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Neural networks for short-term memory for order differentiate high and low proficiency bilinguals

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ABSTRACT

Short-term memory (STM) for order information, as compared to STM for item information, has been shown to be a critical determinant of language learning capacity. The present fMRI study asked whether the neural substrates of order STM can serve as markers for bilingual language achievement. Two groups of German–French bilinguals differing in second language proficiency were presented STM tasks probing serial order or item information. During order STM but not item STM tasks, the high proficiency group showed increased activation in the lateral orbito-frontal and the superior frontal gyri associated with updating and grouped rehearsal of serial order information. Functional connectivity analyses for order encoding showed a functional network involving the left IPS, the right IPS and the right superior cerebellum in the high proficiency group while the low proficiency group showed enhanced connectivity between the left IPS and bilateral superior temporal and temporo-parietal areas involved in item processing. The present data suggest that low proficiency bilinguals activate STM networks for order in a less efficient and differentiated way, and this may explain their poorer storage and learning capacity for verbal sequences.

Introduction

The factors underlying bilingual language acquisition remain a central issue of investigation in cognitive neuroscience despite the extensive research that has taken place. Most studies have focused on factors such as age of acquisition, quantitative and qualitative parameters of second language exposure and the question whether bilingual language acquisition leads to the development of language-type specific or language-type independent lexicons and neural substrates (e.g., Chee et al., 2004; De Bleser et al., 2003; Kim et al., 1997; Klein et al., 1999, 2006; Kovelman et al., 2008; Mahendra et al., 2003; Perani et al., 2003; Wartenburger et al., 2003). The aim of the present study is to treat bilingual language acquisition not as a special situation leading to potentially specific brain activation profiles relative to monolingual language acquisition, as has been the focus in most previous studies. Rather, we consider here individual differences in bilingual language acquisition in the light of individual differences in general cognitive factors underlying monolingual and bilingual language learning. Among these cognitive factors, short-term memory (STM) has been proposed as being a major determinant of lexical language acquisition, in both monolingual and bilingual populations. The present study explores the role of verbal STM as a determinant of bilingual language proficiency, by studying the variation of neural correlates for order and item STM as a function of lexical bilingual proficiency.

Many studies have shown a consistent association between performance on standard verbal short-term memory (STM) tasks such as digit span or nonword repetition and lexical language achievement measures. For example, STM performance at an early age predicts later native and second vocabulary knowledge in young children, and STM performance in monolingual adults correlates with tasks simulating the learning of a new vocabulary (e.g., Baddeley et al., 1988; Gathercole et al., 1992; Service et al., 1992). These data have led to the position that verbal STM capacity is causally related to lexical learning abilities in both monolingual and bilingual populations and that the phonological store and the articulatory

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rehearsal components posited by the phonological loop model (Baddeley and Hitch, 1974) are critical for the learning of new information (Baddeley et al., 1998). The phonological store is assumed to allow the creation of a temporary representation of the new word form to be learned while the rehearsal component refreshes the temporary representation by reintroducing it repeatedly in the phonological store. The more detailed and precise the temporary representation, the more likely this representation will be transformed to a stable long-term representation in the language system.

Early neuroimaging and neuropsychological findings provided supporting evidence for this position. First, neuropsychological studies have shown that patients with lesions in the left inferior parietal area display reduced verbal STM capacity associated with impaired new word learning abilities (e.g., Baddeley et al., 1988). Neuroimaging studies showed that the left lateral inferior parietal area (supramarginal gyrus) was specifically involved in verbal short-term storage tasks, and it was hypothesized that this region subtends the function of the phonological store component proposed in Baddeley and Hitch's (1974) framework (e.g., Paulesu et al., 1993; Salmon et al., 1996). A recent neuroimaging study with high and low proficiency bilingual participants showed that high proficiency bilinguals showed more extensive recruitment of anterior inferior prefrontal areas, and more specifically the left insula, during a short-term verbal storage task (Chee et al., 2004). These inferior frontal areas have been shown to be involved in subvocal rehearsal processes (Paulesu et al., 1993). These different studies suggest that inferior parietal and prefrontal areas involved in verbal STM tasks are related to language learning proficiency. By extension, neural networks of STM might serve as markers of bilingual proficiency, as has been proposed (e.g., Chee et al., 2004).

The aim of the present study is to investigate the proposed link between bilingual proficiency and neural markers of STM, in the light of contemporary theoretical views of STM and recent neuroimaging findings that have raised considerable doubts about the precise neural underpinnings of verbal STM. First, our understanding of the role of left inferior parietal areas during verbal STM processing has considerably evolved. Recent fMRI studies show that the anterior left intraparietal sulcus (IPS), rather than the lateral inferior parietal area, is most consistently activated in verbal STM tasks, and is the only inferior parietal area to show STM load dependency (e.g., Becker et al., 1999; Ravizza et al., 2004). The lateral inferior parietal cortex, most frequently impaired in patients with verbal STM deficits, has been shown to respond to phonological linguistic processing requirements rather than STM load (e.g., Majerus et al., 2005, 2006a,b,c; Martin et al., 2003; Wise et al., 1991; Zatorre et al., 1992). However, even the left IPS does not seem to be specific for verbal short-term storage as it appears to be evenly sensitive to visual STM load (Corbetta et al., 1993; Ravizza et al., 2004; Todd and Marois, 2004). In this context, it has been proposed that this area could exert a more general role of attentional focalization during both verbal and visual STM processing (Majerus et al., 2006a,b,c, 2007; Collette et al., 2005). Second, the relation between language proficiency, STM performance and its neural correlates is difficult to interpret since typical STM tasks also involve a considerable amount of language processing. Behavioural studies have shown that language knowledge is actively recruited during verbal STM tasks, as evidenced by a recall advantage for word lists as opposed to nonword lists in an immediate serial recall task, or by a recall advantage for words of high lexical frequency versus low lexical frequency (Gathercole et al., 1999; Hulme et al., 1991; Roodenrys et al., 1994). Neuroimaging studies have confirmed this, by showing that regions in the superior, middle and inferior temporal lobes, supporting phonological and semantic processes, are actively recruited during verbal STM tasks (e.g., Collette et al., 2001; Fiebach et al., 2007; Ruchkin et al., 1999). Hence, differences in neural substrates during verbal STM tasks observed between high and low proficiency bilinguals could be confounded by underlying differences in basic language processing abilities, which are also recruited during verbal STM processing. This argument could be partly applied to the results reported by Chee et al. (2004). They used unfamiliar words as stimuli in their STM experiment in high and low proficiency bilinguals. The main difference in activation between the two groups was observed in the insula. This area has been shown not only to support subvocal rehearsal during STM, but also to support the coordination of complex articulatory programs as needed during nonword processing (Ackermann and Riecker, 2004; Riecker et al., 2000). Hence, it could be argued that the high proficiency bilinguals in the study by Chee et al. showed higher activation in the insula not because of higher STM capacities but because of more efficient phonological processing abilities, which in turn will enhance processing and rehearsal of these stimuli in STM.

The present study investigated the link between neural markers of STM processing and bilingual proficiency, by using a methodology that has recently been shown to be able to achieve a separation of processes potentially specific to STM processes and those involving more general linguistic and attentional processes, and hence has the potential to achieve a clearer understanding of neural substrates involved during STM processing and their relation to interindividual differences in language learning capacity. This methodology involves the separation of the different types of information to be retained in verbal STM: item information concerning the phonological and semantic properties of the individual verbal items to be retained, and order information concerning the sequential order of presentation of the items within a list. Behavioural studies have shown that language knowledge affects primarily recall of item information relative to recall of order information (e.g., Poirier and Saint-Aubin, 1996; Saint-Aubin and Poirier, 2000, 2005). Recent theoretical models of STM also consider that storage of item information depends on temporary activation of the language network while storage of order information is supported by a specialized order processing and maintenance STM system, although models differ with respect to the precise implementation of this system (e.g., Burgess and Hitch, 1999, 2006; Brown, Preece and Hulme, 2000).

In line with this distinction between item and order information, Majerus et al. (2006a,b,c) compared brain activation in monolingual participants while they performed either a short-term serial order recognition task (e.g., does the order of two probe words match the order of the words within the memory list?) or a short-term item recognition task (e.g., do the probe words match the identity of the words within the memory list?). For both tasks, they observed an extensive fronto-parietal network centered around the left IPS, revealing a network typically observed during verbal STM tasks (Cairo et al., 2004; Chen and Desmond, 2005; Fiez et al., 1996; Majerus et al., 2003; Paulesu et al., 1993; Ravizza et al., 2004; Salmon et al., 1996). At the same time, regions in the fusiform gyri and the superior temporal lobe, associated with orthographic and phonological processing, were more activated during item recognition relative to order recognition. For the order condition relative to the item condition, greater activation was observed in the right intraparietal sulcus and the right superior cerebellum, which is associated with sequential, numerical and temporal processing during the processing of order information (Cabeza et al., 1997; Chochon et al., 1999; Desmond et al., 1997; Rao et al., 2001). This distinction was confirmed by functional connectivity analysis, showing that the left IPS was specifically associated with fusiform and temporal areas during the item STM condition and with right parietal and cerebellar areas during processing of order information. Thus item STM seems to be specifically associated with activation in language processing areas, while order STM is associated with areas involved in sequential and temporal analysis needed for processing order information. At the same time, the left IPS was activated across all conditions. Given that the same left IPS area was also activated across item and order conditions in a similar experiment using visual stimuli (Majerus et al., 2007), it has been suggested that the left IPS plays a more general, amodal role during STM tasks, such as attentional focalization to the types of information to be processed in the STM task (Majerus et al., 2007, 2008).

In sum, recent studies suggest that different networks are involved in verbal STM, (1) a serial order processing network linked to right IPS and cerebellar areas linked to sequential processing, (2) an item processing network closely linked to language processing areas, and (3) information-independent recruitment of the left IPS possibly involved in task-related attention. The specific focus of the present study was to determine which neural STM network is able to differentiate high and low proficiency bilinguals. The most critical test here was the relation between neural substrates for order STM and bilingual lexical proficiency. Recent theoretical models suggest that order processing is one of the main functions of a specialized STM system, and that order retention is causally involved in new word learning as it allows the ordered replay of new verbal sequences during the learning process, and hence increases the likelihood that the new sequence is transformed in a stable long-term memory representation (Gupta, 2003). Hence, if there is a specific causal connection between verbal STM and lexical bilingual proficiency, high and low proficiency bilinguals should specifically differ with respect to serial order STM networks. Behavioural studies have indeed shown that in monolingual children and adults, order STM measures (e.g., serial order reconstruction) but not item STM measures (e.g., single item delayed recall, item errors) are most consistently associated with existing vocabulary knowledge or new word learning performance (Majerus et al., 2006b,c). Furthermore, Majerus et al. (2008) observed that in bilingual speakers, serial order STM but not item STM was associated with new vocabulary learning performance, explaining up to 35% of variance in the new vocabulary learning task. On the other hand, finding group differences for item-specific STM networks in high versus low proficiency bilinguals would be in some sense trivial, given that item STM is supposed to rely at least partly on language processing neural substrates and hence group differences in these areas would mainly reflect the fact that high proficiency bilinguals have better language capacities rather than STM capacities.

The present study explored neural activation associated with order STM and item STM networks in German–French bilinguals, differing in second language lexical proficiency, by presenting order probe recognition and item probe recognition tasks for word sequences in their native language (German). The STM tasks used native language stimuli in order to measure basic order and item STM capacities as directly as possible, while avoiding any confounding effects at the level of stimulus processing that would have occurred if the stimuli had been presented in the second language, for which the participants differed in lexical proficiency. The tasks were very similar to those used by Majerus et al. (2006a,b,c) and implied the presentation of short lists of familiar words, followed by probe stimuli probing either order or item information. For the order condition, the probe stimuli consisted of two words of the list presented in the same order or the reversed order, relative to their order in the list (see also Marshuetz et al., 2000, for a similar procedure). In a first item condition, the probe stimuli consisted of the presentation of the same word twice, differing in 50% of trials from one of the target words by a single letter and phoneme. This was the purest item condition, given that detailed item STM representations had to be formed and to be compared to a single probe item (but presented twice in order to match the amount of visual information of the order probe condition). A second item condition was slightly more hybrid given that the probe stimulus was comprised of two different items and both had to be compared to the items of the stimulus list. This condition allowed us to check for any differences between the item and order conditions that might have been created by the fact that the probe condition necessarily implies the presentation of two different words while only one different word had to be processed in the first item condition.

Our working hypotheses were the following: (1) if serial order STM differentiates high and low proficiency bilinguals, group differences should be observed specifically during the order STM condition, involving a network centered around the left IPS and including the right IPS and superior cerebellar regions; (2) if item STM differentiates high and low proficiency bilinguals, group differences should be observed specifically during the item STM condition, involving item processing areas in the bilateral temporal lobes; (3) if information-independent STM processes, such as attentional control and rehearsal, differentiate high and low proficiency bilinguals, then differences should be observed in the left IPS and inferior prefrontal regions, and this across all conditions.

Methods

Participants

Twenty-two right-handed native German-speaking young adults, with no diagnosed psychological or neurological disorders, were recruited from the undergraduate student population of the French-speaking city of Liege. The participants originated from the German-speaking part of Belgium (Deutschsprachige Gemeinschaft Belgien) and had German-speaking parents, ensuring that they were raised in a mainly German-speaking environment. All participants had learned French as part of their obligatory primary and secondary education, starting to learn French at the same age (about 6 years of age) and for the same time (at least 12 years). At the time of the study, all were undergraduate students at an exclusively French-speaking tertiary higher education institution in Liege. This selection procedure ensured that all participants had equal pressure and opportunity to master French as a second language. The groups were divided in high and low proficiency bilinguals according to their performance on a productive vocabulary task, while matching the two groups on all other parameters (see Table 1). The productive vocabulary task was a selection of 48 pictures from the Snodgrass and Vanderwart (1980) drawings database, allowing us to measure naming (in German and French) for objects from the lowest to the highest lexical frequency ranges (German frequency mean and range: 68.44, 1–434; Baayen et al., 1995). Participants were also administered a questionnaire estimating the number of hours of extrascholar French exposure (e.g., occasional visits to French-speaking friends or French-speaking distant relatives) from infancy to the date of the study, as well as self-rated general French proficiency (on a scale ranging from 1 (very low proficiency) to 7 (like native language)) and self-rated French sentence processing proficiency independently of lexical knowledge (on a scale from 1 (telegraphic-style sentences, no syntax) to 6 (perfect sentences)). French and English productive phonological abilities were assessed via a French and German speaking psycholinguist who rated the correct responses in the productive vocabulary task for phonological clarity and deviancy (on a scale from 1 (all phonemes deviant) to 5 (all phonemes accurate)). General semantic processing abilities were assessed by a semantic category fluency in German task, requiring the participants to generate as many words as possible for concrete and abstract categories during 2 min for each category ('professions', 'personality traits', 'kitchen tools'). Furthermore, verbal and visuo-spatial STM performance was assessed using a German word span task (recall of auditorily presented sequences of increasing length containing words of unpredictable semantic category; this task had greater item STM requirements), a digit span task (recall of auditorily presented digit sequences of increasing length; due to the repeated sampling of the same digits, this task had greater serial order STM requirements) and the Corsi block tapping task (recall of visuo-spatial sequences of increasing length performed by the experimenter on a set of blocks fixed on a wooden base). Finally, general intellectual efficiency was measured using the Raven's standard progressive matrices (Raven et al., 1998). These assessments allowed us to form two groups differing in their level of French productive vocabulary and self-rated general French proficiency, while being matched on other variables (see Table 1). In order to achieve this, we divided the group by performing a median split on French vocabulary scores and we considered differences in extrascholar French exposure which slightly varied between participants. For each participant with a given vocabulary score and a given estimated amount of extrascholar French exposure in the low proficiency group, we chose another participant with the closest matched amount of extrascholar French exposure but higher vocabulary scores for the high proficiency group. Although this procedure led to a small degree of overlap in raw vocabulary scores between both groups, it actually ensured that the participants differed to a maximal extent at the level of second language lexical learning capacities. This was further confirmed by the administration of a task simulating new vocabulary learning for French-like nonwords: a list of four word–nonword paired associates was presented auditorily five times; the words were familiar German words and the nonwords obeyed to French phonotactics (e.g., Steinpilz – jezkol). After each presentation of the list, the participant was presented with the four German words and he/she had to recall each associated nonword. In a control condition, a list of four word–word paired associates was presented following exactly the same procedure, all words being familiar German words. This showed that the high and low proficiency groups actually differed with respect to learning capacities for new word forms.[1] Note also that there was a group difference for the digit span STM task, which had the greater sensitivity to serial order STM requirements relative to the word span task.

Table 1
Demographic, language and cognitive measures

	High proficiency	Low proficiency	*T* value[*] (probability)
N	11	11	
Age (years)	19.42 (±1.34)	19.62 (±1.21)	<1 (n.s.)
Gender	9 f	7 f	
Numbers of languages learnt	2.91(±.54)	2.91(±.54)	<1 (n.s.)
Onset of French education (years)	6 (±.00)	5.82 (±.60)	1.00 (n.s.)
Years of education in French	12.18 (±.60)	12.27 (±1.27)	<1 (n.s.)
Extrascolar French exposure (hours)	3404 (1248–6240)	3044 (1248–8320)	<1 (n.s.)
Self-rated general French proficiency	4.86 (±.77)	4.22 (±.51)	2.26 ($p<.05$)
Self-rated French sentence processing	4.64 (±.67)	4.73 (±.10)	<1 (n.s.)
French vocabulary	37.18 (±4.79)	31.81 (±6.23)	2.26 ($p<.05$)
German vocabulary	47.45 (±1.21)	47.45 (±1.04)	<1 (n.s.)
French phonological score	4.71 (±.13)	4.73 (±.18)	<1 (n.s.)
German phonological score	5	5	–
Semantic fluency	65.90 (±14.43)	64.45 (±16.99)	<1 (n.s.)
Raven's Standard Progressive Matrices	55.55 (±3.33)	54.09 (±3.61)	<1 (n.s.)
Word span	5.63 (±.50)	5.18 (±.87)	1.49 (n.s.)
Digit span	6.81 (±.56)	5.45 (±.35)	6.85 ($p<.01$)
Spatial span (Corsi)	5.55 (±.93)	5.18 (±.87)	<1 (n.s.)
Word–word paired associate learning	16.50 (±2.67)	16.17 (±2.63)	<1 (n.s.)
Word–nonword paired associate learning	10.90 (±1.95)	7.50 (±2.20)	2.17 ($p<.05$)

[*] $df=20$, except for the word–word and word–nonword paired associate learning tasks where $df=14$.

All participants gave written consent prior to inclusion in the study. The study was approved by the Ethics Committee of the Faculty of Medicine of the University of Liege and was performed in accordance to the ethical standards described in the Declaration of Helsinki (1964).

Task description

For each trial, the encoding phase consisted of the visual and sequential presentation of four German words (duration for each word: 900 ms), followed by a maintenance phase indicated by the display of a fixation cross (variable duration: random Gaussian distribution centered on a mean duration of 4500 ms). The retrieval phase consisted of an array of two German words ordered horizontally (see Fig. 1). Participants indicated within 3000 ms if the probe words were matching (by pressing the button under the third finger) or not (by pressing the button under the index) the target information in the memory list. In one condition (order), the participants judged whether the probe word presented on the left of the screen had occurred before the probe word presented on the

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[1] This task was administered as an a posteriori validation procedure of the group constitution procedure, after the collection of initial behavioural and neuroimaging data. Due to the administration of this task at a later time point, data could not be obtained for three participants in each group.

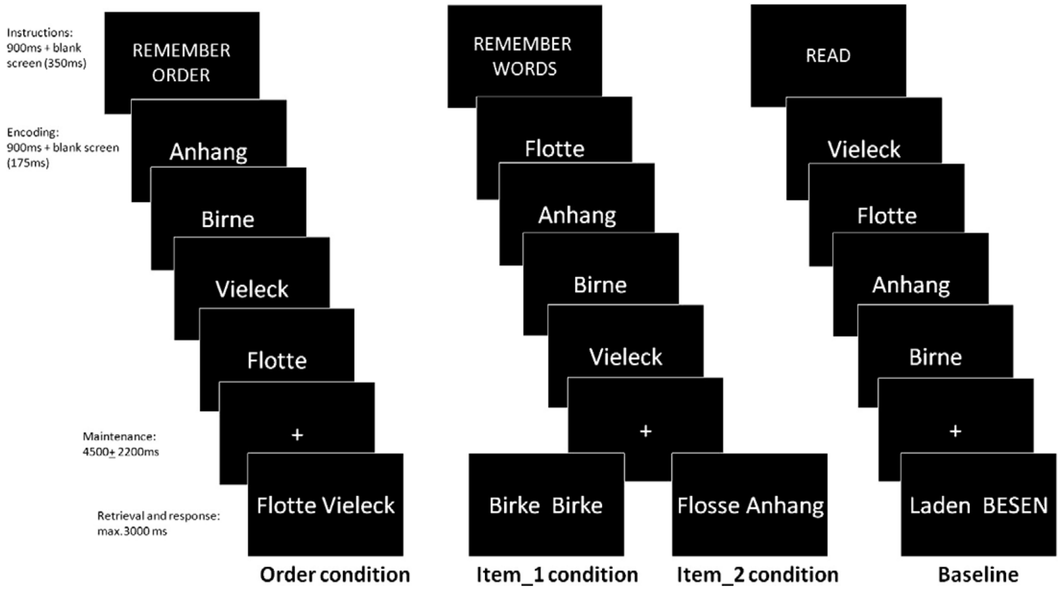

Fig. 1. Event sequences and timing for the experimental and baseline conditions. The figure depicts one negative trial for each condition. All words are German words.

right, relative to the order of presentation of the two words in the memory list. In a second condition, the participants judged whether the two probe words were identical to the words in the memory list; the two probe words where either twice the same word (item_1) or two different words (item_2). The words for the order, item_1 and item_2 lists were pseudo-randomly sampled from a pool of 60 bisyllabic concrete words. This pool consisted of 30 pairs of words that differed by a single phoneme and by a single letter, forming 30 minimal word pairs (e.g., Blume–Bluse, Schaufel–Schaukel). As in Majerus et al. (2006a,b,c), this enabled us to increase the difficulty of the two item STM conditions by constructing negative probes that differed only very minimally from the target word: negative probe trials consisted of the presentation of one member of the minimal pair in the memory list and the other member in the probe array (for the item_1 probe array, this distractor word was presented twice; for the item_2 probe array, this distractor word and one target word were presented; see Fig. 1). Mean lexical frequency was matched within the minimal word pairs: for the first and second words of the pairs, mean lexical frequency was 65.23 (range: 1–909) and 80.43 (range: 2–1020), respectively (Celex database, Baayen et al., 1995); all words were bisyllabic and counted exactly 5 phonemes. For the order condition, the probe trials always contained two adjacent words of the target stimulus list, but they were presented either in the same or the reversed order, like in Majerus et al. (2006a, b,c). Each of the 60 words of the stimulus set occurred exactly twice in each of the three STM conditions, with the restriction that the two words of a minimal pair could never occur together in the same trial, except for the negative probe trials in the item STM conditions where one word of the pair occurred in the target list and the other in the probe array. There were an equal number of positive and negative probe trials, probing all item positions equally. A baseline condition, controlling for perceptual, language and motor response processes not of interest to aims of the study, was used to match the experimental conditions in the sense that, for each trial, four different words, selected from the same pool of words as the items in the experimental conditions, were presented sequentially, followed by a fixation cross of variable duration, followed by the presentation of two new words written either in capitals or small font (see Fig. 1). The participants had to detect whether the two probe words were written in the same font. This condition exactly matched language processing requirements of the STM conditions given that the same amount of different verbal items had to be processed; however, none of the items nor their order had to be retained in STM since the instruction was to read the words and then to make the capital versus small font decision.

The three STM conditions and the baseline condition were presented in a single session, using an epoch-related design. There were 30 trials for each STM condition and 16 trials for the baseline condition. The different trials were presented in pseudo-random order, with the restriction that two successive trials of the same condition could not be separated by more than 6 trials of a different condition (i.e., by more than 90 s on average). The variable interval duration between the encoding and retrieval phases ensured minimal temporal autocorrelation between the encoding and retrieval phases and allowed us to measure brain activation for encoding and retrieval phases separately (Cairo et al., 2004; Majerus et al., 2007; Ollinger et al., 2001; see also below for further technical details). Before the start of a new trial, a brief instruction appeared on the centre of the screen informing the participant what type of information he/she had to retain (order trials: “remember the order”; item trials: “remember the words”; control trials: “read the words”). The duration of the inter-trial interval was also variable (random Gaussian distribution centered on a mean duration of 2000 ms). A practice session outside the MR environment, prior to starting the experiment, was implemented in order to familiarize the participants with the specific task requirements and presentation rate. In the practice session, the participants were presented at least 10 practice trials of each condition.

MRI acquisition

Data were acquired on a 3 T scanner (Siemens, Allegra, Erlangen, Germany) using a T2* sensitive gradient echo EPI sequence (TR = 2130 ms, TE = 40 ms, FA 90°, matrix size

$64 \times 64 \times 32$, voxel size $3.4 \times 3.4 \times 3.4$ mm^3). Thirty-two 3-mm thick transverse slices (FOV 22×22 cm^2) were acquired, with a distance factor of 30%, covering nearly the whole brain. Structural images were obtained using a T1-weighted 3D MP-RAGE sequence (TR = 1960 ms, TE = 4.4 ms, FOV 23×23 cm^2, matrix size $256 \times 256 \times 176$, voxel size $0.9 \times 0.9 \times 0.9$ mm). In each session, between 658 and 732 functional volumes were obtained. Head movement was minimized by restraining the subject's head using a vacuum cushion. Stimuli were displayed on a screen positioned at the rear of the scanner, which the subject could comfortably see through a mirror mounted on the standard head coil.

fMRI analyses

Data were preprocessed and analyzed using SPM5 software (Wellcome Department of Imaging Neuroscience, http://www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB version 7.0.4 (Mathworks Inc., Sherbom, MA). Functional scans were realigned using iterative rigid body transformations that minimize the residual sum of square between the first and subsequent images. The scans were screened for motion artefacts and all time series with motion exceeding 3 mm (translation) or 3° (rotation) were discarded; this resulted in the removal of the data of 2 participants not presented here. They were normalized to the MNI EPI template (voxel size: $2 \times 2 \times 2$ mm) and spatially smoothed with a Gaussian kernel with full-width at half maximum (FWHM) of 8 mm (in order to minimize noise and to assure that the residual images conform to a lattice approximation of Gaussian random fields).

For each subject, brain responses were estimated at each voxel, using a general linear model with epoch regressors. For each condition (order, item_1, item_2), separate regressors were defined to cover encoding and retrieval phases, permitting the modeling of phase specific STM-related brain activity. The encoding epoch regressor ranged from the time of the onset of each trial until the onset of the fixation cross of the maintenance interval; the retrieval epoch regressor ranged from the time of onset of the probe display until the participant's response. In order to explicitly model all STM-related brain activity, we also modeled the maintenance phase. Boxcar functions representative for each regressor and each STM condition were convolved with the canonical hemodynamic response. Due to unavoidable multi-collinearity between the maintenance phase and the two other STM phases, the maintenance regressor was orthogonalized relative to the other two regressors, attributing possible shared variance between the early maintenance phase and the encoding phase to the encoding regressor, and possible shared variance between the late maintenance phase and the retrieval phase to the retrieval regressor; the resulting orthogonalized but modified maintenance regressor was not further explored in the analyses reported here. The design matrix also included the realignment parameters to account for any residual movement-related effect. A high pass filter was implemented using a cut-off period of 128 s in order 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 (+white noise). On this basis, fourteen linear contrasts were performed. The first six contrasts looked for the simple main effect of order encoding, item_1 encoding, item_2 encoding, order retrieval, item_1 retrieval and item_2 retrieval, by comparing each condition to baseline activity. The eight remaining contrasts looked for the differential main effects between the different STM conditions, as a function of STM phase ([Order$_{\text{(encoding)}}$>Item_1$_{\text{(encoding)}}$]; [Order$_{\text{(encoding)}}$ > Item_2 $_{\text{(encoding)}}$]; [Item_1 $_{\text{(encoding)}}$ > Order$_{\text{(encoding)}}$]; [Item_2 $_{\text{(encoding)}}$ > Order $_{\text{(encoding)}}$]; Order $_{\text{(retrieval)}}$ > Item_1 $_{\text{(retrieval)}}$]; [Order $_{\text{(retrieval)}}$ > Item_2 $_{\text{(retrieval)}}$]; [Item_1 $_{\text{(retrieval)}}$ > Order $_{\text{(retrieval)}}$]; [Item_2$_{\text{(retrieval)}}$ > Order $_{\text{(retrieval)}}$]). The resulting set of voxel values constituted a map of t statistics [SPM{T}]. These summary statistics images were smoothed again (6-mm FWHM Gaussian kernel) in order to reduce remaining noise due to inter-subject differences in anatomical variability in the individual contrast images. They were then entered in a second-level analysis, corresponding to a random effects model, in order to account for inter-subject variance in each contrast of interest. One-sample t-tests assessed the significance of the effects separately for each group. Conjunction analyses assessed the commonality of activations in both groups (null conjunction; Friston et al., 2005). Two-sample t-tests assessed group differences for the different contrasts. As a rule, statistical inferences were performed at the voxel level at $p < 0.05$ corrected for multiple comparisons across the entire brain volume. Given that *a priori* knowledge was available about the potential response of a given area in our different STM conditions, a small volume correction (Worsley et al., 1996) was computed on a 10-mm radius sphere around the previously obtained coordinates for the corresponding locations of interest (see below for details).

We also investigated differential functional connectivity patterns between activity in the left IPS and distant brain regions involved in order STM processing, as a function of group membership. Using psychophysiological interaction, this analysis determined whether the correlations between activity in the left IPS and other brain regions during order STM differed across groups (Friston et al., 1997; Gitelman et al., 2003). The analysis was restricted to the encoding phase, given that the relatively short duration of the recognition regressor (less than 2 s on average) is suboptimal for this type of analysis. Two types of new linear models were constructed for each subject, using three regressors (plus the realignment parameters as covariates of no interest, as in the initial model). One regressor represented the STM condition of interest (order encoding) relative to the other conditions. The second regressor was the activity in the reference area. The third regressor represented the interaction of interest between the first (psychological) and second (physiological) regressors. Significant contrasts for this psychophysiological regressor indicated a change in the regression coefficients between any reported brain area and the reference region, in the order encoding condition. After smoothing (6-mm FWHM Gaussian kernel), these contrast images were then entered in a second-level (random effects) analysis. A one-sample t-test was performed to assess the functional connectivity pattern during order encoding for each group separately; two-sample t-tests determined between group differences in functional connectivity patterns for order encoding (voxelwise threshold, $p < 0.05$ corrected for whole brain volume, or small volume corrections at $p < 0.05$ for *a priori* locations of interest).

A priori locations of interest

The following *a priori* locations of interest were used for small volume corrections, based on published coordinates in the literature for verbal STM recognition tasks similar to those used in the present study. These regions concerned primarily the left IPS, bilateral premotor, dorsolateral prefrontal, inferior frontal, subcortical and cerebellar regions which are consistently activated in verbal STM recognition tasks. Other regions of interest concerned more specifically areas in the temporal lobe and inferior parietal lobule documented to underlie phonological, lexico-semantic and orthographic processing during item STM. Finally, the right IPS and the right superior cerebellum (area VI) were regions of interest for the order STM condition. All stereotactic coordinates refer to the MNI space. The *a priori* locations of interest were the following:

Order STM: right IPS [40, −42, 44; 44, −56, 44; 28, −50, 38] (Majerus et al., 2006a,b,c, 2007); cerebellum area VI [26, −58, −38; 18, −54, −22; 2, −78, −34] (Cairo et al., 2004; Majerus et al., 2006a,b,c, 2007)

Item STM: superior temporal gyrus/planum temporale [−54, −14, −2; 59, −33, 2; 44, −16, 16] (phonological/phonetic processing: Binder et al., 2000; Majerus et al., 2006a,b,c; Scott et al., 2000), fusiform gyrus [−32, −46, −12; −40, −55, −17; 30, −56, −8] (orthographic processing: Majerus et al., 2006a,b,c; Price et al., 1996), lateral inferior parietal cortex [−52, −27, 22; 68, −45, 26] (Becker et al., 1999; Majerus et al., 2007), inferior occipital gyrus [12, −94, −8] (Majerus et al., 2006a,b,c).

STM (general/encoding and retrieval): SMA [−12, −1, 61; 0, 18, 54] (Cairo et al., 2004; Majerus et al., 2006a,b,c); middle frontal gyrus [−50, 26, 32; 48, 34, 30] (Majerus et al., 2006a,b,c); lateral orbito-frontal cortex [−48, 44, 2; −48, 36, −22; −44, 4, 26] (Elliott and Dolan, 1999; Majerus et al., 2006a,b,c); insula [−32, 22, 0; 34, 22, −4] (Majerus et al, 2006a,b,c); left IPS [−38, −46, 50] (Majerus et al., 2006a,b,c, 2007); *Encoding phase:* middle frontal gyrus [−44, 4, 26] (Cairo et al., 2004; Majerus et al., 2006a,b,c); caudate [−16, 24, 18; 26, −34, −11] (Cairo et al., 2004; Chen and Desmond, 2005; Majerus et al., 2007); pallidum [−14, 0, −6] (Majerus et al., 2007; hippocampus [24, −34, −4] (Chen and Desmond, 2005) *Retrieval phase*: inferior frontal [−34, 18, −16] (Chen and Desmond, 2005; Majerus et al., 2007; Cairo et al., 2004); medial frontal [8, 38, 20] (Majerus et al., 2007); cerebellum [−36, −50, −26; 34, −44, −34] (Majerus et al., 2007).

Results

Behavioral data

A mixed ANOVA assessed response accuracy as a function of group and STM condition. The group effect, $F(1,20)=2.45$, $p=0.13$, the condition effect, $F(2,40)<1$, n.s., and the group × condition interaction, $F(2,40)<1$, n.s., were all non-significant, showing that task difficulty was matched across conditions and groups. Overall, response accuracy was high (greater than 81%; see Fig. 2 for details) and comparable to response accuracy levels obtained in previous studies for similar tasks. A similar mixed ANOVA was performed on reaction times. The group effect, $F(1,20)<1$, n.s., was not significant but there was a significant condition effect, $F(2,40)=66.55$, $p<.001$; the group × condition interaction was not significant, $F(1,20)=1.30$, n.s. (see Fig. 2 for details). A condition effect was expected here as in the item_2 and the order conditions, two different items had to be processed whereas in the item_1 condition, only one item (presented twice) had to be processed; furthermore, the order condition should lead to slower reaction times due to the recruitment of serial order scanning processes. Planned comparisons confirmed this showing significant differences between conditions item_1 and item_2, $F(1,20)=67.90$, $p<.001$, item_1 and order, $F(1,20)=93.28$, $p<.001$, and item_2 and order, $F(1,20)=31.50$, $p<.001$.

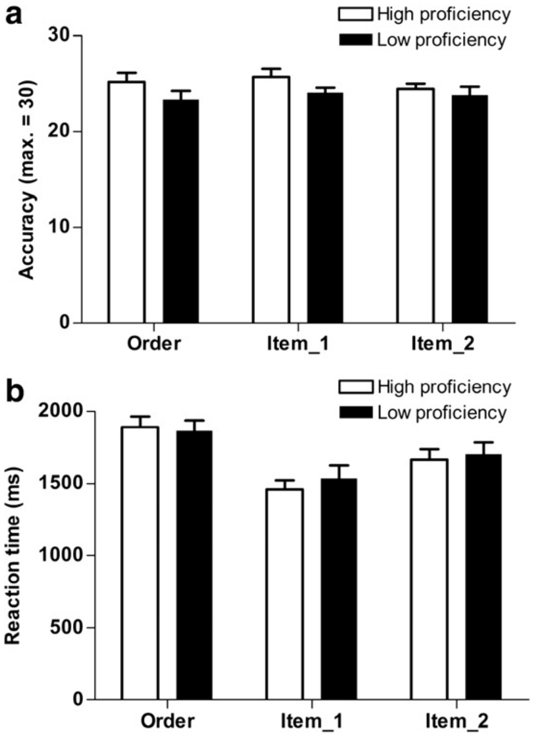

Fig. 2. Response accuracy and reaction times (mean, SEM) for the three experimental conditions, as a function of bilingual proficiency group.

Imaging data

Simple main effects — encoding

First, we assessed the one-sample *t*-tests looking at overall activation patterns for encoding during the three STM conditions, as a function of bilingual group. The commonality of activations across the two groups was further assessed via conjunction null analyses. Please note that for all analyses reported in this and following sections, all reported contrasts reflect brain activation relative to a linguistic baseline task. For the three STM conditions, both groups showed activation in insular, anterior cingulate/supplementary motor and hippocampal areas during encoding (see Table 2). During order encoding, additional activation was observed for both groups in a wider network of prefrontal areas including the left superior frontal gyrus, the left precentral gyrus (dorsal premotor cortex), the left inferior frontal cortex and the right middle frontal gyrus as well as the left IPS. Right IPS activation was also expected for this condition as it has been shown to be specifically involved in order STM, as noted earlier. However, only the high proficiency group showed significant activation in the right IPS. Overall, results for each group as well as conjunction analyses revealed that both groups showed expected fronto-parietal and prefrontal networks, during order and item encoding respectively, except for the right IPS during order encoding which was most consistently activated only in the high proficiency group. It should be noted that the networks involved in item encoding

Table 2
Maxima within regions showing BOLD signal changes in the different short-term memory conditions for the encoding phase, as a function of group (high or low proficiency bilinguals) ($p<.05$, corrected for whole brain volume, if not otherwise specified)

Anatomical region	High proficiency							Low proficiency					Conjunction				
	Vox.		*x*	*y*	*z*	*BA*	*Z*-value	Vox.	*x*	*y*	*z*	*Z*-value	Vox.	*x*	*y*	*z*	*Z*-value
Order																	
SMA/anterior cingulate	409	B	−6	22	42	6/32	5.67	127	−6	16	52	3.85*	368	−2	18	54	4.72
Superior frontal gyrus	333	L	−14	0	62	6	5.08	295	−6	8	62	4.57	408	−24	4	58	4.89
Precentral gyrus	250	L	−54	8	6	6	5.21						104	−52	10	14	3.97*
Inferior frontal gyrus	410	L	−48	8	34	44	4.36*	94	−44	6	28	3.94*	81	−46	6	32	3.76*
Insula	309	L	−40	20	−2		4.63*	301	−36	20	−6	4.56	472	−34	22	0	5.14
Middle frontal gyrus	138	R	54	36	30	9	3.99	71	40	44	28	4.57*	51	40	42	30	4.42*
Insula	439	R	38	22	−2		4.97	143	34	22	2	4.05	221	36	22	−2	4.94
Intraparietal sulcus (ant)	339	L	−40	−48	50		3.85	222	−30	−52	46	3.95	246	−38	−40	50	4.26
Intraparietal sulcus (ant)	139	R	40	-48	46		3.64*										
Hippocampus								214	30	−42	4	4.14	23	30	−44	4	3.46*
Caudate (tail)		L						47	−12	−30	18	3.66*					
Caudate (tail)		R						99	22	−38	14	3.96*	25	14	−24	20	3.66*
Pallidum	19	L	−12	0	−4		3.41*										
Pallidum	161	R	14	2	−4		4.60										
Cerebellum	287	B	2	−60	−16	IV	3.74						26	34	−58	−36	3.29*
	679	R	26	−64	−38	VI	3.83										
1-item																	
SMA/anterior cingulate	19	B	−4	16	58	6/32	3.23*	9	−6	14	60	3.37*	5	−4	20	52	3.20*
Insula	28	L	−28	24	−6		3.67*	24	−32	24	−2	3.30*	45	−32	22	−4	3.44*
Hippocampus								97	28	−42	8	4.04*	7	30	−42	6	3.33*
Cerebellum	67	R	30	−60	−34	VI	3.89*										
2-item																	
SMA / anterior cingulate	16	B	−6	14	54	6/32	3.18*	103	−6	14	60	3.74*	90	0	26	48	3.45*
Middle frontal gyrus						9		11	−46	30	24	3.30*					
Insula	11	L	−26	22	−4		3.42*	71	−30	24	−2	3.44*	85	−32	22	0	3.54*
Insula	41	R	34	24	−4		3.44*						12	34	24	−4	3.37*
Hippocampus								182	22	−36	18	4.18	5	14	−28	20	3.34*
Cerebellum	64	R	30	−60	−34	VI	3.76*										

Note that the contrasts reflect activity relative to a linguistic baseline task. All coordinates refer to MNI voxel space.
* Significant at $p<.05$ after applying small volume corrections (see Methods section for details).

were generally less extensive and did not include the left IPS in comparison to previous studies using a similar design (Majerus et al., 2006a,b,c, 2007). This was partly expected because the baseline condition of the present study provided a maximal control of language analyses and encoding processes in order to be able to study group differences in STM specific networks that are not related to underlying differences in basic language processing abilities. However, if item STM relies primarily on the activation of language representations and their attentional focalization (the latter aspect being subserved by the left IPS) as suggested in the Introduction, then the neural substrates underlying these processes will already have been captured to some extent by our more demanding control condition; in previous studies the control condition implied the presentation of the same word presented four times across all control trials while in the present study four different and new words had to be processed in each encoding control trial.

Simple main effects — retrieval

The *t*-tests for order, item_1 and item_2 retrieval revealed in both groups a broad network of activation encompassing the anterior cingulate, the bilateral inferior frontal gyrus close to the anterior part of the insula, the inferior occipital cortex and superior cerebellar areas, reproducing previous findings of retrieval related cortical activity (see Table 3). In addition, as expected both groups activated the right IPS during the order retrieval condition and fusiform areas involved in orthographic processing during both item retrieval conditions. Hence, both groups globally conformed to expected brain activation patterns for STM retrieval.

Differential group effects

Next, we performed the critical two-sample *t*-tests exploring group differences for the different STM conditions (contrasts: [Order$_{\text{(encoding – bil. high)}}$ vs. Order$_{\text{(encoding – bil. low)}}$], [Item_1$_{\text{(encoding – bil. high)}}$ vs. Item_1$_{\text{(encoding – bil. low)}}$], [Item_2$_{\text{(encoding – bil. high)}}$ vs. Item_2$_{\text{(encoding – bil. low)}}$], [Order$_{\text{(encoding – bil. high)}}$ > Order$_{\text{(encoding – bil. low)}}$] vs. [Item_1$_{\text{(encoding – bil. high)}}$ > Item_1$_{\text{(encoding – bil. low)}}$], [Order$_{\text{(encoding – bil. high)}}$ > Order$_{\text{(encoding – bil. low)}}$] vs. [Item_2$_{\text{(encoding – bil. high)}}$ > Item_2$_{\text{(encoding – bil. low)}}$]; voxelwise threshold, $p<0.05$ corrected for whole brain volume, or small volume corrections at $p<0.05$ for *a priori* locations of interest; see methods section for more details). As shown in Table 4, for STM encoding, group differences were observed only in the order encoding condition: high and low proficiency bilinguals showed different levels of activation in the bilateral lateral orbito-frontal cortex, the praecentral gyrus, the right temporo-parietal area and the right cerebellum. The interaction contrast [Order$_{\text{(encoding – bil. high)}}$ > Order$_{\text{(encoding – bil. low)}}$] > [Item_1$_{\text{(encoding – bil. high)}}$ > Item_1$_{\text{(encoding – bil. low)}}$] revealed a group by condition interaction for the left lateral orbito-frontal cortex. The directionality of this interaction was explored via an analysis of parameter estimates showing that this interaction reflected increased activation in the lateral orbito-frontal cortex

Table 3
Maxima within regions showing BOLD signal changes in the different short-term memory conditions for the retrieval phase, as a function group (high or low proficiency bilinguals) ($p<.05$, corrected for whole brain volume, if not otherwise specified)

Anatomical region	High proficiency							Low proficiency					Conjunction				
	Vox.		*x*	*y*	*z*	*BA*	*Z*-value	Vox.	*x*	*y*	*z*	*Z*-value	Vox.	*x*	*y*	*z*	*Z*-value
Order																	
Medial frontal/anterior cingulate	29	B	10	44	26	9/32	3.60*	402	6	40	28	3.78	146	8	42	26	3.57*
Orbito-frontal		L				11		160	−44	50	−6	4.11					
Orbito-frontal		R				11		539	42	58	−4	4.47					
Middle frontal gyrus		R				6		98	48	26	36	4.09*	69	42	28	40	3.34*
Inferior frontal gyrus	592	L	−36	18	−14	47	4.46	274	−38	18	−18	4.52	548	−36	20	−14	5.02
Inferior frontal gyrus	452	R	36	20	−16	47/45	4.96	406	40	24	−2	5.25	1019	32	20	−16	5.81
Insula	81	L	−34	18	−8		3.96*										
Insula	180	R	28	22	4		3.52*	282	28	26	4	3.38*					
Intraparietal sulcus (anterior)	90	R	52	−50	44		3.64*	406	44	−52	50	3.90	105	46	−52	48	3.40*
Lingual gyrus	450	R	18	−50	−10	19	5.39										
Inferior occipital cortex						18		352	−12	−96	−6	4.52		−12	−92	−10	5.07
Cerebellum	142	R	34	−60	−32	VI	4.12*							32	−60	−34	3.91*
	29	R	16	−46	18	V	3.88*										
	381	R	8	−76	−24	VI	4.41*	155	8	−76	−26	4.00*		8	−76	−26	4.36*
1-item																	
Medial frontal/anterior cingulate	8	B	6	42	26	9/32	3.21*	301	8	34	20	3.75	172	6	42	28	3.75*
Middle frontal gyrus		R				9/46		852	56	38	24	4.43					
Inferior frontal gyrus	513	L	−34	20	−14	47	4.34	382	−42	18	−18	4.10*	779	−34	22	−12	4.75
Inferior frontal gyrus	473	R	36	20	−14	47	4.77	433	36	20	−10	4.37	1121	34	20	−12	5.41
Praecentral gyrus		L				6		511	−46	−2	32	5.34	265	−42	−6	22	3.77
Praecentral gyrus		R				6		169	56	−6	24	3.83					
Superior temporal gyrus/planum temporale	406	L	−36	−16	12	22/41	4.27										
Fusiform gyrus	181	L	−24	−52	−12	37	4.30*	265	−34	−54	−18	3.95*					
Fusiform gyrus	359	R	20	−56	−8	37	4.70*	193	26	−58	−16	3.95*		28	−58	−18	4.71*
Inferior occipital cortex	502	L	−10	−70	−8	18	5.40	510	−4	−98	0	4.92		−10	−96	0	5.47
Inferior occipital cortex	515	R	16	−72	2	18	5.34	460	16	−94	−12	4.61*		14	−92	0	5.15
Cerebellum	354	L	−38	−48	−26	VI	4.42							−38	−50	−24	4.48*
	368	R	16	−54	−16	VI	5.04	364	36	−52	−30	4.44		34	−46	−32	4.14*
2-item																	
Medial frontal/anterior cingulate	337	B	6	38	46	9/32	3.95	446	8	36	44	3.78	461	6	38	44	4.32
Orbito-frontal						11		583	30	50	−10	3.89					
Middle frontal gyrus	227	R	34	10	42	9	4.14						841	42	16	40	3.97
Inferior frontal gyrus		L				44/45		360	−42	18	18	4.21					
Inferior frontal gyrus	367	L	−32	20	−14	47	4.92	414	−32	22	−10	4.97	916	−32	20	−12	5.87
Inferior frontal gyrus	435	R	38	28	−2	47	4.78	404	38	20	−4	4.97	1452	36	26	0	5.74
Postcentral gyrus	155	L	−28	−32	46	2/40	4.56										
Inferior parietal lobule		R				40		216	50	−42	28	4.00					
Intraparietal sulcus (posterior)	152	L	−22	−60	50		4.08	575	−26	−64	42	4.58	241	−26	−62	52	4.09
Intraparietal sulcus (anterior)	357	R						44	50	−48	44	3.72*	112	48	−50	50	3.76*
Fusiform gyrus	88	L	−34	−50	−20	37	4.07*	272	−46	−50	−20	4.02*		−34	50	−22	4.53*
Fusiform gyrus	158	R	26	−64	−12	37	3.58 *	143	32	−56	−18	3.87*		22	−50	−14	3.61*
Lingual gyrus	515	L	−10	−84	−6	18	5.12										
Cuneus	489	L	−6	−92	26	19	5.09										
Cuneus	467	R	6	−78	26	19	5.23							6	−76	26	3.98*
Inferior occipital cortex	51	L	−16	−94	−4	18	3.89	462	−2	−98	−0	5.07		−12	−92	−8	5.62
Inferior occipital cortex	413	R	12	−84	−8	18	4.53*	201	16	−98	−14	5.24		14	−94	−2	4.61*
Substantia nigra	231	L	−6	−24	−10		3.91										
Cerebellum	35	L	−28	−52	−34	VI	3.22*	343	−36	−54	−24	4.27*		−34	−50	−34	3.26*
	54	R	34	−44	−24	VI	3.50*	258	34	−52	−28	4.07*		32	−54	−30	4.29*

Note that the contrasts reflect activity relative to a linguistic baseline task. All coordinates refer to MNI voxel space.

* Significant at $p<.05$ after applying small volume corrections (see Methods section for details).

in the high proficiency group and only during order encoding (Fig. 3) [$F(1,20)=5.87$, $p<.05$; all other F's<1, n.s.]. Furthermore, there was a positive relationship between brain response in the lateral orbito-frontal cortex and the behavioural measures of new French-like vocabulary learning capacity (Fig. 3).

The same two-sample t-tests were performed for the retrieval phase at identical statistical thresholds (t-contrasts: [Order$_{\text{(retrieval – bil. high)}}$ vs. Order$_{\text{(retrieval – bil. low)}}$], [Item_1$_{\text{(retrieval – bil. high)}}$ vs. Item_1$_{\text{(retrieval – bil. low)}}$], [Item_2$_{\text{(retrieval – bil. high)}}$ vs. Item_2$_{\text{(retrieval – bil. low)}}$], [Order$_{\text{(retrieval – bil. high)}}$ > Order$_{\text{(retrieval – bil. low)}}$] vs. [Item_1$_{\text{(retrieval – bil. high)}}$ > Item_1$_{\text{(retrieval – bil. low)}}$], [Order$_{\text{(retrieval – bil. high)}}$ > Order$_{\text{(retrieval – bil. low)}}$] vs. [Item_2$_{\text{(retrieval – bil. high)}}$ > Item_2$_{\text{(retrieval – bil. low)}}$]. A similar picture emerged, the most reliable increases of activation being observed for the high proficiency group in the order retrieval condition, except for an increase in insular activation also in the item_2 condition (Table 5). During order retrieval, the high proficiency group showed higher activation relative to the low proficiency group in the posterior cingulate, the lateral orbito-frontal gyrus and the bilateral cerebellum. The interaction contrast [Order$_{\text{(retrieval – bil. high)}}$ > Order$_{\text{(retrieval – bil. low)}}$] > [Item_2$_{\text{(retrieval – bil. high)}}$ > Item_2$_{\text{(retrieval – bil. low)}}$] revealed a group by condition interaction in the bilateral superior frontal gyrus (supplementary motor area). The directionality of this interaction was explored

Table 4
Maxima within regions showing BOLD signal changes in the different encoding short-term memory conditions for high proficiency versus low proficiency bilinguals ($p<.05$, corrected for whole brain volume, if not otherwise specified)

Anatomical region	High proficiency > Low proficiency							Low proficiency > High proficiency				
	Voxels		*x*	*y*	*z*	*BA*	SPM {*Z*}	Voxels	*x*	*y*	*z*	SPM {*Z*}
Order												
Lateral orbito-frontal	41	L	−48	44	12	10	3.42*	/				
Lateral orbito-frontal	217	R	40	34	−12	11	4.03					
Praecentral	256	L	−10	−28	66	6	3.94					
Inferior parietal cortex/ temporo-parietal junction	224	R	68	−32	18	40	3.93					
Cerebellum	53	R	26	−56	−48	VI	3.83*					
1-item								/				
/												
2-item												
/								/				
Order > 1-Item												
Lateral orbito-frontal	94	L	−46	40	−20	11	3.82*	/				
Order > 2-Item												
/												
Item_1 > Order												
/								/				
Item_2 > Order												
/								/				

Note that the contrasts reflect activity relative to a linguistic baseline task. All coordinates refer to MNI voxel space.

* Significant at $p<.05$ after applying small volume corrections (see Methods section for details).

via analyses of parameter estimates, showing greater activation in the bilateral superior frontal gyrus in the high proficiency group relative to the low proficiency group, and this selectively in the order retrieval condition [$F(1,20)=5.73$, $p<.05$ for the left superior frontal gyrus; $F(1,20)=5.66$, $p<.05$ for the right superior frontal gyrus; all other Fs <1, n.s.]. There was no consistent relationship between brain response in these areas and new French-like vocabulary learning performance (Fig. 3).

Psychophysiological interaction

In order to further understand the group differences observed during order STM, a psychophysiological interaction analysis was conducted in each bilingual group, in order to determine whether each group showed the expected functional connectivity between the left IPS, the right IPS and the right superior cerebellum, based on previous studies by Majerus et al. (2006a,b,c, 2007) showing this network to be specifically involved in order STM encoding. As shown in Table 6 and Fig. 4, although both groups showed functional connectivity between the left IPS and right superior cerebellum, only the high proficiency group showed also functional connectivity between the left IPS and the right IPS. Furthermore, when directly comparing the groups, the low proficiency group showed differential functional connectivity with the left supramarginal gyrus, the right superior temporal gyrus and the right temporo-parietal junction. These regions have been shown to be associated with functional connectivity during item processing in Majerus et al. (2006a,b,c, 2007). Hence only the high proficiency group showed the expected network of bilateral intraparietal and right cerebellar areas while the low proficiency group showed less differentiated functional connectivity patterns during order encoding.

Discussion

The present study explored the relation between bilingual lexical proficiency and neural substrates of order and item STM networks, based on recent behavioural and theoretical studies which suggest that order STM is a particularly important determinant of lexical learning capacity. High and low proficiency groups activated expected fronto-parietal and fronto-temporal networks during encoding and retrieval of order and item information, which indicate a similar recruitment of general encoding and retrieval STM networks. At the same time, the low and high proficiency groups differed specifically for the order STM condition, with the high proficiency group activating to a larger extent the left orbito-frontal cortex during encoding and the bilateral superior frontal cortex during order retrieval. Psychophysiological interaction analysis for the order encoding condition further revealed that, contrary to the high proficiency group, the low proficiency group showed greater functional connectivity between the left IPS and superior temporal and lateral inferior parietal areas associated with item processing.

Do neural markers of order STM differentiate high and low proficiency bilinguals?

In this study, we had considered three factors possibly underlying differences in neural substrates for verbal STM in high and low proficiency bilinguals: (1) differences in serial order STM capacity, which should lead to differing activation patterns during the order STM condition in the right IPS and superior cerebellar areas associated with serial order processing; (2) differences in item STM capacity, which should lead to differing activation patterns during the item STM conditions in inferior and superior temporal areas associated with item processing; (3) differences in general STM capacity, as reflected by differing activation patterns in left IPS and prefrontal areas associated with attentional and executive control and rehearsal processes, and this during all STM conditions.

The results of the present study are most in line with the first hypothesis. Group differences were most consistently observed during the order STM condition, both at encoding and retrieval stages. High proficiency bilinguals activated to a larger extent the left orbito-frontal cortex during order encoding and superior frontal areas during order retrieval.

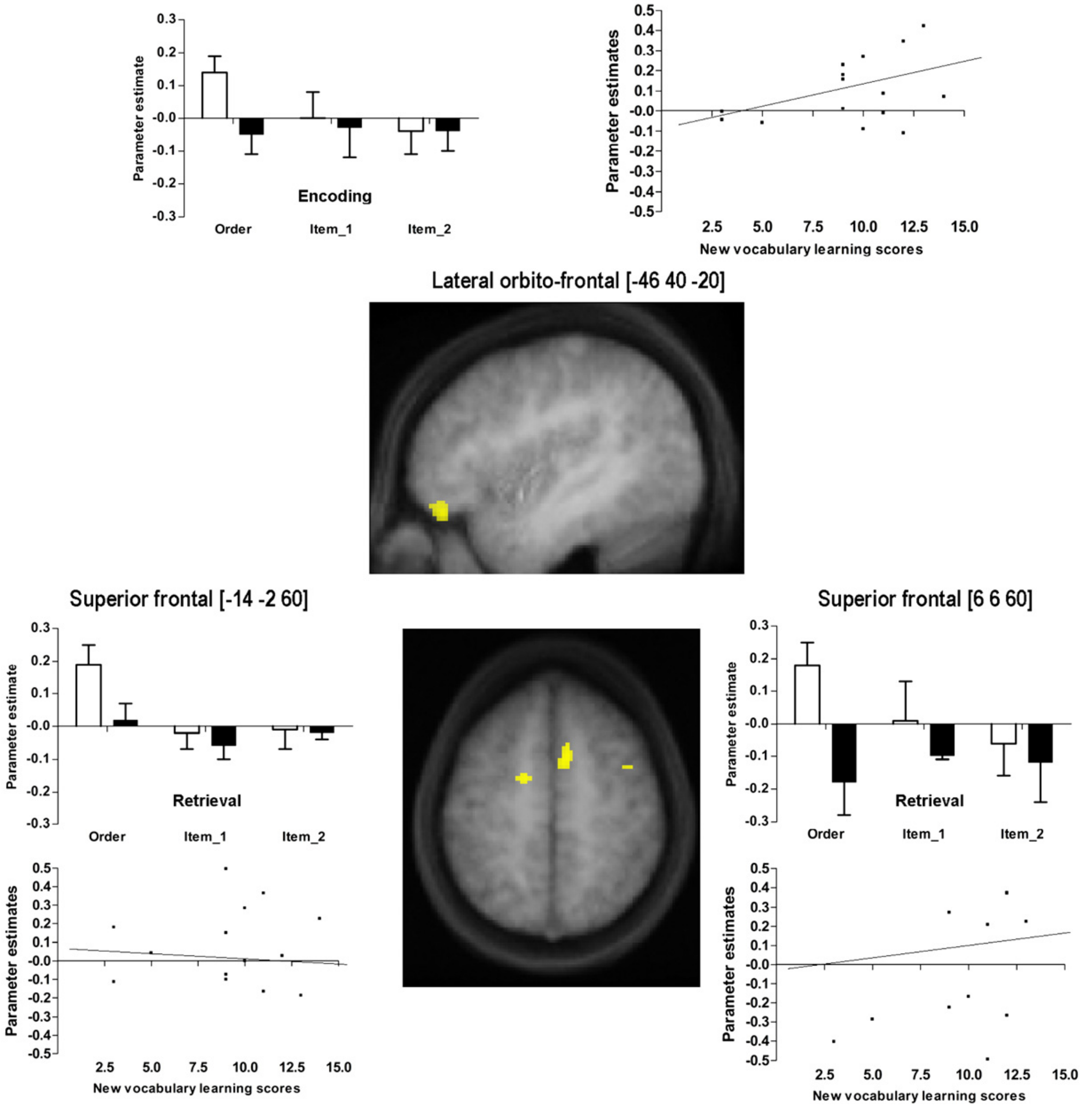

Fig. 3. Significant peak activation foci plotted on sections of an averaged T1 structural image of participant brains and parameter estimates of activation (mean, SEM), for areas showing a significant interaction with short-term memory condition and bilingual group. The figure also displays scatterplots of the relation between parameter estimates of the order encoding/retrieval conditions (both groups confounded) and performance on the new French-like word learning task; the correlations are .53 ($p<.05$, $df=15$), −.10 (n.s., $df=15$) and .12 (n.s., $df=15$), for the orbito-frontal, the left superior frontal and the right superior frontal areas, respectively. Results are shown at a statistical threshold of $p<.001$, uncorrected.

Lateral orbito-frontal areas have been shown to be involved in executive processes during working memory tasks, in particular during updating as compared to inhibition or shifting (Collette et al., 2005; Elliott et al., 2000). In the context of the present study, this suggests that the high proficiency group was possibly involved to a greater extent in updating processes, and this most specifically for the order STM condition. A larger recruitment of updating processes in the order condition, relative to the item condition, is likely given that for the order condition entire list and order information has to be retained and hence serial order information has to be updated after each new incoming stimulus; for the item condition, detailed processing of each individual item does not necessarily involve updating of the entire list information. Alternatively, this region has also been shown to be involved in grouping processes. Henson et al. (2003) observed that the right orbito-frontal cortex was selectively more activated for STM of sequential information presented in a grouped manner. Hence, the higher recruitment of this area could also reflect the explicit use of a grouped rehearsal strategy by the high proficiency group. The use of any of these strategies (controlled updating or grouped rehearsal) will lead to more efficient encoding of serial order information. The larger activation of superior frontal areas (part of supplementary motor areas) during order retrieval in the high proficiency group could also be involved in serial rehearsal and scanning of the target sequence information to be compared to the probe stimulus. In previous fMRI studies on item and serial order STM networks in monolingual participants, these areas have been shown to be specifically involved in the serial order STM conditions, possibly underlying grouped rehearsal processes (Marshuetz et al., 2000; Marshuetz, 2005; Majerus

Table 5
Maxima within regions showing BOLD signal changes in the different short-term memory conditions (retrieval phase) for high proficiency versus low proficiency bilinguals ($p<.05$, corrected for whole brain volume, if not otherwise specified)

Anatomical region	High proficiency > Low proficiency							Low proficiency > High proficiency				
	Voxels		*x*	*y*	*z*	*BA*	SPM {Z}	Voxels	*x*	*y*	*z*	SPM {Z}
Order												
Posterior cingulate	739	R	22	−22	38	31	4.86	/				
Lateral orbito-frontal	10	L	−50	36	−12	11	3.56*					
Cerebellum	516	L	−26	−40	−46	VI	4.74					
	371	R	4	−36	−14	III/IV	4.23					
1-Item								/				
/												
2-Item												
Insula	368	R	32	−4	22		4.02	/				
Order > 1-Item												
/												
Order > 2-Item												
SMA	39	L	−14	−2	60	6	3.62*					
SMA	198	R	6	6	60	6	3.60					
Item_1 > Order												
/								/				
Item_2 > Order												
/								/				

Note that the contrasts reflect activity relative to a linguistic baseline task. All coordinates refer to MNI voxel space.
* Significant at $p<.05$ after applying small volume corrections (see Methods section for details).

et al., 2006a,b,c, 2007). In sum, high proficiency bilinguals do not only recruit right IPS and right superior cerebellar areas shown to be essential for order STM processing, but they also activate other areas in superior and lateral orbito-frontal areas that contribute to more efficient order encoding via updating and grouped rehearsal processes of order information.

Furthermore, functional connectivity analysis showed that in the low proficiency group, the left IPS area, supposed to subtend attentional focalization during STM, was preferentially connected with right and left temporo-parietal areas during order encoding, relative to the high proficiency group. Previous studies have shown these areas to be associated with phonological analysis of item information and item STM (Martin et al., 2003; Majerus et al., 2002, 2005, 2007; Zatorre et al., 1992). Hence, the low proficiency group appeared to use less specialized and less differentiated order encoding processes, recruiting to a larger extent item analysis and encoding processes during order STM, relative to the high proficiency bilingual group.

Our results are less consistent with the second hypothesis. Relative to order STM, we observed no differences between high and low proficiency bilinguals in neural networks associated with item STM processing. However, it should be noted here that the baseline condition we used controlled for language processing components associated with item STM to a maximal extent. In contrast to previous work (e.g., Chee et al., 2004), we used this baseline in order to be able to reveal differences in STM-related neural processing between high and low proficiency bilinguals that cannot be accounted for by pre-existing differences in basic language capacity. However, this methodological precaution could have led to an overall diminished brain response in the item STM condition relative to the baseline condition if item STM is partly temporary language activation maintained by focused attentional processes, as discussed in the Introduction. We indeed observed overall lower brain activation in both groups for the item encoding conditions, relative to the order encoding condition. Hence, our study does not allow us to discard the existence of possible differences between high and low proficiency bilinguals for basic item-related language processing capacities, common to the baseline and item STM tasks used in this study (e.g., Masoura and Gathercole, 2005). We should note, however, that the aim of the present study was to specifically address the existence of STM-related neural differences in high and low proficiency bilinguals, and not differences in basic native language processes (although these were controlled for as far as possible via the language tasks used for the group matching procedure and via the baseline condition in the scanner). In sum, we assume that general STM neural substrates associated with item encoding, other than basic language activation, do not appear to be altered in low proficiency bilinguals. Furthermore, the item retrieval conditions yielded very broad activation patterns, comparable to those of the order retrieval condition. Critically however, no group differences were observed for brain activation associated with the item retrieval condition.

Finally, the last hypothesis considered the existence of bilingual proficiency group differences in general STM processes, independent from processes specific to item and

Table 6
Maxima within regions correlating with BOLD response in the left intraparietal sulcus during encoding of order information in STM, as a function of group (high versus low proficiency bilinguals) ($p<.05$, corrected for whole brain volume, if not otherwise specified)

Anatomical region	Voxels		*x*	*y*	*Z*	*BA*	SPM {*Z*}-value
High proficiency							
Intraparietal sulcus (post)	21	R	20	−60	50		3.18*
Cerebellum	88	R	36	−62	−42	VI	3.24*
Low profiency							
Cerebellum	22	R	40	−54	−46	VI	3.51*
High > Low							
/							
Low>High							
Superior temporal gyrus/ planum temporale	93	R	46	−18	14	22	3.57*
Temporo-parietal junction	22	R	66	−30	4	22/40	3.56*
Supramarginal gyrus	25	L	−62	−24	24	40	3.51*

All coordinates refer to MNI voxel space.
* Significant at $p<.05$ corrected for small volume (see Methods section for details).

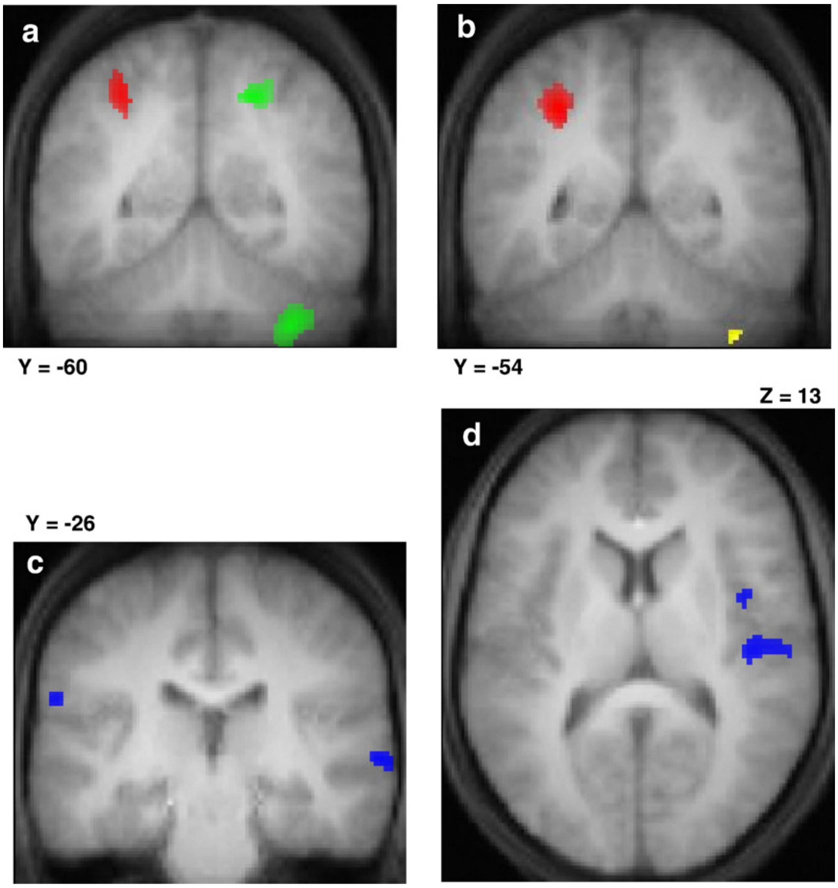

Fig. 4. Horizontal, sagittal and coronal sections depicting activation in the left intraparietal sulcus (in red) and regions that are functionally connected to this region during order encoding in the high proficiency group (in green, panel a), in the low proficiency group (in yellow, panel b) and regions showing greater functional connectivity with the left IPS in the low proficiency group relative to the high proficiency group (in blue, panels c and d). Results are shown at a statistical threshold of $p<.001$, uncorrected.

order storage. A target region here was the left IPS which has been proposed to play a general role in task-related attention during STM tasks, as well as during other tasks involving task-related attention (Iidaka et al., 2006; Majerus et al., 2007; Muller et al., 2003; Todd and Marois, 2004; Todd et al., 2005). No group difference was observed for activation in the left IPS. However, we should again remain cautious here as the left IPS was only activated in the order encoding condition, but not during the item encoding conditions at selected statistical thresholds. Again, the lack of activation in the latter conditions is most probably related to the attentional processing requirements already recruited in the baseline condition. As such, we cannot exclude the possibility that there are differences in basic attentional focalization processes that could affect STM processing in high and low proficiency bilinguals. On the other hand, general activation patterns in insular, cerebellar and anterior prefrontal areas associated with encoding, retrieval and general rehearsal stages across all STM conditions were similar in the two groups, showing that both groups did not differ with respect to these general STM processes.

Relations between neuroimaging findings, serial order STM capacity and bilingual lexical proficiency

The present study shows that the neural network underlying serial order STM in the low proficiency bilingual group appears to be less specialized and differentiated, leading to less efficient processing of serial order information in STM. Hence we might also expect poorer order STM performance at the behavioral level in the low proficiency group of this study. With respect to the behavioural results obtained for the task performed in the scanner, no group differences were observed, for neither the serial order nor the item STM tasks. This was to some extent expected given that the tasks had a relatively low memory load (four order positions or four items to be retained) in order to achieve high levels of accuracy in both groups; this reduces noise in brain activation profiles that could be caused by task difficulty differences between groups (see also Chee et al., 2004, for similar behavioural results). On the other hand, for the tasks performed outside the scanner, both groups differed significantly for the digit span task which had the greater serial order retention requirements as the same digits were presented repeatedly and the positions in which they occurred had to be memorized (see also Majerus et al., 2006a,b,c, 2008). We observed no group differences for the word span task, which had higher item retention requirements because the words to be retained were sampled from random semantic categories that could not be predicted in advance. However, a post-hoc error analysis for the word span task showed a group by error type interaction: high proficiency bilinguals showed a higher amount of item errors relative to order errors, as expected, while the low proficiency group showed a higher amount of order errors relative to item errors.[2] At the same time, both groups differed in their level of second language knowledge and new word learning capacity, while being matched for native vocabulary knowledge and general non-verbal cognitive efficiency. Furthermore, we observed a positive correlation between performance on the new vocabulary learning task and the level of activation in inferior frontal cortices that differentiated high and low proficiency groups during order encoding. In light of these conjoined neuroimaging and behavioural results, we submit that the differences observed for neural substrates of serial order processing in high and low proficiency bilinguals are the neuroanatomical counterpart of behavioural differences observed in serial order STM capacity and new word learning capacity.

The nature of the observed brain activation differences is also consistent with theoretical models of the relation between serial order STM processes and new word learning. According to one of the most precise models with respect to this issue (Gupta, 2003; Gupta and MacWhinney, 1997), the purpose of a specialized serial order STM component is to encode the order of presentation of language stimuli and to reactivate the stimuli in the language system in their correct order during rehearsal. The same mechanism is supposed to ensure the encoding and serial rehearsal of order information at the list level, that is, the order of words in a list) and the sublist level, that is, the order of phonemes of an unfamiliar word, although the order of phonemes additionally will be constrained by sublexical phonological knowledge about possible and frequent phoneme associations in a given language (i.e., phonotactic knowledge). The order STM trace allows reactivating lexical items and their underlying phonological representation, thereby rehearsing the temporary lexical representation for a new word form, and hence increasing the likelihood that it will be accurately encoded as a stable long-term memory representation in the language system. Thus in this model, the vector of the causal relation between serial order STM and new word learning is represented by serial rehearsal processes. The areas more activated in the high proficiency group during order STM were indeed inferior and superior frontal regions associated with grouped sequential rehearsal processes.

In this sense, our results agree with Chee et al. (2004) who argued that high and low proficiency bilinguals could be differentiated during a general verbal STM task in inferior frontal and insular regions associated with subvocal rehearsal processes. However, our study shows that this is specific to the processing and rehearsal of serial order information, a memory function that was not controlled by Chee et al.

It must be noted that differences in inferior frontal cortex are frequently observed between high and low proficiency bilingual groups, and this also outside the context of STM tasks. For example, Kovelman et al. (2008) observed that Spanish–English bilinguals showed greater recruitment of the left inferior frontal cortex (area 45; $x=-48$, $y=38$, $z=-4$) when judging English sentences, relative to monolingual English speakers; this region was very close to the left orbito-frontal cortex differentiating high and low proficiency bilinguals in the present study. Similarly, Klein et al. (2006) observed larger activation of the insular cortex and the ventral premotor area when English–French bilinguals who had acquired French after the age of 5 had to repeat French words rather than English words. Similar differences in the inferior frontal cortex were observed for lexical processing of English words in native Russian speakers with later acquired, and less proficient, English (Marian et al., 2003; see also Dehaene et al., 1997; Kim et al., 1997; Weber-Fox and Neville, 2001; Yokoyama et al., 2006, for related results for sentence comprehension and listening-to-stories tasks). Although the tasks used in these different studies were quite diverse and the interpretations provided were equally variable, we must note that all required passive listening to sequences of verbal information and hence also recruited item and order STM capacities. While the studies interpreted the bilingual proficiency-related differences in inferior frontal and prefrontal areas as reflecting special neural substrates for processing a second language, an alternative interpretation could be provided in the light of the data obtained in our study: less proficient bilinguals will process the second language in a less automized and efficient manner, needing the information to be stored and rehearsed for a longer duration, the time the less efficient language analysis and comprehension processes are completed. Hence differences in inferior prefrontal activation observed in previous studies could also reflect the greater serial rehearsal demands when less proficient bilinguals have to process second language information. Furthermore, as our study shows, levels of bilingual language proficiency eventually attained, all other parameters relative to language exposure and age of acquisition being controlled for, depend on the efficiency with which these serial rehearsal processes can be recruited. With respect to the present study, we can also affirm that the differences in inferior frontal cortex were not related to the recruitment of special neural correlates for second language processing given that the STM task was administered in the native language of the participants.

Finally, this study has implications not only for bilingual learning, but also for any lexical language learning situation, including monolingual speakers learning native vocabulary. As mentioned before, our participants were tested on order and item STM tasks for their native language and hence the differences in neural substrates for STM processing are not specific to storing second language information. Furthermore, we showed that these differences correlated with an experimental task providing a direct measure of new vocabulary learning performance. Hence this study shows the universal importance of order STM and its neural substrates for lexical language learning more generally. This is also in line with a recent behavioural study we conducted in English–French bilinguals learning a new vocabulary sharing French phonological characteristics: serial order STM capacity explained up to 30% of variance in new vocabulary learning performance, after accounting for the influence of existing French phonological knowledge and item STM capacity (Majerus et al., 2008). The present study also extends earlier studies that showed close relations between order STM measures and vocabulary learning in monolingual children and adults (Majerus et al., 2006a,b).

In sum, the present study highlights the special status of serial order STM capacities and their neural substrates as a factor associated with group differences in bilingual lexical proficiency. The neuroanatomical differences we have observed are consistent with theoretical models lending a specific importance to sequential rehearsal processes during

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[2] High proficiency group, order errors = 3.27 (+2.05), item errors = 5.27 (+4.45); low proficiency group, order errors = 5.00 (+2.23), item errors = 3.09 (+1.45); $F(1,20)=4.71$, $p<.05$.

STM as mediating the learning of new sound sequences. However, future studies should try to determine whether these differences are related to constitutional biological factors or to strategically controllable factors whose efficiency could be improved by remediation procedures.

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