Working memory and syntax interact in Broca's area

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Comprehension of filler–gap dependency relations (as in *this is the man who the woman is touching* □) is supported by Broca's area. There are two views regarding the processing role of this brain region in comprehending these dependencies. *Specifists* hold that Broca's area plays a specific syntactic role in processing filler–gaps. *Generalists* maintain that as the on-line linking of fillers and gaps taxes Working Memory (WM) resources, Broca's area supports a domain general WM. The current fMRI study tested these two views in a grammaticality judgment task, where participants were presented with two syntactically distinct dependency relations: (a) Filler–Gap and (b) Reflexive Binding. The distance between the dependent elements within each of the constructions was varied, to parametrically vary WM demands. The *Generalists* would expect parametric variation of distance in both dependencies to lead to a linear increase in activation of Broca's area. Our results support the *specifists*' view, however: the left inferior frontal gyrus demonstrated an interaction between distance and dependency type with a positive linear effect only for Filler–Gaps. A positive linear effect of distance across both dependencies was only found in the bilateral parahippocampal/fusiform gyri. Therefore the role of Broca's area in WM is syntactically specific to filler–gap relations.
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The need for Working Memory (WM) during sentence comprehension is evident in sentences that contain dependency relations. The complex sentence (1) contains both a relative clause and a dependency between the constituent **the woman**, which is heard or read early, and the position where it is later interpreted semantically as the recipient of the pinching action at the end of the [bracketed] relative clause (marked by "□"). This displaced constituent (or, to be precise, the relative pronoun *who* which relates to it) is referred to as the Filler, and the position of interpretation ("□") as the Gap. Understanding of this rather complex point is easier if one examines sentence (2), which like (1)

has an embedded complement clause (hence 2 verbs), but no displacement (hence no gap).

(1) John loves **the woman** who [David pinched □]

(2) John said that David pinched the woman

Filler–Gap dependency relations (here annotated with an arrow) are best known as syntactic Movement, a linguistically defined relation which extracts the filler out of the position marked by the gap. Comprehension of such sentences requires that the gap be filled with content, which presupposes the establishment of a link between the filler and the gap. While linguistic arguments in favor of the existence of gaps abound, psycholinguistic experimentation has shown that fillers are active at the position of the gap, but not immediately before, since healthy participants demonstrate priming for a semantically related target at the gap and not earlier (e.g., Nicol and Swinney, 1989; Swinney and Zurif, 1995; Love and Swinney, 1996; Clahsen and Featherston, 1999; Nakano et al., 2002). This cannot take place without a memory of some sort, in fact one that fits the definition of WM: The memory required to link a gap to a filler must maintain a limited amount of information active over a short (intra-sentential) temporal delay.

Evidence from pathology and health suggests that Broca's area is critical for comprehending filler–gap dependencies: Sentences containing them have repeatedly produced chance comprehension performance in Broca's aphasia (cf. Grodzinsky, 2000; Drai and Grodzinsky, 2006a,b for reviews), a syndrome in which the psycholinguistic indices for gap-filling are not observed (Zurif et al., 1993). In addition, activation of Broca's area in healthy subjects is correspondingly found in fMRI (e.g., Röder et al., 2002; Ben-Shachar et al., 2003, 2004; Santi and Grodzinsky, in press). Such experiments typically use minimal contrasts like the one between (1) and (2). These facts has led to the view that in sentence processing, Broca's area is entrusted with handling displacement, or gap-filling (Zurif et al., 1993; Grodzinsky, 2000). We call it the *Specifist* view.

Against this background, it has been claimed that the functional role of Broca's area is more general. PET and fMRI experiments that tax WM incrementally in tasks other than gap-filling, or even outside the sentence processing domain, have nonetheless monitored activations in Broca's region and its vicinity (Braver

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et al., 1997; Druzgal and D'esposito, 2001). These experiments have typically, but not exclusively, used *n*-back tasks with letters and figures (Smith and Jonides, 1999). These results have led to a *Generalist* view of Broca's area, according to which this brain region supports a domain-general WM (either verbal or syntactic), not a particular syntactic process. The syntactic effects reported above, on the Generalist view, are consequences of a linguistically non-selective role of this brain region (Just and Carpenter, 1992; Caplan and Waters, 1999; Smith and Jonides, 1999; Ranganath et al., 2003).

Specifists do not deny that memory tasks and sentence tasks do activate similar loci in fMRI. Yet, do these results necessarily argue against their position? Note that Specifists propose that *within the domain of sentence processing*, the role of Broca's area is specialized to syntactic Movement relations. Indeed, they support their view with evidence from sentence processing studies that use sentences with and without Movement.

To the Specifists, then, Broca's area may be multi-functional, having modules that support a specialized role in sentence comprehension and a general WM. However, the evidence cited to bolster the Generalist claim contains materials from domains other than sentence processing (i.e., the processing of letters, shapes, etc.). The large distance between the materials and the tasks in question thus increases the likelihood that the purported generalization, which annuls the syntactic role of Broca's region, is actually spurious. For these views to be distinguished, then, evidence of a different kind is needed.

Our goal in this paper is to provide new fMRI evidence that bears on this debate. It is simply a matter of logic that in order to extend the scope of an account of the role played by a brain region in processing, the move from specific to broad must systematically proceed from particular to general. An attempt to adjudicate between the Specifist and Generalist views must begin by making comparisons *within* the sentence processing domain.

To this end, we need an intra-sentential dependency relation that, like filler–gap relations, requires WM, but at the same time is syntactically distinct from them. Such sentences would allow us to see whether the WM resource recruited for the processing of non-Movement dependencies is the same as the WM involved in the standard Movement sentences like (1). Once it has been shown that there is a WM generalization within the syntactic domain through the systematic study of different syntactic dependencies (i.e., through a minimal contrast), the Specifist claim would have to be modified. Such a result would moreover lead us to test whether the function of this WM generalizes further to modality of input (i.e., verbal) or other cognitive domains and so on (Just and Carpenter, 1992; Caplan and Waters, 1999; Friedmann and Gvion, 2003). This experimental direction, then, has the potential of progressively testing the degree of involvement of the WM resource in Broca's area in cognitive processing.

Natural language avails us of dependency relations other than Movement, which is where we start. To appreciate the syntactic distinctions that exist between dependencies, we should consider a concrete example. Two distinct intra-sentential dependency relations are presented in (3) and (4) (Lasnik and Uriagereka, 1988).

(3) John knows that **Mary** pinched **herself**   Binding

(4) John loves **the woman** that David pinched ■   Movement

Like before, both sentences have a main clause and an embedded clause. Yet here, they both contain a dependency relation. In (3), a reflexive depends on an antecedent NP for reference. This relation is called *Binding*. The gap in (4) likewise depends on a filler, maintaining a *Movement* relation as discussed above. The rough-and-ready Generalist WM-perspective of Broca's area puts these two dependencies on a par. Both require the rapid, temporary establishment of a link between two non-adjacent elements in a sequence, and hence a comparison between activations due to sentences containing them (all else equal) should yield at a minimum activation overlap in Broca's region, but possibly greater activation within this overlap for one dependency over the other depending on putative differences in difficulty between them. Comprehension impairments in Broca's aphasia should likewise be on a par in (3)–(4).

The Specifist view maintains that these two relations are not alike. Important syntactic and processing differences between the two dependencies could require distinct computational mechanisms that embed separate WM resources. Syntactically, the antecedent of a reflexive (**Mary** in (3)) is in a position that is part of a canonical ordering of the elements in a sentence (an argument position), whereas in Movement, a displaced filler (**The woman**, **who**, in (4)) is not. In the Binding relation in (3), the reflexive **herself** must agree in number and gender with its antecedent **Mary**, and the latter must be the structurally nearest NP. Binding requires the antecedent to be structurally close to the reflexive (cf. the ungrammaticality of **John knows Mary pinched himself*), while Movement is exempt from such restrictions (cf. **Which student** *did Bill say that Fred claimed that Sue thought John loves* ■?). In terms of processing, the 2 dependencies differ with regards to whether they can be readily identified early on in processing, or only in retrospect. In Movement, the need to search for a gap is revealed as soon as the processor encounters the filler (roughly, displaced and cued by **who** in (4)); but no such cues are available for Binding (the reflexive in (3) may be replaced with a lexical NP such as a name, and the sentence would still be grammatical). It is not until processing reaches the reflexive in (3) that the dependency relation becomes evident.

This last distinction seems to reflect in the demands that the processing of these two dependencies make on WM. Movement seems to place greater demands on storage processes (as processing includes a search for a gap after the filler has been identified and stored in WM), whereas Binding appears to put greater demands on retrieval processes (while still requiring a WM resource) as anaphoric reference to the reflexive is assigned only in retrospect (there is a backwards search for an antecedent). Given on-line studies show that the filler cannot be accessed at any point between its initial presentation and its gap, one may want to argue that retrieval processes are primarily engaged in filler–gap dependencies and not storage ones. This argument is curtailed by considering that in order to have reactivation, there must be storage and that only certain syntactic cues allow for semantic reactivation.

The above differences between the two types of dependencies – especially those that are linguistic in nature – lead the Specifists to expect a neurological separation between WM for Binding and for Movement. Generalists, by contrast, deny the neurological relevance of the distinction between the two. The minimal contrast between Binding (3) and Movement (4) thus seems appropriate to distinguish between the approaches in neuroimaging and in aphasia experiments.
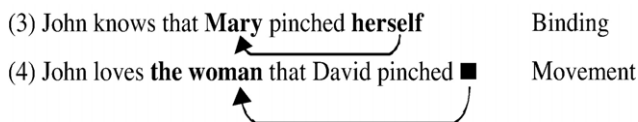
The results of a recent combined aphasia and fMRI study provide preliminary support to the Specifist view: the two syntactic dependencies were found to activate distinct cortical regions in healthy subjects (different parts of Broca's area, and of the left middle/superior temporal cortex, see Santi and Grodzinsky, in press). Likewise, the aphasics' behavioral performance distinguished between these two syntactic pairs.

These results are inconsistent with the Generalist view, which assumes a common neurological WM resource for language. They are, moreover, bolstered by findings from two additional recent studies, which only used Movement sentences, but increased WM demands by adding a phrase (adjectival, prepositional and/or adverbial) between the filler and the gap while controlling for absolute sentence length (Cooke et al., 2001 in English and Fiebach et al., 2005 in German). Longer filler–gap distance led to greater activation within the left inferior frontal gyrus (LIFG; BA 47 and BA 44, respectively) and temporal cortices (BA 21, 22, and 39) than shorter distances.

While these results are suggestive, they are not conclusive. All three studies used a subtractive method, and Cooke et al.'s (2001) and Fiebach et al.'s (2005) only increased filler–gap distance (WM) once compared to baseline. The following are limitations: the subtractive method assumes that the only difference between the two conditions is the manipulated variable – the distance between the filler and the gap. In fact, the manipulation in itself can affect strategies used in the various conditions as well as other task-related variables (McClelland, 1979). Studies that parametrically vary the experimental factor of interest and look for regions that demonstrate corresponding modulations in the hemodynamic response circumvent these limitations. In terms of WM studies, a parametric design requires that distance be stretched twice relative to baseline and each time it must be stretched by the same amount. A parametric design is a more robust design than a subtractive one since it better avoids confounding effects. Indeed, such designs have been used successfully by nonlinguistic WM studies with the *n*-back task (Braver et al., 1997; Druzgal and D'esposito, 2001). In fact, the latter verbal

WM study showed increasing activation in the LIFG with greater WM load. This finding combined with those of the two syntactic WM studies provides some tentative reason to believe that there is a general verbal WM in the LIFG. However another limitation of Cooke et al.'s (2001) and Fiebach et al.'s (2005) studies is that they increased distance in filler–gap dependencies only rather than investigating other syntactic dependencies to test its specificity. Thus, if we wish to be convinced that the LIFG sustains general WM processes in sentence comprehension we need to see if such results are maintained when sophisticated parametric designs are applied to linguistic experiments that manipulate more than one type of dependency.

The current fMRI experiment combines these two features. We contrasted Binding and Movement, and increased WM demands by parametrically varying the length of the dependency link in both (antecedent–reflexive distance in Binding; filler–gap distance in Movement). We tested whether or not this parametric variation of distance interacts with syntactic type. To create a distance gradient in a structured manner, a choice must be made: one can vary the number of syllables, number of words, or number of adjectival or prepositional phrases. We chose to increase the distance between the dependent elements by modifying the number of intervening NPs (Table 1), while keeping overall sentence length constant. We chose NPs because they are of the same category as fillers and antecedents to reflexives. That is, unlike prepositional, adjectival and adverbial phrases, NPs require greater processing since they act as potential antecedents since they intervene between the filler and its gap, or between the antecedent and the reflexive it binds, and, thus, are very good candidate elements to vary in a parametric study. Importantly, the multiplicity of potential antecedents created no ambiguities, as the sentences were structured such that grammatical considerations always ensured a unique link.

This parametric design leads to an appropriate test. If Broca's area acts as a general WM, it should demonstrate linear increase in BOLD response as dependency distance (i.e., the number of NPs intervening between the two dependent elements) goes up, for both

Table 1
Example sentences from each of the six experimental conditions in their grammatical (+G) and ungrammatical (−G) versions

Conditions		Example sentences
A. BIND 0	+G	The sister of Kim assumes that Anne loves **the mailman** who □ burnt **himself**
	−G	*The sister of Kim assumes that Anne loves **the mailman** who □ burnt **herself**
B. BIND 1	+G	The sister of Kim assumes that **the mailman** who □ loves Anne burnt **himself**
	−G	*The sister of Kim assumes that **the mailman** who □ loves Anne burnt **herself**
C. BIND 2	+G	Anne assumes that **the mailman** who □ loves the sister of Kim pinched **himself**
	−G	*Anne assumes that **the mailman** who loves the sister of Kim pinched **herself**
D. MOV 0	+G	The mailman and the mother of Jim love **the woman** who Kate burnt □
	−G	*The mailman and the mother of Jim love **the woman** who Kate laughed **t** and burnt □
E. MOV 1	+G	The mother of Jim loves **the woman** who the mailman and Kate burnt □
	−G	*The mother of Jim loves **the woman** who the mailman laughed **t** and Kate burnt □
F. MOV2	+G	Kate loves **the woman** who the mailman and the mother of Jim pinched □
	−G	*Kate loves **the woman** who the mailman laughed **t** and the mother of Jim pinched □

0NP is the baseline and 1NP, and 2NP indicate the number of additional noun phrases (NP) from the baseline structure that intervene between the two dependent elements in each dependency relation (intervening NPs are marked in green).

Movement and Binding. A specific role in comprehending sentences with filler–gaps would lead to a linear increase in BOLD response for filler–gaps only, and, hence, a distance by type interaction. We thus looked for a linear effect in Movement that was greater than that for Binding and vice versa, as well as linear effects that cut across both dependencies.

Materials and methods

Subjects

Eleven students in Linguistics at McGill University volunteered. All participants were right-handed with normal hearing (7 females; $\bar{X}_{age}=23.05$ years). They gave informed consent in accordance with the ethics committee of the Montreal Neurological Institute (MNI).

Task and stimuli

The subjects performed an auditory grammaticality judgment task, which required that they press one of two buttons on a response box to indicate whether the sentence they heard was grammatical or not. All ungrammatical trials were excluded from fMRI analyses. There were 12 conditions, resulting from a 2 Syntax (BIND, MOV)×3 Distance (0 – baseline, and 1, or 2 additional intervening NPs)×2 Grammaticality (+GRAM, −GRAM) design (see Supplementary material; see Table 1). Distance between the filler/antecedent and gap/reflexive was parametrically varied through the number of intervening NPs. Sentence length remained the same across all conditions (13 words, 16–17 syllables), although syntactic structure was slightly modified in order to increase the number of intervening NPs, grammaticality was preserved.

In Binding (BIND), the antecedent–reflexive dependency is constrained by a locality condition. Thus, in order to increase the distance between the antecedent and its reflexive pronoun in the BIND condition, it was necessary to use a relative clause and, hence there is a subject filler–gap dependency, e.g., *…the mailman who □ loves Anne…*, in all BIND conditions. Critically, however, the distance between the subject and its gap was not parametrically varied. Distance in BIND, began at a baseline where no NPs intervened between the antecedent and reflexive (see Table 1A – BIND0), and was then increased as the link crossed a relative clause, e.g., *…who loves Anne…* which had 1 intervening NP (see Table 1B – BIND1), and whose subject was further made into a complex noun phrase *…the sister of Kim…*, leading to 2 intervening NPs (see Table 1C – BIND2). This linear increase should linearly tax WM because gender and number information that the reflexive pronoun is checked with becomes further away linearly with the more NPs in the embedded relative of the antecedent. In Movement (MOV), distance began at a baseline where there was 1 NP intervening between the filler and the gap (see Table 1D – MOV0), and then distance increased by making the filler–gap relation cross 2 conjoined NPs (see Table 1E – MOV1), and by further making one of these two conjoined noun phrases a complex one (see Table 1F – MOV2). Here, too, WM is taxed as the number of potential antecedents grows.

Ungrammatical sentences for BIND were produced by switching the gender of the reflexive to produce a gender mismatch between the reflexive and its appropriate antecedent (in bold). For MOV, the ungrammatical sentences were produced by creating a coordinate structure mismatch (Lasnik and Uriagereka, 1988). By creating a coordinate structure with an intransitive verb in addition to the transitive verb, Movement of the transitive verb's object (marked in bold) from the coordinate structure creates a Movement violation.

There were 12 sentences for each grammatical condition and 8 sentences for each ungrammatical condition. We decided to use fewer ungrammatical than grammatical trials to maximize the number of informative trials (i.e., grammatical trials) while minimizing the duration the subject must be in the scanner. Given that the stimuli sequence was random, the subject could not predict when there would be a grammatical or ungrammatical sentence.

Procedure

One or two days prior to scanning the subject was provided with task instructions and given a short practice session. This practice session provided an opportunity to address any questions participants may have about the task prior to them being inside the imaging machine. On the day of scanning the subject was positioned on the bed of the MRI machine. Headphones were given to them for stimuli presentation and their head was placed on an air–vacuum pillow that was used to minimize head Movement. A high-resolution anatomical scan was first acquired, followed by a short practice run of 10 sentences. The practice session provided an opportunity to confirm that the volume was sufficient and that all equipment was properly connected, in addition to giving the subject a chance to warm up to the task. The subject then performed the task across two runs of stimuli. Each run was blocked into 10 sentences with 2 frames of silence interleaving the blocks. All sentences in a block were of the same condition with exception of grammaticality. Of the 10 sentences 4 were ungrammatical. Intermittent scanning was used such that the scanner noise would not interfere with the subject's ability to hear and comprehend the sentences being presented. On average the middle of the scan occurred 3150 ms after the end of the sentence. This delay was chosen since it has been shown that 3000 ms is the approximate delay in the hemodynamic response to peak (Belin et al., 1999) and the end of the sentence is where memory load will be highest since that is where linking occurs. Jitter in the delay by +500 ms or −500 ms was used to increase the probability of capturing the peak of the hemodynamic response since the reported 3000-ms delay represents an average. The stimuli in each run were identical but the block ordering was varied. Presentation order of the runs was counterbalanced across subjects.

fMRI parameters

Image acquisition was performed with a 1.5 T Siemens Vision imager at the MNI in Montréal, Canada. A localizer was performed followed by whole-brain T1-weighted imaging for anatomical localization (256×256 matrix; 160–176 continuous 1.00 mm sagittal slices). Each functional volume was acquired with a 64×64 matrix size and a total volume acquisition time of 1700 ms with an acquisition delay of 7800 ms. Each imaging run produced 147 acquisitions of the brain volume (20 slices, 5 mm slice thickness, TE=50 ms, TR=1.7 s, FA=40°, FOV=320×320 mm).

Behavioural data analysis

The behavioral Percent Correct Grammaticality Judgment data and Reaction Time data were submitted to a 2 Syntax (MOV, BIND)×3 Distance (0 – baseline and, 1, or 2 additional NPs)×2

Grammaticality (+GRAM, −GRAM) repeated measures ANOVA in SPSS.

fMRI data analyses

The data were preprocessed with a spatial filter (FWHM = 8 mm) and motion corrected. Statistical analyses were performed in FMRISTAT, which is based on the general linear model (Worsley et al., 2002). For the primary contrasts the first two frames of silence and all ungrammatical frames were excluded from the analysis. Since we are interested in syntactic processing under normal conditions, the grammatical trials are the only truly informative trials, thus, all ungrammatical trials were excluded from all fMRI analyses. The ungrammatical trials were included solely to give the subject a task that forces them to actively process the stimuli. The design matrix was not convolved with a hemodynamic response function (hrf) since there was one acquisition per event and its position within the trial was based on assumptions about the hrf. In fitting the linear model, linear drift in the data was removed. Based on the model's predictor weightings, contrasts were computed.

Two types of analyses were conducted: (1) linear effect analyses and (2) direct contrasts between the two types of dependencies. The primary aim of the current study was to parametrically manipulate distance within each of the two dependencies. Thus, the results of the linear effect analyses are of most relevance. Further, in parametrically varying dependency distance multiple differences between the BIND and MOV conditions were generated, including right-branching relative clauses versus center-embedded relative clauses, coordination of NPs or not, and subject versus object Movement. Critically within the parametric variation only one variable changed, but when directly comparing the dependencies these additional variables become an issue. Thus, the results of the direct contrasts between conditions are of less interest. The primary reason for conducting these contrasts is to see whether an area of right middle frontal cortex is activated more by BIND than MOV, as it was in a previous experiment (Santi and Grodzinsky, in press).

Three main design matrices were computed, modeling: (1) a linear effect of distance regardless of syntactic structure, (2) a linear effect of distance separately for Binding and Movement, and (3) a difference between the two constructions not considering distance (for this design matrix all frames of silence were removed). The first design matrix consisted of 3 predictors: (1) coded by 1 s when the scan corresponds to BIND and 0 otherwise, (2) coded by 1 s when the scan corresponded to MOV and 0 otherwise, and (3) coded by 1, 2, 3, or 4 according to the number of intervening NPs within the dependency plus 1. The second design matrix consisted of four predictors: (1) coded by a 1 when the scan corresponded to BIND and 0 otherwise, (2) coded by a 1 when the scan corresponded to MOV and 0 otherwise (3) coded by 1, 2, or 3 when BIND had 0, 1, or 2 intervening NPs, respectively, and (4) coded by 2, 3, or 4 when MOV contained 1, 2, or 3 intervening NPs. The third design matrix had 1 predictor: (1) coded by 1 when MOV and 0 when BIND. The first design matrix was used to test for an effect of distance that cut across the two syntactic dependencies (i.e., contrast (0 0 1)). The second design matrix was used to determine if the variables, distance and syntactic type, interacted. Specifically, we looked for a linear effect in Movement that was greater than that for Binding and vice versa (i.e., contrast (0 0 −1 1) for linear effect MOV > linear effect BIND and contrast (0 0 1 −1) for linear effect of BIND > linear effect MOV). Furthermore, the second design matrix tested for which areas demonstrated a linear effect of distance for each of the dependencies

(i.e., contrast (0 0 1 0) to investigate a linear effect of BIND, and contrast (0 0 0 1) to investigate a linear effect of MOV). An area not only had to show that there was a greater linear effect for the one dependency over the other (i.e., linear MOV > linear BIND) but also that the same dependency demonstrated a linear effect (i.e., linear MOV) in that area to be reported as showing an interaction effect. The third design matrix was used to determine if there was an overall difference between the two types of syntactic dependencies (i.e., contrast (1) for MOV greater than BIND and (−1) for BIND greater than MOV).

The contrasts from the two runs for each subject were combined in a weighted average, transformed to a standardized space (MNI coordinates) using in-house software (Collins et al., 1994), and then entered into group maps (fixed effect). The group maps were searched for clusters with minimum volumes of 100 mm^3 and $p < 0.005$ (uncorrected).

In order to obtain a better visualization of the effects, the t-values for each condition were extracted from the group map. The t-value for each individual condition were computed from a fourth design matrix with 6 predictors: (1) coded with 1 s when BIND0 and 0 otherwise, (2) coded with 1 s when BIND1 and 0 otherwise, (3) coded with 1 s when BIND2 and 0 otherwise, (4) coded with 1 when MOV0 and 0 otherwise, (5) coded with 1 when MOV1 and 0 otherwise and (6) coded with 1 when MOV2 and 0 otherwise. The t-values corresponding to all voxels in a region of interest were then averaged within a condition and plotted.

For precise localization, we computed the probability that activation within LIFG lies within Broca's area through the use of Amunts et al.'s (1999) cytoarchitectonic probability maps of BA 44 and BA 45 (http://www.bic.mni.mcgill.ca/cytoarchitectonics/). The MNI Coordinates of our LIFG ROIs were converted into the voxel coordinates of the probability maps. These coordinates were then used in extracting values from these voxels in the probability maps. The values were then averaged. The value at each voxel in Amunts et al.'s (1999) map corresponds to the number of subjects with overlapping cytoarchitectonic structure. Therefore, the average value for the ROI needed to be divided by the number of brains ($n = 10$) entered into the probability map in order to derive a percentage.

Results

Behavioural

Despite the fact that the stimuli were cumbersome, mean percent correct grammaticality judgments in all twelve conditions were > 90% (see Fig. 1). None of the main effects or interactions was significant. There was neither a significant linear effect of distance nor an interaction between the linear effect of distance and syntactic construction.

The reaction time data (see Fig. 2) demonstrated a 3-way interaction of syntax × distance × grammaticality ($F(2,20) = 4.91$, $p = 0.018$). The 2-way interaction between syntax and distance was investigated at each level (i.e., 0 – baseline, and 1 and 2 additional NPs) of the distance variable. There was a significant interaction between syntax and grammaticality at Distance = 1 ($F(1,10) = 8.68$, $p = 0.015$) and Distance = 2 ($F(1,10) = 10.395$, $p = 0.009$). The 2-way interaction at Distance = 1 and Distance = 2 was due to a main effect of grammaticality for the Movement condition, whereby at both Distance = 1 ($F(1,10) = 10.379$, $p = 0.009$) and Distance = 2 ($F(1,10) = 12.92$, $p = 0.005$) the reaction time for the ungrammatical condition was faster than the grammatical condition. There was no
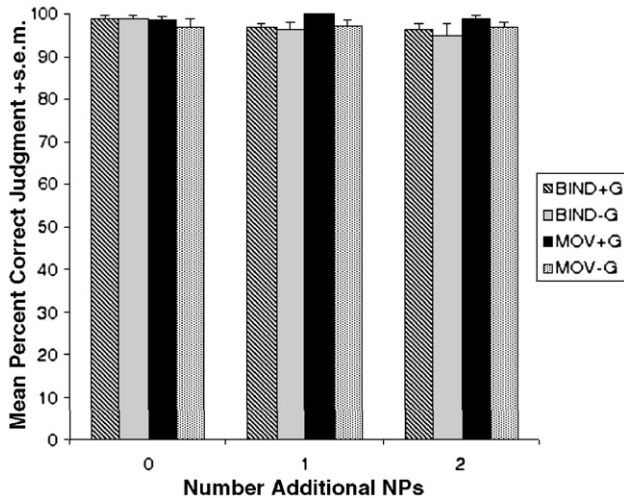
Fig. 1. Mean percent correct grammaticality judgments±S.E.M. across all conditions. BIND+G, grammatical binding condition; BIND−G, ungrammatical binding condition; MOV+G, grammatical Movement condition; MOV−G, ungrammatical Movement condition.

main effect of grammaticality at either Distance=1 or Distance=2 for binding. Critically, however, there was no main effect of syntax, indicating that the WM-load was equivalent in the two dependencies. The only difference between the two dependencies was at Distance=1 and Gram=Ungrammatical, where Movement had a faster RT ($F(1,10)=9.13$, $p=0.013$), although there was a marginal effect of syntax at Distance=2 and Gram=Grammatical ($F(1,10)=4.505$, $p=0.060$). This marginal effect was due to the Movement condition having a slower RT than the Binding condition (see Fig. 2).

fMRI

We report four relevant results of two kinds: A. Linear Effects: (1) Left Inferior Frontal Gyrus (LIFG): a positive linear effect for Movement and a negative linear effect for Binding created an interaction between distance (i.e., WM) and syntactic type, (2) Right Inferior Temporal Gyrus (RITG): a positive linear effect for Binding and no linear effect for Movement led to an interaction between WM and syntactic type, (3) bilateral Parahippocampal Gyrus/Fusiform Gyrus (PHG/FG): a main linear effect of distance (i.e., across syntactic type). B. Direct Contrast Effect: (4) Right Middle Frontal Gyrus (RMFG): greater activation for Binding than Movement led to a main effect of syntactic type. Each of these will be discussed in turn below.

LIFG

WM selectivity in this region was demonstrated in 2 ways: an interaction effect between dependency and linear effect of distance (see Fig. 3; Table 2); moreover, the maps of a positive linear effect of movement and a negative linear effect of binding were located within Broca's area. A precise localization of these results was obtained with the help of Amunts et al.'s (1999) cytoarchitectonic probability map of these areas: according to this map, the positive distance effect for Movement is contained within BA 45 with a probability of 47.01%, while the negative distance effect of Binding is more medial and within BA 44 with a probability of 23.30%.

An elaboration of these probability values and how they are obtained is necessary. Amunts et al.'s (1999) map is created by

superimposing the cytoarchitectonic borders of BA 44 and 45 onto a template brain. These evince a high degree of variability – there is no single voxel in the probability map in which BA 44 of all 10 subjects overlap. The highest number of subjects with overlapping cytoarchitectonics at any one voxel in this map is 9 (though there is a small area in the map of BA 45 in which all 10 subjects overlap). This provides a first hint of the variability in the location of Brodmann areas among subjects.

The threshold for the probability map must be set at 5 of the 10 subjects used by Amunts et al. (1999), in order to get a volume the size of an average BA 44 or 45. Thresholding it at a lower value increases the number of voxels beyond the size of a typical BA 44 or BA 45. This, again, is due to the great variability between subjects.

The numbers we provide for Movement in BA 45 and Binding in BA 44 reflect a high degree of overlap between the activations and the respective areas, although they may seem quite low. Critically, in no activated voxel for the positive linear effect of movement did we find in the BA 45 probability map zero subject overlap. Only 1 voxel of those activated by a negative linear effect for binding corresponded to 0 subject overlap in the probability map of BA 44. Secondly, the cluster for the positive linear effect of movement contains 3 voxels corresponding to seven subject overlap, a relatively high value, and the most frequent subject overlap value was 5. Based on our calculations, we can assert with confidence that the positive Movement effect was in BA 45, and the negative Binding effect in BA 44.

RITG

A positive linear effect of distance for the Binding stimuli that was greater than that in the Movement stimuli. In looking at the maps of the linear effects of each structure, only the positive linear effect for Binding was significant. There was no linear effect of distance for the Movement stimuli (either positive or negative) within this region.

Bilateral PHG/FG

This region demonstrated increasing activation with increasing distance (i.e., number of intervening NPs) irrespective of construction type (see Fig. 3; Table 2). While the right hemisphere
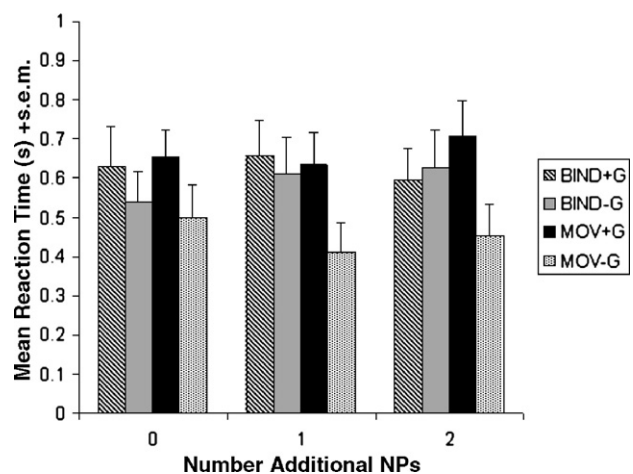

Fig. 2. Mean reaction time (s)±S.E.M. across all conditions. BIND+G, grammatical binding condition; BIND−G, ungrammatical binding condition; MOV+G, grammatical Movement condition; MOV−G, ungrammatical Movement condition.
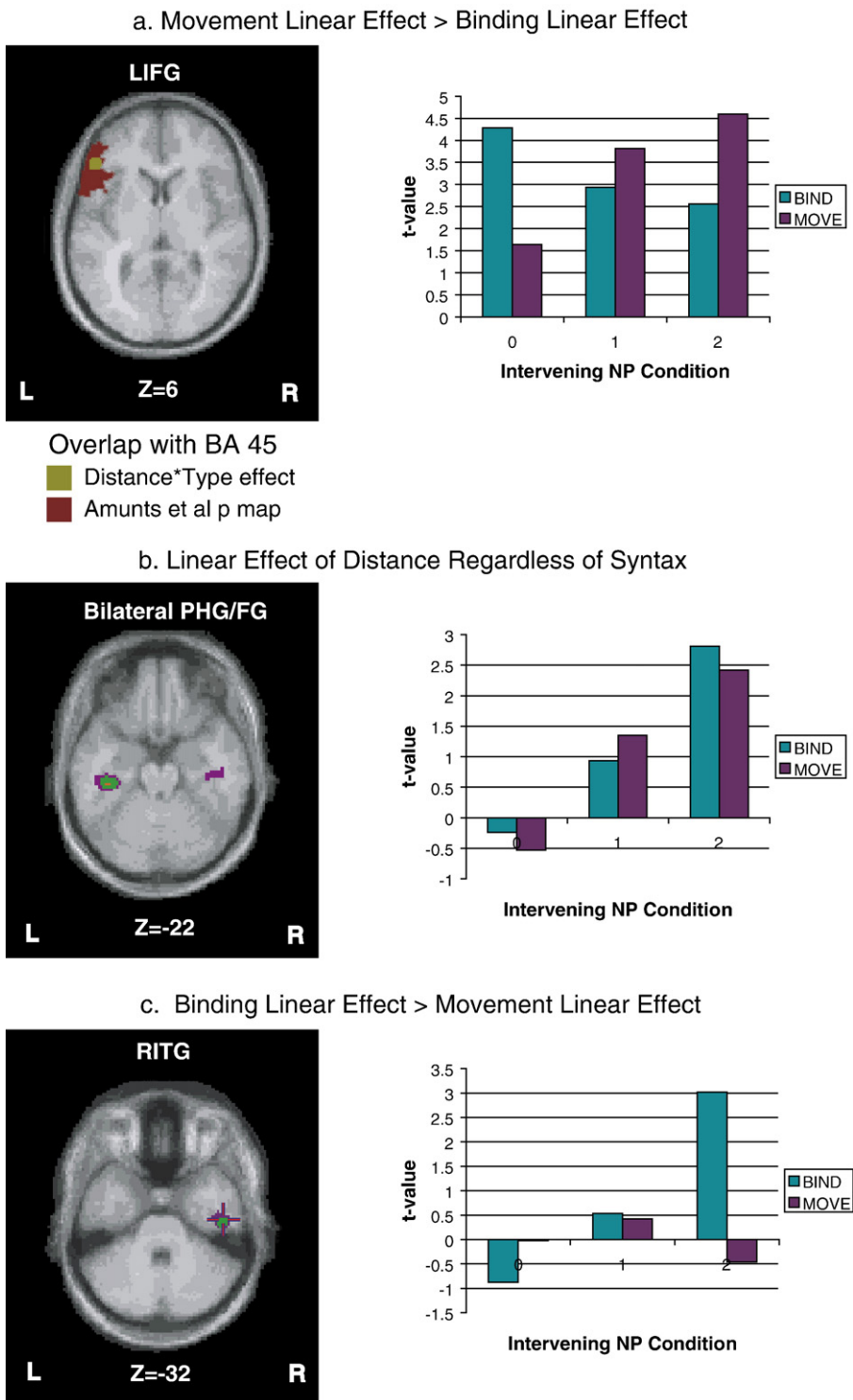
Fig. 3. Regions demonstrating a linear effect of distance with charts identifying the average *t*-value from the group map for each condition. The left inferior frontal gyrus (LIFG) demonstrated an interaction between distance and sentence type (map searched for clusters above a threshold of $t(1826)=2.5762$, $p=0.005$). The LIFG ROI is presented in green and Amunts et al.'s (1999) probability map of BA 45 is presented in red. In LIFG, a positive linear effect of distance was produced by the Movement stimuli (a). A linear effect of distance regardless of sentence type was produced bilaterally in the parahippocampal gyrus/fusiform gyrus (LPHG/FG; b; map searched for clusters above a threshold of $t(1848)=2.5762$, $p=0.005$). The average *t*-values are for the LPGH/FG only. The right inferior temporal gyrus (RITG) demonstrated a linear effect of distance for the binding condition (map searched for clusters above a threshold of $t(1826)=2.5762$, $p=0.005$) but not the Movement condition (c).

Table 2
Description of the regions activated by the linear effect analyses

Linear effect	Gyrus	BA	Volume (mm³)	X	Y	Z
MOV > BIND	LIFG	45	328	−50	32	6
MOV positive	LIFG	45	128	−50	33	8
BIND negative	LIFG	44	224	−39	19	10
General positive	LPHG/FG	36	1712	−40	−28	−22
General positive	RPHG/FG	36	704	44	−22	−26
BIND > MOV	RITG	20	1296	48	−16	−32
BIND positive	RITG	20	2752	46	−18	−29

The type of analysis (i.e., Effect), the gyral location, Brodmann area (BA), volume (in mm³), and mean *X*, *Y*, and *Z* Montreal Neurological Institute (MNI) coordinates are presented.
RPHG, Right Parahippocampal Gyrus; FG, Fusiform Gyrus; LIFG, Left Inferior Frontal Gyrus; LPHG, Left Parahippocampal Gyrus; RITG, Right Inferior Temporal Gyrus.

activation is in close proximity to the RITG region that demonstrated an interaction effect of distance by syntactic type, the two regions only share 6 voxels (out of 88 voxels in the map of a linear effect across dependency and 162 voxels in the map of linear BIND > linear MOV) in common clearly identifying their distinctness (see Fig. 3; Table 2). This seems to suggest that Binding produces greater spatial extent of activation in the right medial temporal lobe.

RMFG

This showed greater activation for one dependency over another without there being a linear increase in activation with distance (see Table 3). RMFG is of interest, as it is similar to a region that likewise demonstrated a main effect of Binding in a previous study (Santi and Grodzinsky, in press). Like these previous results with 0 additional intervening NPs, the *t*-values for Binding are around silence, whereas the non-Binding *t*-values are negative (see Fig. 4). Although the *t*-value increases with 1 additional intervening NP or more, this difference did not come out significant in the computed group map when contrasting the two conditions directly.

Discussion

The results of this parametric study point toward a syntactically specialized WM in Broca's area, one that is involved in the processing of filler–gap, or Movement relations. The linear effect of distance interacted with syntactic type within BA 45. Specifically, the Movement structure demonstrated a positive linear effect of distance, but the Binding structure did not. If Broca's area responded generically to WM demands we would not expect to see an interaction but simply a linear effect regardless of syntactic type, as we did bilaterally in the PHG/FG.

These findings are consistent with results from aphasia, whereby Broca-lesioned patients' comprehension of sentences with filler–gaps is impaired but preserved on sentences with reflexive binding (Grodzinsky et al., 1993; Ruigendijk et al., 2006). Additionally, they nicely complement studies in aphasia, which show a double dissociation between general verbal WM (assessed with digit-span word-span and *n*-back tests) and comprehension of filler–gap dependencies. Conduction and anomic aphasics with impaired verbal WM do not show impaired comprehension of filler–gap dependencies, whereas agrammatic aphasics with more limited general verbal WM impairments do show impaired

comprehension of filler–gap dependencies (Martin, 1987; Miera and Cuetos, 1998; Friedmann and Gvion, 2003).

While these results clearly point to a specialization, and argue against a common WM resource for the processing of the 2 dependencies in Broca's area, there are regions that respond generically to WM demands (i.e., do not discriminate between syntactic differences). The fact that the PHG/FG responded is not surprising, given that it is activated by a variety of other verbal (Rama et al., 2001; Sakai et al., 2002) and visual (Wager and Smith, 2003; Ranganath and D'esposito, 2005) WM tasks. However, the activation of the PHG/FG might be a bit surprising from the perspective of the literature on the neuroimaging of sentence comprehension. Medial inferior temporal regions are reported less frequently by neurological studies of language than are superior temporal and inferior frontal regions (Caplan et al., 1998; Cooke et al., 2001). Furthermore, when medial temporal regions are reported they are not given much focus. Its sparse appearance in the literature might be related to the subtractive designs, which might not be as sensitive to the WM demands, as is a parametric design. Furthermore, the literature puts greater focus on activation within Broca's and Wernicke's area given their theoretical focus that developed from earlier work in aphasia.

While there was a bilateral linear effect of distance in the medial temporal cortex, Binding demonstrated a greater spatial distribution in the right hemisphere. This was determined, through an interaction between distance and syntactic type in cortex adjacent to the main effect of distance in the RPHG/RFG. This region demonstrated a positive linear effect to Binding only.

A region that was more sensitive to the needs of Binding than Movement is the RMFG. Although the RMFG seemed, based on the *t*-value scores, sensitive to WM demands in a step fashion (from 0 to 1 additional intervening NPs), the differences were not significant in the group maps that compared the individual conditions. Thus, we cannot conclude that it is involved in WM processes, but rather that it is recruited by some other need in Binding constructions.

Table 3
Description of the regions activated by the difference between the two syntactic dependencies

Effect	Gyrus	BA	Volume (mm³)	X	Y	Z
BIND > MOV	RMFG	10	832	42	58	−8
BIND > MOV	LSTG	21	5160	−62	−40	0
BIND > MOV	LiPCS	4/6	1240	−52	14	28
BIND > MOV	RSTG	21	472	70	−42	0
BIND > MOV	RITG	36	864	48	−28	−16
MOV > BIND	RIns	13	3344	44	−20	24
MOV > BIND	LSFG	9	944	−34	28	42
MOV > BIND	CingG/RSFG	32/9	3840	6	58	2
MOV > BIND	RMTG	21	168	59	−3	−14
MOV > BIND	RITG	38/21	528	36	3	−32

The type of analysis (i.e., Effect), the gyral location, Brodmann area (BA), volume (in mm³), and mean *X*, *Y*, and *Z* Montreal Neurological Institute (MNI) coordinates are presented.
RMFG, Right Middle Frontal Gyrus; LSTG, Left Superior Temporal Gyrus; LiPCS, Left Inferior Precentral Sulcus; RSTG, Right Superior Temporal Gyrus; RITG, Right Inferior Temporal Gyrus; RIns, Right Insula; LSFG, Left Superior Frontal Gyrus; CingG, Cingulate Gyrus; RSFG, Right Superior Frontal Gyrus; RMTG, Right Middle Temporal Gyrus.
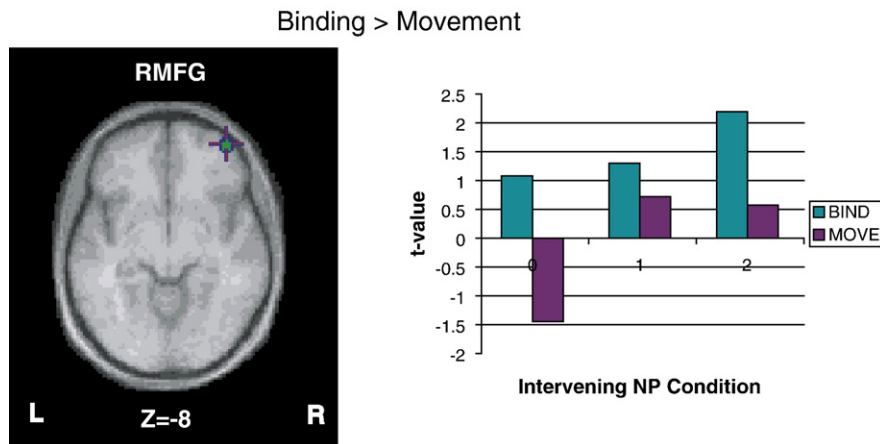
Fig. 4. Activation of the right middle frontal gyrus (RMFG) for the [Binding − Movement] contrast (map searched for clusters above a threshold of $t(1386) = 2.5762$, $p = 0.005$). The average t-value for each of the conditions within the region is presented.

While there were additional areas activated by the direct contrast of [BIND − MOV] as well as [MOV − BIND], they should not be focused on. The reason being, that the primary aim of the current study was to parametrically manipulate distance within each of these dependencies. In doing so, multiple differences between the BIND and MOV conditions were generated, including right-branching relative clauses versus center-embedded relative clauses, coordination of NPs or not, and subject versus object movement. The critical point is that within the parametric variation only one variable changed, but when directly comparing the dependencies these additional variables become an issue. Despite these various differences, it is nice to see the replication of the RMFG activation by the binding contrast.

Finally, the negative linear trend for Binding in a region of LIFG is more difficult to understand. Although negative trends associated with increasing WM load have been reported in the literature previously, they have thus far resisted explanation. In the current study, the combination of two factors of the design could account for this negative linear effect: (1) intermittent scanning and (2) subject filler–gap in the binding condition (see description of the stimuli in Materials and methods). Since intermittent scanning was used, it is possible that the negative linear trend was due to the subject filler–gap becoming increasingly further away from the point of scanning and thus having the scan capturing a point along the hrf that is further and further from its peak. Put another way, the decreasing activation could be related to the peak of activation to the subject filler–gap becoming temporally further offset from the onset of the scan.

There may be an inclination towards an alternative interpretation of this negative linear trend for binding, which is to associate the binding dependency with cases in which processing dependent final elements becomes easier with greater distance from the dependent initial item (i.e., so-called antilocality effects; Konieczny, 2000). This alternative interpretation is problematic, since the antilocality effects critically require the dependent final element to be predicted at the dependent initial element. For example, a verb is predicted whenever there is a subject. In verb final languages, such as German, the distance between the subject and the verb can be increased by having a direct object and relative clause intervene between the two. Effects have been observed whereby it is easier to process the verb the greater the distance it is from its subject, and have thus been

referred to as antilocality effects. Critically the verb can be predicted as soon as the subject is processed. Since in the case of binding there is no way to predict the reflexive pronoun, an argument for antilocality (i.e., the reflexive becomes easier to process the further it is from its antecedent) cannot account for the negative linear effect observed with increasing distance between the reflexive pronoun and its antecedents.

In sum, then, this study set out to determine whether there are associations/distinctions with regards to WM in syntax. The complicated picture we found has a little of both. Most critical was the distinction within LIFG. Contrary to some current views the LIFG region that is activated by syntactic Movement is not simply due to a role in general WM. Further, this result is inconsistent with the perspective that Broca's area is only sensitive to the linearization of arguments in a sentence (Bornkessel et al., 2005; Grewe et al., 2006). While the filler–gap distance was parameterized, there was no parametric variation in the complexity of argument linearization. The result demonstrates that Broca's area is specific to the WM needs of syntactic Movement rather than general to dependency relations. The degree of specificity requires further testing. As was mentioned in the Introduction the two dependencies differ with respect to their demands on WM. Binding taxes retrieval processes, whereas Movement (at least in the cases tested here) taxes storage processes. Thus, it may be the case that this region is specific to storage processes across syntactic type or possibly even across modality. A variety of additional studies is required to dissociate these possible alternatives. Another novel finding from the current study was that WM load had a significant effect in bilateral medial temporal lobes for both dependency relations.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2007.04.047.

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