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Neural Patterns in Linguistic Cortices Discriminate the Content of Verbal Working Memory

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Abstract

An influential theoretical account of working memory (WM) considers that WM is based on direct activation of long-term memory knowledge. While there is empirical support for this position in the visual WM domain, direct evidence is scarce in the verbal WM domain. This question is critical for models of verbal WM, as the question of whether short-term maintenance of verbal information relies on direct activation within the long-term linguistic knowledge base or not is still debated. In this study, we examined the extent to which short-term maintenance of lexico-semantic knowledge relies on neural activation patterns in linguistic cortices, and this by using a fast encoding running span task for word and nonword stimuli minimizing strategic encoding mechanisms. Multivariate analyses showed specific neural patterns for the encoding and maintenance of word versus nonword stimuli. These patterns were not detectable anymore when participants were instructed to stop maintaining the memoranda. The patterns involved specific regions within the dorsal and ventral pathways, which are considered to support phonological and semantic processing to various degrees. This study provides novel evidence for a role of linguistic cortices in the representation of long-term memory linguistic knowledge during WM processing.

Key words: psycholinguistic, running span, working memory

Introduction

Working memory (WM), the ability to temporarily hold information in mind, is considered to rely on direct and obligatory activation of corresponding representations in long-term memory (LTM) by a number of theoretical accounts (Cowan 1995, 1999, 2001; Martin et al. 1996; Oberauer 2002; Nee and Jonides 2011, 2013; Majerus 2013, 2019). In the visual domain, this position is supported by studies showing that WM content can be decoded by neural patterns in visual sensory cortices (Harrison and Tong 2009). In the verbal domain, this view is most strongly supported by behavioral evidence showing that LTM linguistic knowledge impact WM performance (Brener 1940; Poirier and Saint-Aubin 1995; Hulme et al. 1997; Walker and Hulme 1999), but little evidence in the neuroimaging literature supports this

theoretical position. This is a particularly critical theoretical question, as some models assume that LTM linguistic knowledge is not accessed in a direct and obligatory manner during WM processing (Hulme et al. 1991; Schweickert 1993). The aim of this study was to assess whether verbal stimuli that differ in their lexico-semantic content (i.e., word and nonword) could be differentiated based on their pattern of neural activation within linguistic cortices, and this in WM encoding conditions relying on fast activation of memoranda.

In the verbal domain, interactions between WM and corresponding representations in linguistic LTM are supported by the fact that verbal items associated with richer lexico-semantic representations, such as words, lead to strongly increased WM recall performance as compared to stimuli with minimal

lexico-semantic content, such as nonwords (Brener 1940; Jefferies et al. 2006a). Similar observations have been made through the manipulation of other linguistic contents, such as high versus low frequency words (Hulme et al. 1997), semantically related versus unrelated words (Poirier and Saint-Aubin 1995), and high versus low imageability words (Walker and Hulme 1999). Although there is little doubt that these psycholinguistic effects reflect the influences of LTM knowledge stored within the linguistic system, current theoretical models do not agree as regards the moment at which these influences occur. On the one side, language-based models of WM (Martin et al. 1996; Acheson and MacDonald 2009; Majerus 2013, 2019) consider that these influences stem from the direct activation occurring within the linguistic system. For this family of models, as soon as a verbal item is presented for encoding in WM, underlying language representations at phonological, lexical, and semantic levels are activated. This will directly lead to the linguistic knowledge effects observed in WM as stimuli associated with richer or more stable representations will be encoded in a more robust manner. On the other hand, redintegration-based models of WM (Hulme et al. 1991; Schweickert 1993) consider that linguistic knowledge effects in WM tasks do not reflect activation of linguistic knowledge at encoding but are the result of a post-encoding reconstruction mechanism occurring only at the moment of recall. More specifically, for redintegration-based models, memoranda are stored within a temporary buffer in a purely phonological format. Over time, these phonological traces will be subject to degradation due to decay or interference. At the moment of recall, the partially degraded phonological traces undergo a clean-up process, whereby they will be compared to lexical representations in the language system. The recall advantage for words over nonwords in WM tasks is explained by the fact that in absence of associated lexical representation, nonwords cannot be reconstructed via the clean-up process, unlike words. Hence, for this family of models, LTM knowledge is accessed only at the moment of recall or when retrieval attempts are possible (e.g., during maintenance).

Behaviorally, language-based and redintegration-based models are difficult to disentangle as there are no behavioral measures that would reflect purely the processes occurring during encoding; both accounts will predict an influence of linguistic knowledge on standard WM recall tasks, which only provide us the information that is available at the moment of retrieval. Language-based and redintegration-based models can, however, be dissociated when using a neuroimaging approach. Language-based models predict that the neural activation associated with the encoding of word and nonword stimuli in WM should differ already at the encoding and maintenance stages of WM processing, as word and nonword stimuli will directly activate their corresponding representations in the language system if available. For redintegration-based models, however, no difference between word and nonword stimuli should be observed at the encoding stage, as the influence of LTM linguistic knowledge is supposed to occur only when retrieval attempts are possible, that is, during the maintenance and recall stages. However, direct neuroimaging evidence for an involvement of linguistic LTM representations in the short-term maintenance of different types of verbal memoranda such as words versus nonwords is still lacking.

At a more general level, the involvement of linguistic cortices in verbal WM tasks is suggested by several lines of evidence. It has been shown that the encoding and short-term maintenance

of phonological information recruit the superior temporal gyrus associated with phonological processing (Buchsbaum et al. 2005; Strand et al. 2008; Ravizza et al. 2011). Ruchkin et al. (2003) compared WM for words and nonwords in an event-related potentials study and observed a larger negativity for words as compared to nonwords during encoding, maintenance, and the retrieval stages of WM processing. In a positron emission tomography (PET) neuroimaging study, Collette et al. (2001) also compared WM encoding and recall for word and nonword lists and found that word lists recruited the left middle temporal gyrus to a greater extent, a neural region proposed to support lexico-semantic processing (Rissman et al. 2003; Gold et al. 2006; Gagnepain et al. 2008; Sabri et al. 2008; Snijders et al. 2009; Whitney et al. 2011; Visser et al. 2012). Using functional magnetic resonance imaging (fMRI), Fiebach et al. (2007) were able to show sustained blood oxygen level-dependent (BOLD) responses in frontal and temporal cortices supporting semantic knowledge during the maintenance of verbal information.

A more recent set of studies has used multivariate voxel pattern analysis (MVPA) techniques, which can inform us about the nature of activity patterns in linguistic cortices during verbal WM tasks. In one of these studies, Lewis-Peacock and Postle (2012) showed that neural patterns in linguistic cortices can distinguish between WM maintenance of word and nonword stimuli. A further study showed that neural patterns in the superior temporal gyrus can differentiate between different types of nonwords at least during the encoding and recall phases of an immediate serial recall task (Kalm and Norris 2014). A very recent study by Yue et al. (2018) showed that a classifier trained on a speech versus nonspeech perceptual task successfully decoded speech and nonspeech stimuli to be maintained in a WM task. At the same time, this study failed to show reliable decoding of speech versus nonspeech stimuli within phonological processing region (i.e., the superior temporal gyrus) during the maintenance period, which is not in line with the hypothesis that the content of WM would be directly represented within linguistic cortices.

In sum, the existing neuroimaging studies tend to show an involvement of linguistic cortices during verbal WM processing, but at the same time, the evidence remains inconclusive. Furthermore, for those studies that showed evidence for an involvement of linguistic cortices in verbal WM tasks, it is difficult to know to what extent these studies reflect the direct and obligatory activation of linguistic representations during WM encoding and maintenance as postulated by language-based models or a more elaborative reconstruction mechanism as postulated by the redintegration hypothesis. In the Collette et al. study, encoding and recall WM phases were confounded due to the poor temporal resolution that characterizes PET neuroimaging technology, which makes it difficult to determine the WM stage at which language cortices were recruited. In the studies by Fiebach et al. and Lewis-Peacock and Postle, participants were instructed to explicitly use a phonological or a semantic processing strategy when encoding the different memoranda. It is thus unknown whether the content of verbal memoranda can be decoded in linguistic cortices when participants are not instructed to use specific linguistic encoding strategies.

The present study tested the direct involvement of lexico-semantic knowledge and associated cortices in WM for word versus nonword stimuli, and this by using a fast encoding, running span procedure (Pollack et al. 1959). This procedure is known to strongly minimize encoding strategies, such as rehearsal, grouping, semantic elaboration, or mental imagery
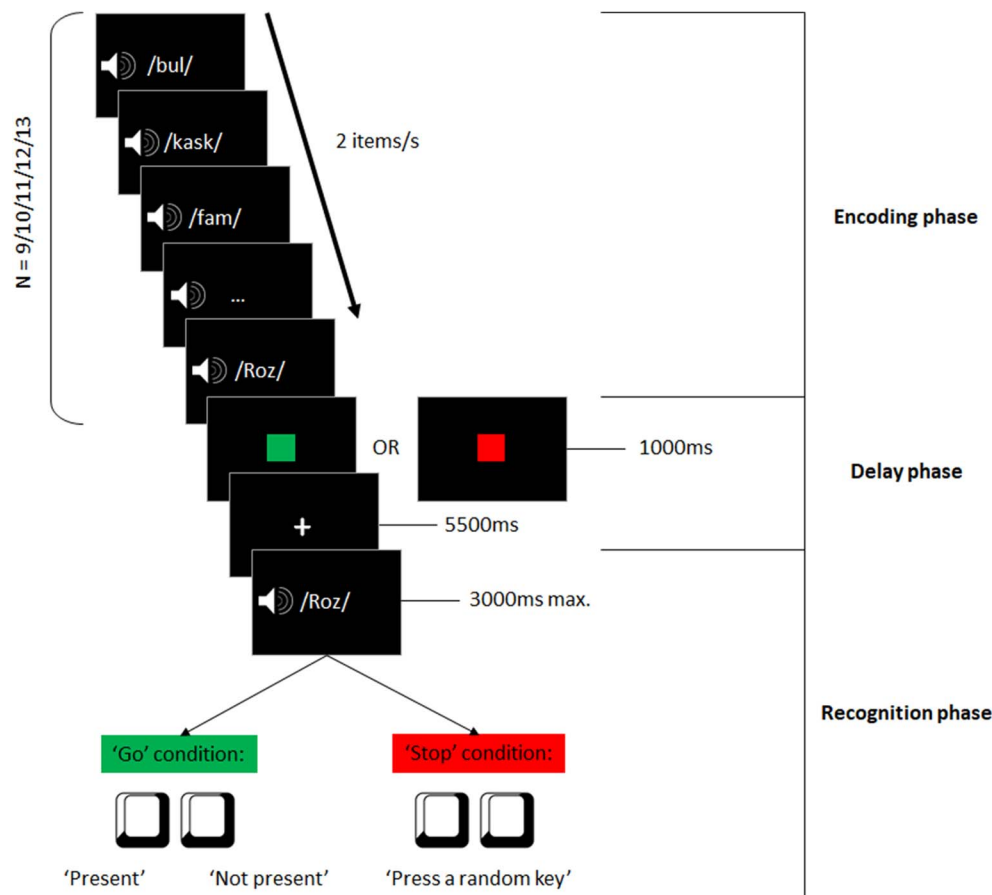
Figure 1. Overview of the running span task design.

(Hockey 1973; Botto et al. 2014; Morrison et al. 2016). The use of this encoding procedure allowed us to conduct a strong test of language-based versus redintegration-based models of WM that classical procedures do not allow. Indeed, in classical WM procedures, participants have the opportunity to reconstruct memoranda during the inter-item interval (Turner and Henry 2004; Jefferies et al. 2006b). Due to the very fast presentation rate and the use of long list lengths that characterizes the running span procedure, any reconstruction attempt will be very difficult to perform (see Fig. 1 for a schematic task description). In these task conditions, as illustrated in Figure 2 (right panel), the redintegration hypothesis predicts that word and nonword stimuli should both be processed at the phonological level during encoding. Hence, we should not be able to decode word and nonword stimuli based on their neural patterns. Language-based models, on the other side, predict that it would be possible to decode the neural patterns of word and nonword stimuli during encoding (see Fig. 2, left panel), since verbal memoranda are supposed to have a direct and obligatory access to all levels of linguistic knowledge as soon as they have been perceived. We examined the extent to which multivariate neural patterns in linguistic cortices are able to differentiate word versus nonword stimuli when participants are invited to encode the stimuli. In addition to an encoding period, we further added a delay interval during which participants were invited either to actively maintain ("Go" condition) or to stop maintaining ("Stop" condition) the memoranda. We expected that if linguistic knowledge also

contributes to WM processing during the maintenance period, neural patterns that discriminate word versus nonword stimuli in linguistic cortices during encoding should also be observable during the maintenance period. Conversely, this should not be the case anymore when participants are invited to stop maintaining the memoranda. During this maintenance period, participants may have the opportunity to use reconstruction mechanisms. Note that the two theoretical accounts predict the same patterns of outcomes at this stage (see Fig. 2). This is however not problematic for the purpose of this study as neural discrimination of words versus nonwords during the encoding period will be most informative for distinguishing between language-based and reconstruction-based models.

We focused on temporal and frontal language regions in the dorsal and ventral language pathways, which are generally considered to be involved in phonological and lexico-semantic processing, respectively (Hickok and Poeppel 2007; Friederici 2012; Friederici and Gierhan 2013). Many studies have shown the involvement of the temporal section of the dorsal pathway (i.e., the superior temporal gyrus) in the processing and representation of phonological information, where fine-grained discrimination of distinct phonological features has shown to be possible (Mesgarani et al. 2014; Arsenault and Buchsbaum 2015). The frontal section of the dorsal pathway (i.e., the pars opercularis), on the other side, has shown to be critical for sensorimotor integration of those phonological information (Restle et al. 2012; Murakami et al. 2015). The temporal section of the
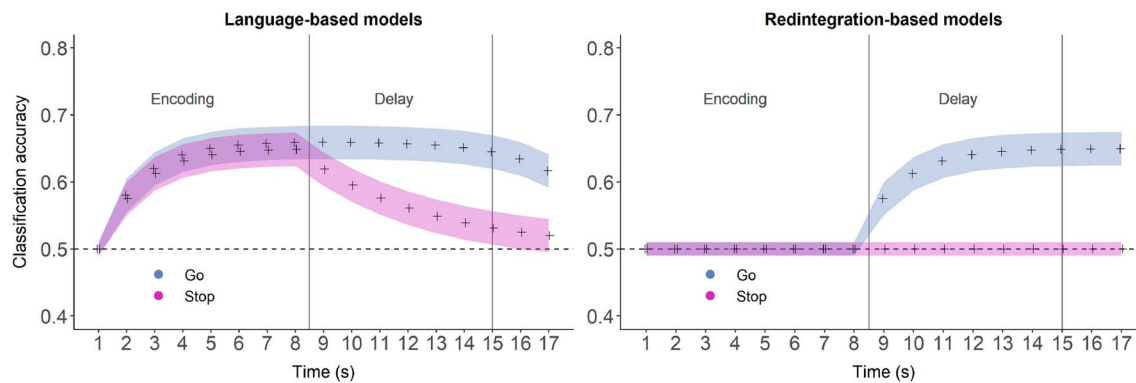
Figure 2. Theoretical word–nonword classification curves as predicted by the two theoretical accounts. Left panel: Predictions for the language-based account. Right panel: Predictions for the redintegration account.

ventral pathway (i.e., the middle temporal gyrus) supports the content of semantic knowledge and encompasses not only the anterior temporal lobe in which amodal semantic knowledge are known to be stored (Visser et al. 2012) but also the middle part of the temporal lobe, which is consistently observed across a wide range of semantic processing tasks (Rissman et al. 2003; Gold et al. 2006; Fiebach et al. 2007; Gagnepain et al. 2008; Sabri et al. 2008; Snijders et al. 2009; Whitney et al. 2011; Visser et al. 2012). The frontal component of the ventral pathway (i.e., the pars triangularis), on the other side, appears to be more specifically involved when semantic control over to-be-processed information is required (Lambon Ralph et al. 2017). In addition, we examined whether the linguistic nature of memoranda could also be decoded in posterior intraparietal sulci (IPS). IPS involvement has been associated with attentional and task control processes in WM (Todd et al. 2005; Emrich et al. 2013; Majerus et al. 2017), and there is conflictual evidence concerning its role in the representation of WM content as opposed to WM task control (Emrich et al. 2013; Bettencourt and Xu 2015; LaRocque et al. 2016; Yu and Shim 2017). For instance, in the visual domain, it has been possible to decode different visual features being maintained in WM, such as line orientation, color, or spatial position (Ester et al. 2015; Peters et al. 2015; Yu and Shim 2017), but this result has not been consistently observed (Linden et al. 2012; Albers et al. 2013; Emrich et al. 2013; LaRocque et al. 2016). Importantly, this question has not been systematically investigated in the verbal domain.

Experiment

Method

Participants
Data were obtained for 31 right-handed native French-speaking young adults (14 males; mean age = 21.42 years; age range 18–29) recruited from the university community, with no history of psychiatric or neurological disorders. The data from 2 participants had to be discarded due to excessive peaks in head movement (volume-to-volume displacement exceeding 4 mm and/or 4°). The data of one additional participant had to be excluded due to difficulties with task compliance, as indicated by response omissions for a significant amount (26.67%) of trials. Functional data acquisition was incomplete for one participant due to premature stopping of the scanner, but resulted in only 5% loss of the whole data set; we decided to retain this participant for data analysis. The final sample was composed of 28

valid datasets. The study was approved by the ethics committee of the Faculty of Medicine of the University of Liège and was performed in accordance with the ethical standards described in the Declaration of Helsinki (1964). All participants gave their written informed consent before their inclusion in the study.

Task Material
The stimuli consisted of 200 words and 200 nonwords. The words were selected from the Lexique 3.0 database and had an average lexical frequency of 18.99 counts per million (standard deviation [SD] = 71.1; New 2006). The nonwords were created by generating under MATLAB a very large ($N > 10^5$) number of stimuli that did not match any entry within the Lexique 3.0 database. The words and nonwords were matched for several critical phonological dimensions: number of phonemes ($M = 4.59$, $SD = 0.65$ and $M = 4.6$, $SD = 0.67$ for words and nonwords, respectively, $BF_{01} = 8.93$), biphone frequency ($M = 726.37$, $SD = 418.51$ and $M = 691.96$ and $SD = 485.05$ for words and nonwords, respectively, $BF_{01} = 8.93$; Tubach and Boë 1990), number of competitors from the same lexical cohort (e.g., *alcove*, *alligator*, *alcohol* … Marslen-Wilson 1987; Tyler et al. 2000) ($M_{log} = 1.92$, $SD_{log} = 0.58$ and $M_{log} = 1.97$, $SD_{log} = 0.55$ for words and nonwords, respectively, $BF_{01} = 6.02$), uniqueness point ($M = 4.17$, $SD = 0.91$ and $M = 4.09$, $SD = 0.81$ for words and nonwords, respectively, $BF_{01} = 5.65$), and phonological structure (the syllabic structure was matched at a pairwise basis for 98.5% of words and nonwords).

The stimuli were recorded by a French-native female speaker using a neutral voice. Each item was recorded as a separate stereo.wav sound file (44 100 Hz sampling frequency). Background noise was removed using Audacity software using a Fourier transform analysis. Each stimulus was normalized to a duration of 475 ms without altering the pitch, using the SBSMS algorithm implemented in Audacity. Task presentation was controlled via the Cogent toolbox implemented under MATLAB.

Task Procedure
Participants underwent a 1-h MRI session during which they performed a running span task. A diagram resuming the different phases of the task is displayed in Figure 1. For each participant, 165 stimuli within each stimulus conditions were randomly sampled from the whole set of data and were used for the running span task, and this in order to include random variability within the dataset for each participant, thereby increasing the generalizability of our results. Each participant

received a different version of the task, with each version being constructed with the constraints mentioned below.

Encoding phase. Each trial started with the presentation of the auditory sequence, pacing at 500 ms/item, where participants were instructed to carefully memorize the items as much as they could. At the start of a trial, the participants were "not" informed about the stimulus (word, nonword) or the delay ("Go" or "Stop" condition, see below) conditions. Auditory sequences were composed of 9, 10, 11, 12, or 13 items, ensuring that participants could not predict the length of a given sequence in advance, furthermore reducing the use of encoding strategies (Palladino and Jarrold 2008; Botto et al. 2014). Each auditory sequence was constructed such that adjacent items could not share their two first or two last phonemes to avoid phonological overlap. Each stimulus was repeated 4 times throughout the task and did not appear twice in the same serial position.

Running span—delay phase. The auditory sequence was followed by an on-screen colored 40×40 pixels square lasting for 1000 ms, directly followed by a white cross at the center of the screen lasting for 5500 ms. If the square color was green, participants were instructed to maintain the items they had heard (Go condition), while if the square color was red, participants were instructed to just rest and do nothing (Stop condition). Critically, during the encoding phase, participants did not know whether they would have to subsequently remember the items or not, making the task requirements during encoding identical to Go and Stop conditions.

Running span—recognition phase. The delay phase was followed by a black screen and an auditory probe stimulus requiring participants, in the Go condition, to judge whether the probe was presented in the list or, in the Stop condition, to just press any key when they heard the auditory stimulus. Consequently, in the Go condition, memory for the auditory sequence was always assessed, while this was never done in the Stop condition. In the Go condition, participants were invited to use their index finger of the right hand for "yes" (the probe appeared in the auditory sequence) and their middle finger for "no" (the probe did not appear in the auditory sequence). During this recognition phase, 60% (36 out of 60) of the active trials were composed of matching probes. This unequal distribution of matching and nonmatching probes ensured that each serial position was sufficiently probed (between 3 and 4 times) to analyze serial position effects (see results). Nonmatching probes were randomly sampled from the pool of stimuli while also ensuring that they never appeared in the current memory sequence. The stimuli were never used twice as a probe. Participants had a 3000 ms upper limit to respond after probe onset. After the participant's response or after the 3000 ms time limit in case of no-responses, the next trial was initiated, separated by an inter-trial interval of 9000 ms (plus or minus a random duration sampled from a normal [Gaussian] continuous distribution with SD = 750 ms).

Sequences were constructed such that any given condition (word/nonword, Go/Stop) could not be repeated on more than three consecutive trials. There were 30 trials per experimental conditions (word—Go; word—Stop; nonword—Go; nonword—Stop), with a total of 120 experimental trials. Participants took approximately 45 min to perform the running span task. To ensure that participants complied with task requirements, they performed a training version of the task (with stimuli not used in the experimental task) outside the scanner during a 1-h information session preceding the session in the scanner by at

least 1 day and a maximum of 7 days. During the MRI session, the instructions were repeated before the beginning of the task.

MRI Acquisition

The experiments were carried out on a 3T whole-body scanner (Prisma, Siemens Medical Solutions) operated with a standard transmit–receive quadrature head coil. Multislice T2∗-weighted functional images were acquired with a gradient-echo echo-planar (EPI) imaging sequence using axial slice orientation and covering the whole brain/most of the brain (30 slices, FoV = 192x192 mm², voxel size 3x3x3 mm³, TR = 1830 ms, TE = 30 ms). The five initial volumes were discarded to avoid T1 saturation effects. After functional acquisition, a gradient-recalled sequence was applied to acquire two complex images with different echo times (TE = 10 ms and 12.46 ms respectively) and generate field maps for distortion correction of the functional images. For anatomical reference, a high-resolution T1-weighted image was acquired for each subject (T1-weighted 3D magnetization-prepared rapid gradient echo (MPRAGE) sequence, TR = 1900 ms, TE = 2.19 ms, inversion time (TI) = 900 ms, FoV = 256x240 mm², matrix size = 256x240x224, voxel size = 1x1x1 mm³). Around 1450 functional images per participants were acquired for the running span task. Head movement was minimized by restraining the participant's head using a vacuum cushion. Stimuli were displayed on a screen positioned at the rear of the scanner, which the participant could comfortably see through a mirror mounted on the head coil.

fMRI Analysis

Image Preprocessing
Data were preprocessed and analyzed using SPM12 software (version 12.0; Wellcome Department of Imaging Neuroscience, www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB for univariate analyses. The default parameters as defined in SPM12 were used. EPI time series were corrected for motion and distortion with "Realign and Unwarp" (Andersson et al. 2001) using the generated field map together with the FieldMap toolbox (Hutton et al. 2002) provided in SPM12. A mean realigned functional image was then calculated by averaging all the realigned and unwarped functional scans and the structural T1-image was coregistered to this mean functional image (rigid body transformation optimized to maximize the normalized mutual information between the two images). The mapping from subject to Montreal Neurological Institute space was estimated from the structural image with the "unified segmentation" approach (Ashburner and Friston 2005). The warping parameters were then separately applied to the functional and structural images to produce normalized images of resolution $2 \times 2 \times 2$ mm³ and $1 \times 1 \times 1$ mm³, respectively. Finally, the warped functional images were spatially smoothed with a Gaussian kernel of 4 mm full-width at half-maximum to improve signal-to-noise ratio while preserving the underlying spatial distribution (Schrouff et al. 2012); this smoothing also diminishes the impact that residual head motion can have on MVPA performance, even after head motion correction (Gardumi et al. 2016).

Univariate Analysis
Univariate analyses first assessed brain activity levels associated with stimulus condition (word vs. nonword) within each

task condition (Go and Stop) in the running span task. For each participant, brain responses were estimated at each voxel, using a general linear model with event-related regressors. The design matrix contained one regressor for the encoding and maintenance phase for each condition resulting from the crossing of stimulus and task conditions (word—hold; word—release; nonword—hold; nonword—release) and a single regressor for the recognition phase (all conditions were confounded for this regressor as this study focused on condition effects for the encoding and maintenance stages). For all models, the time course of the events was convolved with the canonical hemodynamic response function to account for the shape of the BOLD response. Each model also included the realignment parameters to account for any residual movement-related effect. A high-pass filter was implemented using a cutoff period of 128 s to remove the low-frequency drifts from the time series. Serial autocorrelations were estimated with a restricted maximum likelihood algorithm with an autoregressive model of order 1 (plus white noise).

Linear contrasts were defined for each stimulus conditions (word vs. nonword) and this within each task condition (Go and Stop). The resulting contrast images, after additional smoothing by 6 mm FHWM, were entered in a second-level, random effect analysis of variance (ANOVA) to assess the effect of stimulus conditions responsive brain areas at the group level. The additional smoothing was implemented to reduce noise due to intersubject differences in anatomical variability and to reach a more conventional filter level for group-based univariate analyses ($\sqrt{(4^2 + 6^2)}$ = 7.21 mm; Mikl et al. 2008). All the univariate analyses were performed using a cluster-level family-wise error rate corrected threshold at $P < 0.05$, with a voxel-level cluster forming threshold of $P < 0.001$. For regions of interest (ROI) analyses, a small volume correction was applied to the contrasts of interests.

Multivariate Analysis

Multivariate analyses of the 4 mm smoothed functional time series were conducted using PRoNTo, a pattern recognition toolbox for neuroimaging (www.mlnl.cs.ucl.ac.uk/pronto; J. Schrouff et al. 2013). It was used to determine the voxel patterns discriminating between the different stimulus and/or task condition trials at an individual subject level. Binary support vector machines were used to classify whole-brain voxel activation patterns associated with word versus nonword stimuli (Burges 1998). A standard mask removing voxels outside the brain was applied to all images. A first analysis included both the encoding and delay periods as a single event, and this in order to assess general classification accuracy in the running span procedure. We additionally conducted classifications over the time course of the running span task, by assessing classifier accuracies second by second. All models included timing parameters for HRF delay (5 s) and HRF overlap (5 s), ensuring that stimuli from different categories falling within the same 5 s were excluded (Schrouff et al. 2013). Given that image acquisition was performed using a TR of 1830 ms, this also means that adjacent time points over the time course contained partially overlapping signal. This latter point is however not problematic for the purpose of the present study, as we were specifically interested in the evolution of the word/nonword discrimination over the time course of WM processing; adjacent time points were not directly compared. A leave-one-block-out cross-validation procedure was used.

At the group level, classifier performance was tested by comparing the group-level distribution of classification accuracies to a chance-level distribution using a Bayesian one sample t test. Bayesian statistics were used given their robustness in case of small-to-moderate sample sizes and non-normal distributions (Moore et al. 2015) and because, with these analyses, the bias toward accepting or rejecting the null hypothesis does not change with sample size. Furthermore, Bayesian statistics assess evidence for a model under investigation in the light of the data, whereas group-level classical t tests make population-level inferences, which have been shown to be problematic when comparing classification accuracies against chance level (Allefeld et al. 2016). The BF_{10} is used to determine the likelihood ratio of the alternative model (H_1) relative to the null model (H_0) and the BF_{01} to determine the likelihood ratio of H_0 relative to H_1. We use the classification proposed by previous studies (Jeffreys 1998; Wagenmakers et al. 2011): A BF of 1 provides no evidence, $3 > BF > 1$ provides anecdotal evidence, $10 > BF > 3$ provides moderate evidence, $30 > BF > 10$ provides strong evidence, $100 > BF > 30$ provides very strong evidence, and $BF > 100$ provides extreme/decisive evidence. In Bayesian ANOVAs, we performed a Bayesian model comparison using a top–down testing procedure, which first computes the BF value for the most complex model possible (i.e., the model including all main effects and all possible interactions). The BF value for each term is then assessed by directly comparing the full model against the same model but without the term under investigation. In order to minimize error in model estimation, the number of Monte Carlo simulation generated was set to $N_{iterations} = 100\,000$. In all analysis, we used the default Cauchy prior distribution value of $r = 0.707$. We furthermore computed Bayesian credible intervals using the 95% highest density interval on the sampled posterior distribution of the model under investigation ($N_{iterations} = 100\,000$). All the analyses were performed using the BayesFactor package (Morey and Rouder 2014) implemented in R (Development Core 2008). This first overall assessment of the stimulus condition was then followed by a more fine-grained, theoretically driven ROI analysis, and this in order to critically investigate to what extent linguistic cortices support the discrimination of linguistic LTM knowledge.

Regions of Interest

We selected ROIs associated with the dorsal and ventral language pathways (Hickok and Poeppel 2007; Friederici 2012; Friederici and Gierhan 2013; Majerus 2013) using the IBASPM 71 and IBASPM 116 atlases (http://www.thomaskoenig.ch/Lester/ibaspm.htm) using the wfupickatlas toolbox. After the desired regions were selected in the atlases, they were exported as .nifti files and then used as an inclusive mask for voxels on which the multivariate analyses were conducted.

The "dorsal language pathway" was further subdivided according to its temporal and frontal sections given their distinct roles in perceptual versus sensorimotor aspects of phonological processing (Restle et al. 2012; Mesgarani et al. 2014; Arsenault and Buchsbaum 2015; Murakami et al. 2015). The temporal region covered the left superior temporal gyrus, encompassing the anterior temporal sulcus up to the planum temporale region. The frontal region covered the pars opercularis, which is located in the posterior part of the inferior frontal gyrus (BA44).

The "ventral language pathway" was also subdivided as a function of its temporal and frontal components, given their distinct roles in semantic representation and semantic control,

respectively (Rissman et al. 2003; Gold et al. 2006; Fiebach et al. 2007; Gagnepain et al. 2008; Sabri et al. 2008; Snijders et al. 2009; Whitney et al. 2011; Visser et al. 2012; Lambon Ralph et al. 2017). The temporal component covered the middle temporal gyrus, encompassing the anterior temporal lobe up to the posterior middle temporal gyrus, including the middle temporal–occipital junction. The frontal component covered the entire pars triangularis, located in the anterior part of the inferior frontal gyrus (BA45).

ROIs in the intraparietal cortex were defined as 10 mm radius spheres, on mean coordinate values for the left posterior IPS ($x = -25$, $y = -64$, $z = 43$) and the right posterior IPS ($x = 27$, $y = -62$, $z = 38$), taken from previous studies that have focused on interactions between attentional and WM processing (Todd and Marois 2004; Todd et al. 2005; Asplund et al. 2010; Majerus et al. 2012, 2016). The regions were created using the wfupickatlas toolbox.

Finally, we also performed a ROI analysis on the primary visual cortex V1, and this in order to show that discrimination patterns for words versus nonwords were specifically located in the language-related ROIs. The V1 ROI region was defined using the probabilistic atlas Anatomical toolbox (Eickhoff et al. 2005) implemented in SPM. The region covered the whole primary visual cortex region (Amunts et al. 2000) and has shown to successfully decode different visual features such as color, line orientation, or movement direction in visual WM tasks and which should not be relevant for the decoding of word versus nonword stimuli in the present study (Harrison and Tong 2009; Emrich et al. 2013; Ester et al. 2013; Weber et al. 2016). An overview of these ROIs is given in Figure 3.

Searchlight Analysis
Finally, in addition to the ROI analyses, a searchlight decoding approach was used to determine the local spatial distribution of the voxels that discriminate between words and nonwords (Kriegeskorte et al. 2006). Univariate voxel activity levels associated with each event of interest were first estimated at the individual level by using the beta images for each event, resulting in a total of 120 beta images for the encoding phase and 60 images for Go condition of the delay phase (i.e., maintenance). A searchlight sphere of 10 mm was then applied on the whole-brain multivariate feature map built from the extracted beta images, and the classification accuracy of each voxel cluster was determined, using ad hoc code built for the Pronto toolbox and available at https://github.com/CyclotronResearchCentre/PRoNTo_SearchLight. Significance of searchlight classifications was assessed at both individual and group levels using a procedure similar to Majerus et al. (2017), given that analyses of group-level classification accuracies can indicate small above-chance level classifications as being significant while at an individual level, only few (if any) participants may show significant classification accuracies. It is therefore important to also consider the prevalence of the effect across participants and not only the mean classification rate of the group (Allefeld et al. 2016). To obtain significance values for individual-level classification accuracies, we used binomial tests indicating the classification accuracy threshold at which voxels are significant at $P < 0.05$ according to a binomial distribution. For displaying searchlight results, a prevalence image was built on individual searchlight classification maps summarizing the number of individual participants for which a given voxel showed a classification accuracy higher than the binomial significance threshold. This
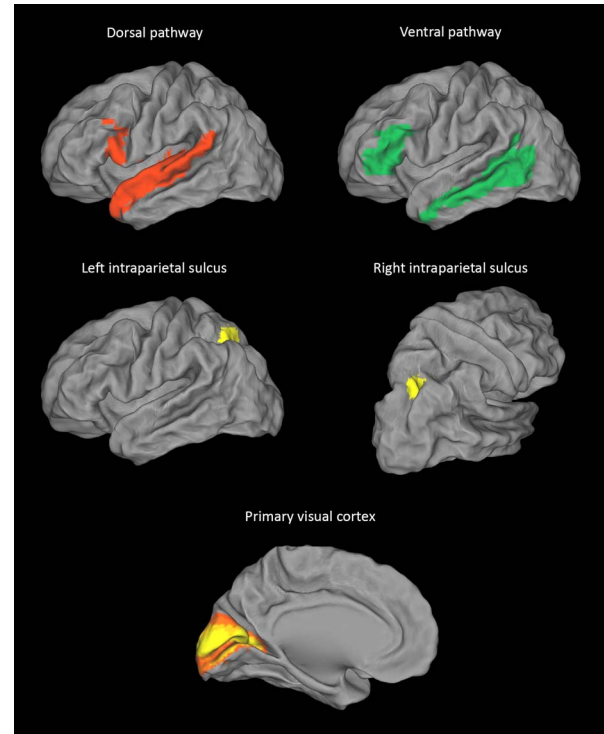

Figure 3. ROI used in the univariate and multivariate analyses. The upper part of the image shows the ROI within the dorsal (left, orange) and ventral language (right, green) pathways, with their respective frontal and temporal components. The middle part of the image shows the left and right IPS ROI. The lower part of the image shows the primary visual cortex (V1) ROI.

led to a prevalence image indicating the proportion of participants showing significant classification accuracies for a given voxel. Note that simulations of this procedure indicated that this method is very conservative; a simulation with 10 000 iterations of classification accuracies over 28 brains, each composed of 1 000 000 voxels, showed that the probability to find by chance one single voxel exceeding the binomial significance threshold ($N_{trial} = 120$) for at least half the participants was virtually 0, given a true null hypothesis.

Results

Behavioral Analysis

A first analysis assessed response accuracy as a function of lexical condition (word vs. nonword) and as a function of the serial position being probed (1 through 9) using a Bayesian repeated measures ANOVA. We found moderate evidence against the presence of a lexical condition effect ($BF_{01} = 4.542$) and decisive evidence supporting the serial position effect ($BF_{10} = 3.199e+10$). We also found very strong evidence against the interaction term ($BF_{01} = 60.652$). As shown in Figure 4 (upper panel), there were strong recency and poor primacy effects. The same pattern of results was observed when running the same analysis on response times. We found moderate evidence against the effect of lexical condition ($BF_{01} = 8.917$), but decisive evidence supporting a serial position effect ($BF_{10} = 2042.802$). We found very strong evidence against the interaction term ($BF_{01} = 53.819$). The serial position effect was characterized by faster responses for the last presented items as compared to items presented

Proportion of HIT responses across serial position

Response times for HIT responses across serial position
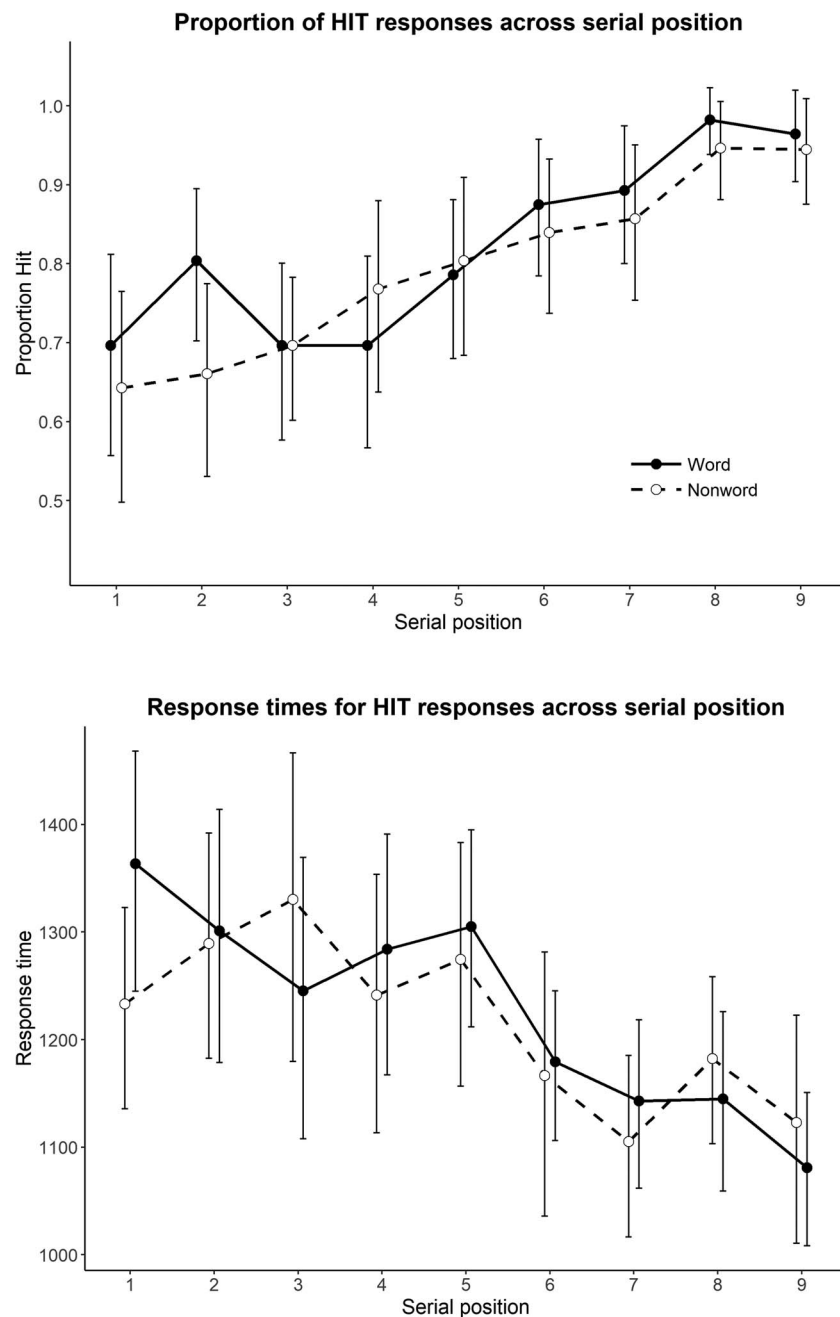
Figure 4. Proportion of hit responses (upper panel) and response times for hit responses (lower panel) across serial position, averaged across participants. Error bars represent 95% Bayesian credible intervals, after controlling for between-subject variability (Cousineau 2005; Morey 2008; Baguley 2012).

in the beginning of the list (Fig. 4, lower panel). In line with our predictions, the strong recency and poor primacy effects that characterize running span procedures for both accuracy and response times show that participants passively encoded each subsequent item without being able to use refreshing or rehearsal strategies for earlier presented items (Ruiz et al. 2005; Ruiz and Elosúa 2013; Botto et al. 2014). Overall, given the very high within-subject variability (as shown by the error bars corrected for between-subject variability in Fig. 4, upper panel), a lexicality effect was not strongly expected. Previous studies have shown reliable lexicality effects when using full recall paradigms

or when using recognition paradigms with a particularly large number of trials (Gathercole et al. 2001; Jefferies et al. 2006b; Kowialiewski and Majerus 2018).

Neuroimaging—Univariate Analyses

No linguistic condition effect was observed when directly contrasting the two (word vs. nonword) stimulus conditions, regardless of the task condition (hold, release) (cluster-level FWE corrected threshold $P < 0.05$, with $P < 0.001$ uncorrected voxel-level cluster-forming threshold). When using the ROIs as defined in
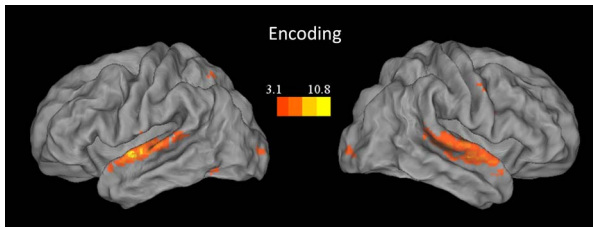
Figure 5. Univariate results for activity peaks during encoding of word and nonword stimuli (null conjunction analysis) in the running span task. The regions are displayed at an uncorrected voxel-level threshold of $P < 0.001$. The scale color indicates minimum and maximum t values, with (1, 108) degrees of freedom.

the Methods section, no linguistic condition effect was observed for both tasks. This finding is in line with the majority of studies showing overlapping univariate neural responses for word and nonword conditions (Newman and Twieg 2001; Kotz et al. 2002; Rissman et al. 2003; Xiao et al. 2005; Orfanidou et al. 2006; Raettig and Kotz 2008; Sabri et al. 2008; Davis and Gaskell 2009). At the same time, when looking at the univariate activity peaks associated with both the word and nonword conditions using a null conjunction analysis, we observed as expected the recruitment of the superior temporal region covering the dorsal language pathways; note that in order to highlight regions associated with encoding of verbal stimuli irrespectively of subsequent WM task demands, this analysis focused specifically on the encoding stage (see Fig. 5).

Neuroimaging—Multivariate Analyses

Overall, robust discrimination of word versus nonword conditions was observed when the encoding and delay periods were considered together. As shown in Figure 6, decisive evidence for above-chance discrimination was found in the hold and release conditions in the whole-brain analysis. For this analysis, all BF values are reported in the figures. When the ROIs were considered, above chance-level discrimination was observed in the temporal and frontal components of both the dorsal and ventral language pathways, and this in both the Go and Stop conditions with strong to decisive evidence for above-chance discrimination being observed for all language regions. Interestingly, the IPS regions presumably involved in attentional and task control also showed decisive evidence for above-chance discrimination in the Go condition, and strong evidence was still observed in the Stop condition. Note that similar results were observed when the linguistic regions of the right hemisphere were explored, but results were overall less robust (see Supplementary Fig. 1).

In a next analysis, we directly compared word versus nonword classification accuracy between the Go and Stop task conditions. As can be seen in Figure 7, classification accuracy dropped in the Go condition as compared to the Stop condition, and this was consistently observed across all ROIs and in the whole-brain analysis, as assessed by Bayesian one sample t tests. This drop of classification accuracy in the Stop condition suggests that participants had stopped maintaining the memoranda, leading to a disappearance of stimulus condition-specific neural activity patterns in linguistic cortices. The results on the right hemisphere are available in Supplementary Figure 2.

In order to obtain a more precise understanding of the moment at which linguistic condition informative neural patterns disappeared, we explored the time course of classification

accuracy over the entire duration of the running span task trials (see Fig. 8). Classification accuracy was assessed for time points ranging from 15 s before and 2 s after the presentation of the recognition probe, to ensure a window of 17 s, thereby covering the entire trial. This procedure ensured that the same time points were examined for each trial despite the variable duration of the encoding event. Note that BF values related to these analyses are reported in supplementary material. Analyses were also performed on linguistic cortices in the right hemisphere and are reported in Supplementary Figure 3.

Dorsal Pathway
For the temporal component of the dorsal pathway, above-chance level discrimination in the Go condition was found over time points 3 through 9 and over time points 11 through 13, corresponding to the encoding and delay phases. In the Stop condition, this was observed only for time points corresponding to the encoding phases and more specifically over time points 2, 4, and 5. Direct comparisons between task conditions showed reliable differences in classification accuracy at time points 8, 9 and 13, corresponding to the delay phase. Over the frontal component of the dorsal pathway, above-chance level discrimination was observed in the Go condition over time points 5 through 13, all located in the encoding and delay phases. In the Stop condition, this was the case only for time points 4 and 5 (encoding phase). Direct comparisons showed that the two task conditions differed at time points 6 to 13, corresponding mostly to the delay phase.

Ventral Pathway
In the temporal component of the ventral pathway, in the Go condition, above-chance level discrimination was found over time points 2 through 11 and 13 (encoding and delay phases). In the Stop condition, this was observed for time points 2 through 6 (encoding phase only). The two task conditions differed over time points 8 through 11 and 13 through 14 (mainly in the delay phase). The same results were observed when focusing on the frontal component of the ventral pathway: above-chance level discrimination was found over time points 2 through 14 in the Go condition (encoding and delay phases) and 2 through 5 in the Stop condition (encoding phase only). The difference between the two delay conditions was observed over time points 6 through 14, corresponding again mainly to the delay phase.

IPS
In the Go condition, above-chance level discrimination was found at time point 2, as well as over time points 4 through 11 (encoding and delay phases). This was observed over time points 2 and 4 only in the Stop condition (encoding phase only). The two task conditions differed over time points 7 through 10, which corresponds to late encoding/early delay phases.

In order to show that the observed discrimination patterns for word and nonword conditions are specific to language and WM-related cortices, we performed a final ROI analysis over the primary visual cortex V1. Given the purely auditory–verbal nature of the stimuli used in this experiment, no discrimination of word versus nonword conditions was expected in this region associated with processing of visual sensory information (Tootell et al. 1998; Kamitani and Tong 2005). As can be seen in Figure 8, classification accuracy was at chance level in both task conditions throughout the entire trial duration.
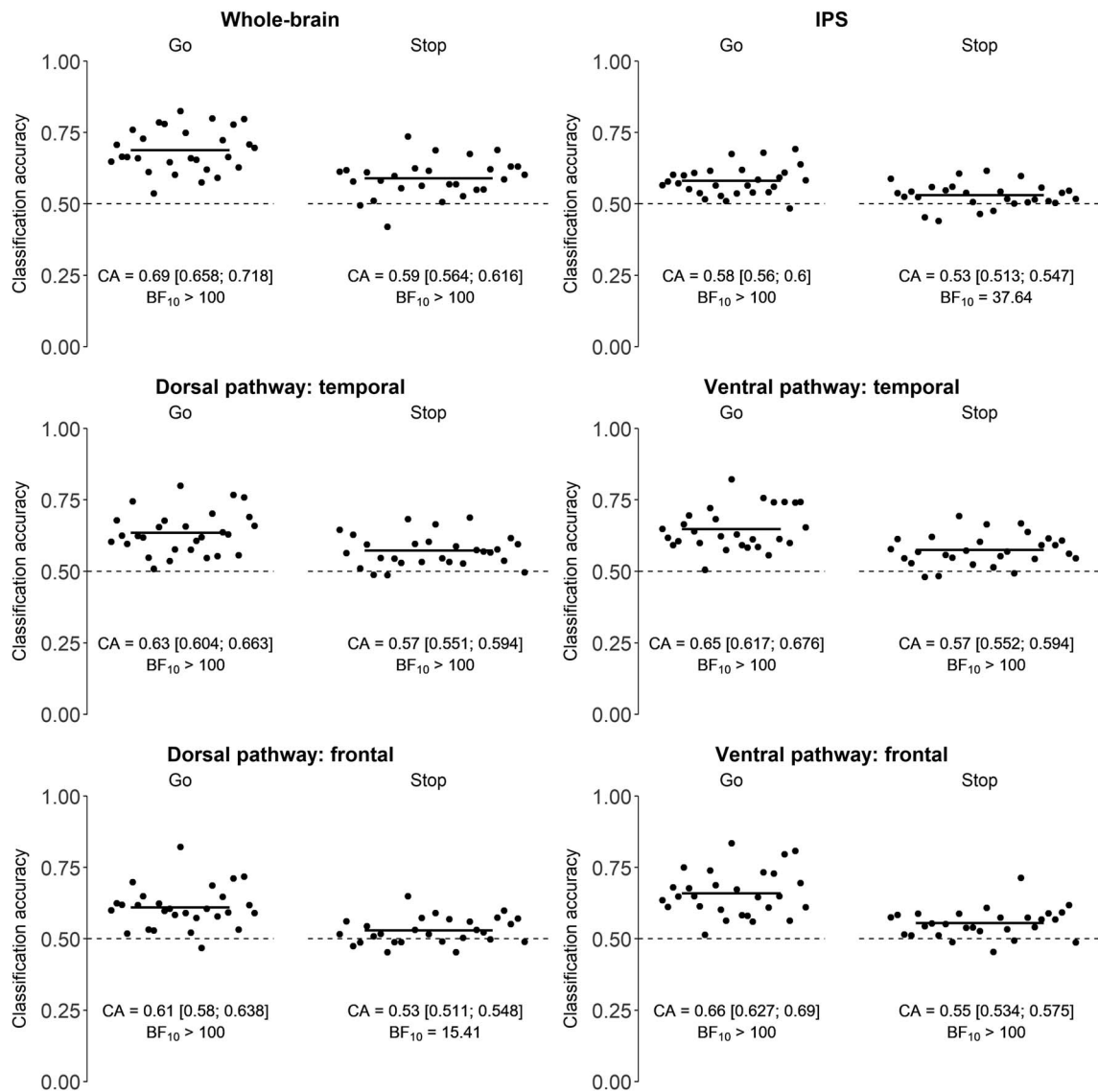
Figure 6. Classification accuracies in the running span task, for whole-brain and ROI analyses. Each point represents classification accuracy for one participant. Chance level classification accuracy is indicated by the horizontal black line. The 95% Bayesian credible intervals are reported in square brackets.
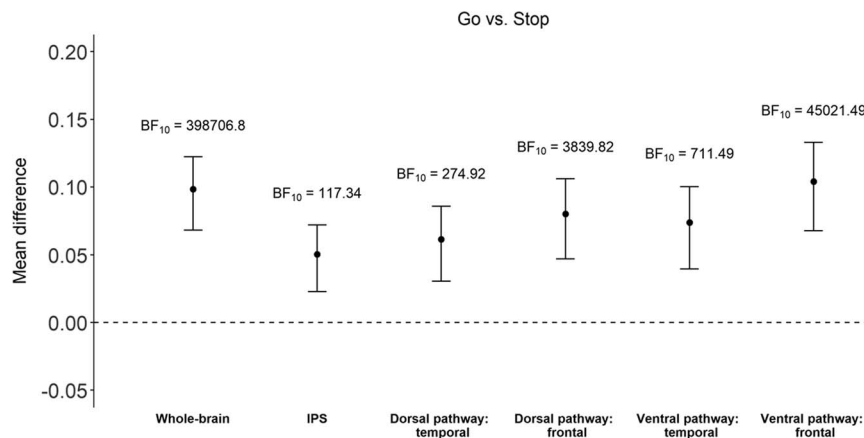
Figure 7. Difference of classification accuracies between the Go and Stop task conditions, for ROI and whole-brain approaches. Error bars represent the 95% Bayesian credible intervals.
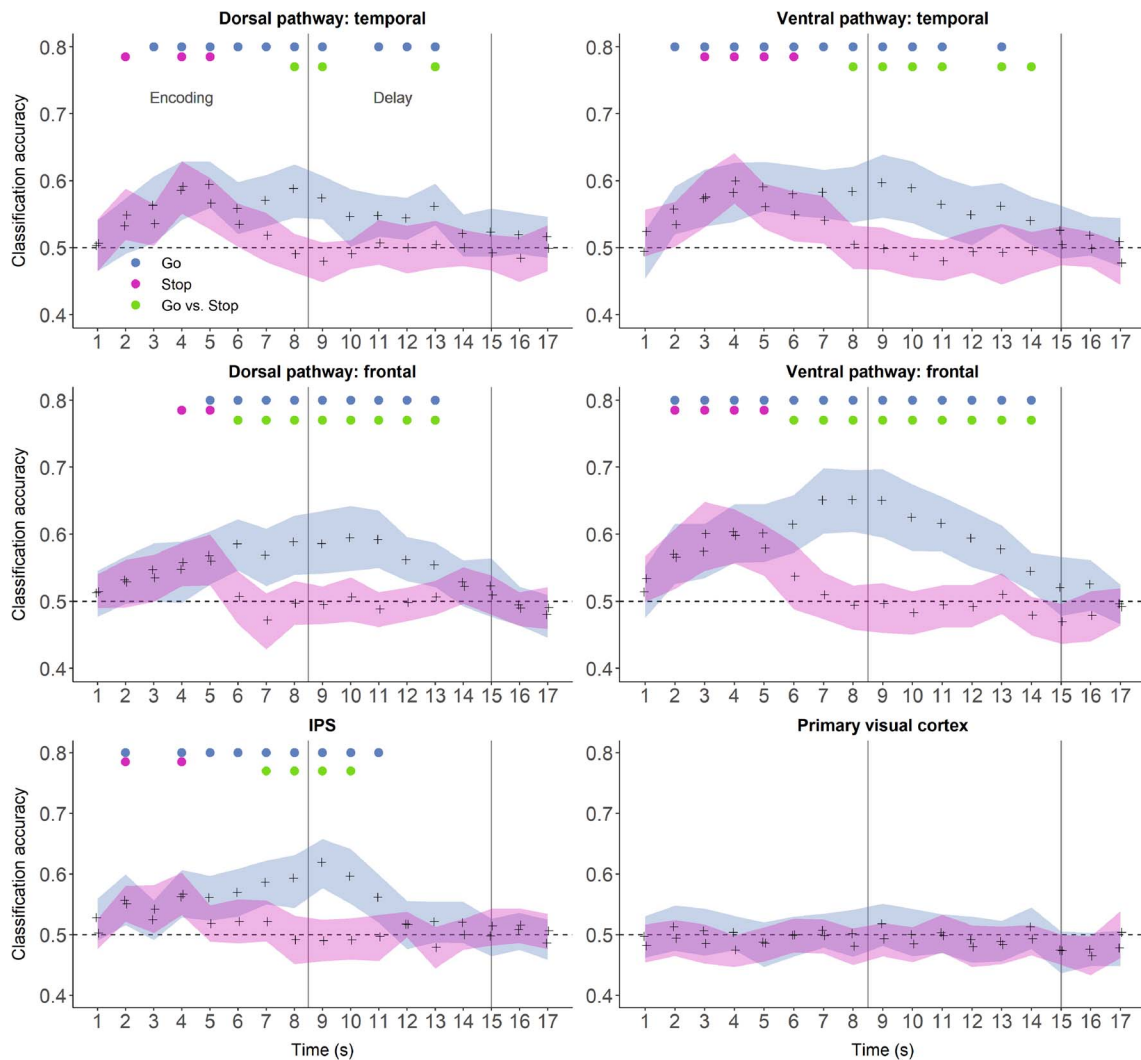
Figure 8. Classification accuracies (word vs. nonword) as a function of trial time in the running span task (in seconds) for ROI and whole-brain approaches. The solid vertical lines represent the beginning and the end of the maintenance phase. The dashed horizontal line indicates chance level. The recognition probe directly appeared after the end of the maintenance phase. BF_{10} values for word–nonword classification accuracies above 3 are indicated via the colored dots on top of the figure. Blue dots: $BF_{10} > 3$ for hold condition (word–nonword classification accuracy relative to theoretical random classification distribution). Purple dots: $BF_{10} > 3$ for release condition (word–nonword classification accuracy relative to theoretical random classification distribution). Green dots: $BF_{10} > 3$ for direct comparison of word–nonword classification accuracies in the hold versus release task conditions. The width of the ribbons corresponds to the 95% Bayesian credible intervals.

Note that in the time course analysis (Fig. 8), classification accuracy for the Go and Stop conditions appears to separate around 2 s before the presentation of the cue. This pattern is not likely due to participants predicting the delay condition since the participants could not be aware of the upcoming condition; the different conditions followed each other in pseudorandom order (see procedure). Instead, this situation is likely due to the fact that adjacent time points contain partially overlapping neural signal preventing a clear separation between conditions for directly adjacent time points.

Neuroimaging—Searchlight Analyses

Finally, we performed a whole-brain searchlight analysis in order to determine more precisely which neural regions reliably contributed to classification accuracy between word and nonword stimuli given the relatively large size of the ROIs.

The ventral/dorsal distinction we made may not delimitate the phonological and lexico-semantic aspects of language processing in a strict manner. It is therefore difficult, based on the ROI analysis, to estimate precisely whether phonological or lexico-semantic regions contributed the most to the word/nonword distinction. The searchlight analysis was performed separately on the encoding and on the Go condition of the delay phase (i.e., when participants had to maintain the stimuli). As can be seen in Figure 9, all the regions that reliably contributed to classification accuracy in this analysis were exclusively located in the left hemisphere. During encoding, the frontal regions that contributed the most to word/nonword classification included the pars triangularis (i.e., the anterior part of Broca's area) and to a very limited extent the pars opercularis (i.e., the posterior part of Broca's area). Temporal regions that contributed to classification accuracy included not only the anterior and the posterior parts of the superior temporal sulcus but also
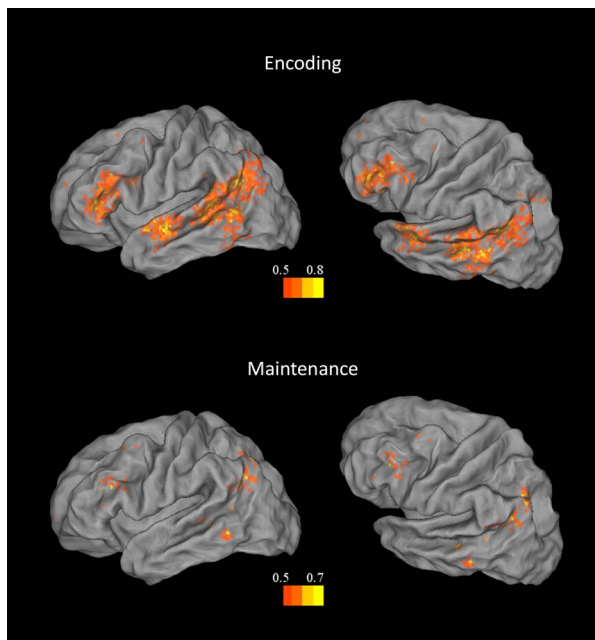
Figure 9. Results of the searchlight analysis discriminating between the word and nonword stimuli during the encoding (upper panel) and maintenance (lower panel) periods. The colors indicate the prevalence of participants showing individual-level significant classification accuracies for a searchlight region around a given voxel.

the posterior part of the middle temporal gyrus, extending to the angular gyrus. Voxels within the left IPS contributed to some very limited extent to classification accuracy. During the maintenance period, the neural regions contributing to classification accuracy were much more limited and included the pars triangularis, the posterior middle temporal gyrus, the angular gyrus, the intraparietal sulcus, and to a limited extent, the posterior part of the superior temporal sulcus. Note however that for the maintenance phase, the number of events was restricted relative to the encoding phase (60 instead of 120 events), which raised the binomial significance threshold at the individual level (i.e., from 0.575 to .6).

In sum, we observed decisive evidence for a differentiation of neural patterns involved in encoding and short-term maintenance of words versus nonwords. These patterns could be found both in dorsal and ventral pathways of the language network, but also in IPS areas presumably associated with WM attentional control processes.

Discussion

This study provides evidence for a nonstrategic involvement of both the dorsal and ventral language pathways, considered to support phonological and lexico-semantic language knowledge, in the encoding and maintenance of verbal information in WM. Some studies have hinted to a role of linguistic cortices during WM tasks, by showing sustained activity in these cortices or by identifying neural patterns that discriminate between different types of verbal memoranda (Buchsbaum et al. 2005; Strand et al. 2008; Ravizza et al. 2011; Lewis-Peacock and Postle 2012; Kalm and Norris 2014; Yue et al. 2018). However, most of these investigations used experimental procedures that allowed participants to reconstruct memoranda during the inter-item interval or that

involved explicit linguistic judgment tasks. The present study shows that linguistic cortices represent the type of verbal stimuli to be held in WM as soon as stimuli are presented for encoding, in the absence of any explicit linguistic encoding strategies, and linguistic cortices continue to represent the type of memoranda over the maintenance stage.

As can be seen when directly comparing Figures 2 and 8, the results do not support redintegration-based models; these models consider that at the moment of encoding, memoranda are maintained via an exclusively phonological format, which should be similar for words and nonwords if matched for phonological familiarity and complexity (as was the case in the present study). In these conditions, lexico-semantic knowledge, distinguishing between words and nonwords, should only intervene at the moment of retrieval (Hulme et al. 1991; Schweickert 1993). Our results, by showing that word and nonword memoranda could be reliably distinguished in both phonological and lexicosemantic language networks, and this right from the moment of encoding, contrast with this prediction. We should however mention here that these findings do not rule out the possibility of redintegration mechanisms operating at the post-encoding and retrieval stages; our results simply show that the redintegration theory, in its original form, is not sufficient for accounting for the intervention of linguistic knowledge in WM. This is also consistent with behavioral evidence suggesting that stimuli with richer lexico-semantic content lead to more stable WM traces already at the moment of encoding (Savill et al. 2015).

These results provide novel and critical support for theoretical models considering that WM involves the temporary activation of LTM knowledge (Cowan 1995, 1999, 2001; Martin et al. 1996; Oberauer 2002; Nee and Jonides 2011, 2013; Majerus 2013, 2019) and, more precisely, the temporary activation of representations in the linguistic system (Martin et al. 1996; Martin and Saffran 1997; Gupta 2003; Acheson and MacDonald 2009; Majerus 2013, 2019). Furthermore, this study suggests that access of lexico-semantic knowledge occurs in a very direct manner, since neural patterns could already be decoded at the moment of encoding during the fast presentation, running span procedure preventing participants from implementing strategic processes. This result goes beyond previous studies which showed an involvement of semantic processing regions when participants were explicitly instructed to use a semantic or phonological strategy when encoding stimuli in WM (Fiebach et al. 2007; Lewis-Peacock and Postle 2012). Overall, our results strengthen the assumption that verbal WM is grounded within the LTM linguistic system, by showing that access to lexicosemantic knowledge occurs in a rapid manner in WM, as it does during language processing. Electrophysiological studies allowing a fine-grained investigation of temporal parameters suggest that lexical access occurs very rapidly during language processing (MacGregor et al. 2012). In agreement with these studies, we observed that lexico-semantic knowledge could be reliably decoded even in a very fast presentation paradigm. The grounding of verbal WM within the LTM linguistic system is also consistent with neuropsychological data showing that patients can show selective impairment for word or nonword stimuli in WM tasks, depending on whether their lesions involve parts of the ventral or the dorsal language pathway, respectively (Patterson et al. 1994; Martin and Saffran 1997; Majerus et al. 2007; Hoffman et al. 2009, 2012; Leff et al. 2009). Our data are also in line with repetitive transcranial magnetic stimulation studies, showing that inhibitory stimulation over the superior temporal gyrus leads to poorer WM performance for nonwords, but not

when stimulation is delivered over the middle temporal gyrus (Acheson et al. 2011). In the same vein, inhibitory stimulation over the left temporal pole leads to poorer performance for words, but not nonwords (Savill et al. 2019), suggesting that linguistic cortices determine WM performance.

Importantly, the searchlight analyses revealed that several regions systematically found in semantic processing tasks, the pars triangularis, the posterior middle temporal gyrus, and the angular gyrus (Binder et al. 2009; Lambon Ralph et al. 2017) reliably contributed to the distinction between word and nonword conditions during encoding and continued to do so over the maintenance period. This is a critical result since it shows that specific semantic processing regions represent the type of verbal stimuli during encoding and continue to do so when the stimuli further need to be actively maintained. In contrast, we found that two regions located in the superior temporal gyrus (i.e., a more anterior and a more posterior region) reliably represented the type of verbal memoranda during encoding but not during the maintenance phase. This result is in line with a previous study showing that perceptual neural regions in the superior temporal gyrus are not necessarily involved in WM maintenance (Yue et al. 2018). The two regions in the superior temporal gyrus identified by the searchlight analysis have been shown to contribute to the perception and phonological analysis of auditory–verbal stimuli, for the posterior region, and to access to word meaning for the anterior superior temporal region (Scott et al. 2000; Dewitt and Rauschecker 2012; Mesgarani et al. 2014; Arsenault and Buchsbaum 2015). On the other hand, the posterior middle temporal gyrus and the pars triangularis also involved in the maintenance phase have been shown to support semantic control (Hoffman et al. 2012; Lambon Ralph et al. 2017) and may be particularly solicited when processing words and nonwords in order to ensure selective activation of the accurate semantic representation for the word stimuli and inhibition of the not relevant semantic representations for the nonword stimuli. The precise role of the angular gyrus in semantic processing is less clear, but it might be involved in the integration of higher order semantic information (Binder et al. 2009).

It is also important to note that in this study word and nonword stimuli could be decoded in phonological processing regions, especially within the posterior part of the left superior temporal gyrus, despite the fact that the word and nonword conditions were equated on a number of important phonological variables. One possibility that could account for this result is that the lexical level of language representation is directly represented at the phonological level, for instance via lateral connection patterns between phonemes. It must be pointed out that there is, up to now, no consensus as regards the neural substrate of representation of lexical information. Indeed, more than two decades of neuroimaging studies have failed to find such a substrate (Mechelli et al. 1999; Binder et al. 2000; Newman and Twieg 2001; Kotz et al. 2002; Rissman et al. 2003; Xiao et al. 2005; Orfanidou et al. 2006; Gagnepain et al. 2008; Raettig and Kotz 2008; Takashima et al. 2014; Bakker-Marshall et al. 2018). Another possibility is that the lexical levels of representation are not explicitly represented within the phonological processing network, but that they are temporarily arise due to top–down feedback activations running from semantic levels of representation (where familiar words are represented in a permanent manner) to phonology (Patterson et al. 1994; Bullinaria 1995; Dilkina et al. 2010). Such top–down feedback processes have been documented in different language processing contexts (Hannemann et al. 2007; Sohoglu et al. 2012; Heald and

Nusbaum 2014; Leonard et al. 2016) and could potentially explain why neural patterns within phonological processing regions can differentiate between word and nonword stimuli while the two classes of stimuli are matched for all other, non-lexical phonological characteristics.

Contrary to the multivariate analysis, the univariate analysis did not result in any reliable differences between the word and the nonword conditions. This result may seem surprising, given that previous studies have consistently found specific neural regions associated with word and nonword processing when using direct univariate contrasts (Newman and Twieg 2001; Kotz et al. 2002; Rissman et al. 2003; Xiao et al. 2005; Orfanidou et al. 2006; Raettig and Kotz 2008; Sabri et al. 2008; Davis and Gaskell 2009), including more recent studies (Bechtold et al. 2019). However, these studies used lexical decision judgments requiring additional controlled processes. This is particularly problematic as word and nonword stimuli are not equivalent as regards their attentional requirement during decision-making, nonwords being more difficult to process. Studies have indeed shown that the same neural regions typically attributed to lexico-semantic processing can be elicited by nonword stimuli during lexical decision judgments, if low-frequency words are used instead of high-frequency words (Graves et al. 2016; Mattheiss et al. 2018). During passive listening, other studies have also found no reliable univariate differences between word and nonword conditions (Binder et al. 2000). In the light of these findings and those of this study, we argue that the word–nonword distinction may differ more at the level of quality of representations than at the level of neuroanatomical location. Nonwords may recruit the same neural regions as those involved in word processing, via automatic search for corresponding representations in lexico-semantic levels of representations (McClelland and Rumelhart 1981), resulting in increased activity peaks for both words and nonwords. However, the types of activity patterns within lexico-semantic processing areas will differ as only for words a corresponding representation can be eventually accessed and selected, and only multivariate analysis techniques can detect these differences in representational patterns.

A further important finding of the present study is that maintenance of word versus nonword stimuli could also be decoded based on neural patterns in IPS regions that have been associated in the past with attentional processes in WM tasks. In the visual WM domain, the role of the posterior intraparietal cortex in the representation of WM content is a highly controversial question (Linden et al. 2012; Albers et al. 2013; Emrich et al. 2013; LaRocque et al. 2016). While a number of studies suggest that the posterior intraparietal cortex is involved in attentional control processes and more precisely the representation of task set (Todd and Marois 2004; Majerus et al. 2010; Cowan et al. 2011), other studies have shown that not only visual features of memoranda, such as line orientations (Bettencourt and Xu 2015; Ester et al. 2015), objects features (Lee et al. 2013), abstract visual patterns (Christophel et al. 2012), and spatial locations (Peters et al. 2015) but also colors (Yu and Shim 2017) can be decoded from patterns in posterior IPS. This raises the important question of the role of the intraparietal cortex in WM: Is it merely involved in attentional and task control (Emrich et al. 2013; Majerus 2019), or does it also have a WM buffering function in which traces of memoranda are stored? The fact that neural patterns in IPS regions were able to decode word versus nonword memoranda in the present study focusing on verbal WM suggests that parietal regions also maintain at least

some characteristics of memoranda in verbal WM. On the other hand, the fact that identical IPS regions and neural patterns are consistently involved in both verbal and visual WM tasks (Majerus et al. 2010, 2016; Majerus 2019) reduces the likelihood of a modality-specific buffering function of the parietal cortex. A possible interpretation of these findings is that the IPS regions maintain information about general characteristics associated with the memoranda, such as the broad category of stimuli to be maintained as well as their processing requirements at the attentional level. A recent study has shown that the posterior IPS is indeed sensitive to both perceptual and attentional loads during WM encoding, which is likely to differ for word and nonword memoranda (Majerus et al. 2017).

Note also that in the present study, decoding of the linguistic condition was particularly weak in the IPS regions during the encoding phase. It could be argued that the IPS regions support a buffering function and that redintegration occurred within this buffer during the delay phase. However, it must be pointed out that neural decoding was also observed to some extent during encoding in the IPS. In addition, it is not clear whether the redintegration hypothesis considers that the IPS supports a buffering function or whether the phonological buffer is supposed to be located in a different region such as the supramarginal gyrus (Yue et al. 2018). A possible explanation is that the weaker decoding of stimulus condition within the IPS region reflects the fact that active maintenance was particularly difficult during the encoding phase of the running span task, participants often reporting to rely on a "passive listening" strategy (Bunting et al. 2006; Morrison et al. 2016). Overall, our results do not allow us to exclude a redintegration function of the IPS during maintenance. The critical finding of this study, however, is the decoding of linguistic content of memoranda in language cortices already during encoding in a fast encoding WM task, which is against the assumptions of redintegration-based models.

Conclusions

This study shows a nonstrategic involvement of linguistic cortices in lexico-semantic processing during verbal WM processing, providing critical support for theoretical statements assuming that verbal WM relies on direct activation of the linguistic LTM system and that this activation supports the representation of WM content.

Supplementary Material

Supplementary material is available at *Cerebral Cortex* online.

Notes

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