communication within a network involved in semantic processing, suggesting that they were better able to use long-term memory stores to generate a more elaborate representation of the meaning of the sentence. We propose that this increased communication within the semantic network may be related to the *binding* of the event representation that is to be held in the episodic buffer.

The second network involves the PCC, IFG (BA44/45) and IPL—connectivity between the PCC and IFG (BA44/45) and the PCC and inferior parietal cortex was correlated with WMC. Both the IFG and IPL have been linked to WM, but for different reasons. As discussed above, the IFG region described here has been linked to a control mechanism involved when there is competing information being held online (Nee et al. 2012). While the exact role of the IPL in verbal WM has recently been disputed (Buchsbaum

and D’Esposito 2008) there is overwhelming evidence of IPL involvement in WM. The finding that the connectivity between the PCC and these two regions that have been linked to WM was modulated by WMC show that individuals with a higher WMC had increased communication between the PCC and IFG than those with lower WMC. As mentioned above, while the binding may involve the semantic network a more expanded WM network, including verbal WM and the episodic buffer, may be involved in keeping this event representation active.

It should also be noted that the negative correlation between the PCC and IPL and positive correlation between PCC and IFG may indicate that these correlations are related to task-negative and task-positive correlations, respectively. This suggests that high capacity readers were either more likely to or better able to disengage the default network and engage the task-related, WM network than lower capacity readers. This interpretation does not negate our proposal. However, further studies are required to test the proposed model and disentangle the episodic, event representation processing and the default mode processing linked to the PCC.

Limitations

An alternative explanation for the PCC/precuneus activation that is related to the default network deserves attention. It is possible that high capacity readers read the sentences much faster than the 5 s it is displayed and then engage the default network earlier, thereby inducing the observed correlation. Although this is a possibility, it is unlikely. The average reading time differences we have observed between object-relative and conjoined active sentences is on the order of 500 ms (high: 4.3 s, and low: 4.8 s capacity readers). Given the sluggishness of the hemodynamic response it is doubtful that earlier engagement of the default network is responsible for the correlation between WMC and PCC/precuneus activation.

A second limitation concerns the use of a language comprehension task with three processing phases. Because the hemodynamic delay is slow it is necessary to place a delay between the sentence and the probe. However, this delay induced an unnatural WM load that has an impact on probe processing and may account for some of the differences observed between the object-relative and conjoined active conditions during the probe.

Conclusions

The results presented here extend those previously reported in that it appears as though two distinct WM systems are involved during sentence comprehension and that the use

of these systems are dependent on WM capacity. We propose that high capacity readers are able to utilize episodic memory systems to generate a representation of the events depicted in the sentence and that this is extremely helpful in the comprehension of non-canonical sentences like object-relative constructions. The results also suggest that at least some of the activation observed in the left IFG is not language specific activation but is instead related to executive processes that are recruited during comprehension. Further studies are needed to explore the relationship between comprehension and WM which takes a closer look at the impact of WM stores other than verbal WM.

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