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Spatiotemporal Dynamics of Bilingual Word Processing

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Abstract

Studies with monolingual adults have identified successive stages occurring in different brain regions for processing single written words. We combined magnetoencephalography and magnetic resonance imaging to compare these stages between the first (L1) and second (L2) languages in bilingual adults. L1 words in a size judgment task evoked a typical left-lateralized sequence of activity first in ventral occipitotemporal cortex (VOT: previously associated with visual word-form encoding), and then ventral frontotemporal regions (associated with lexico-semantic processing). Compared to L1, words in L2 activated right VOT more strongly from ~135 ms; this activation was attenuated when words became highly familiar with repetition. At ~400ms, L2 responses were generally later than L1, more bilateral, and included the same lateral occipitotemporal areas as were activated by pictures. We propose that acquiring a language involves the recruitment of right hemisphere and posterior visual areas that are not necessary once fluency is achieved.

Introduction

More than two-thirds of the global population is proficient in more than one language, yet we do not understand how the brain organizes and processes multiple lexicons. Language processing has been studied extensively in monolingual populations, and it has been shown that for written words, over the course of ~1000 ms, there are multiple stages subserved by different cortical regions and networks that are strongly lateralized to the left hemisphere. For single words out of context, early sensory processing occurs in bilateral primary visual cortex ~100 ms after the word is shown. Before ~200 ms, the information is encoded as words in a particular language in an extended network of regions that receive modulated input from an area of left ventral occipitotemporal cortex (VOT) centered on the fusiform gyrus (McCandliss et al., 2003). While VOT's exact functions in word reading are unknown (Price and Devlin, 2003), the region appears to be a crucial early-stage area for successful visual word encoding,

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which is influenced by both orthographic and lexical manipulations (Miozzo and Caramazza, 1998; Pugh et al., 2001). Finally, lexico-semantic processing is thought to occur at ~400 ms in a network of left fronto-temporal regions including anterior temporal and inferior prefrontal cortex (Halgren et al., 1994b; Marinkovic et al., 2003; Patterson et al., 2007).

Do bilinguals recruit the same left lateralized network for visual word processing? How early does the brain distinguish the language of word presentation? Does the information maintain the posterior-to-anterior flow from early to late processing stages in both languages? During the early visual word encoding stage (~130–200 ms), it has been suggested that the two languages rely on at least partially distinct neural systems, however it is unclear whether areas such as VOT are recruited in both the first (L1, or the language that was first acquired) and second (L2) languages to the same extent (Ohno et al., 2002; Proverbio et al., 2002). Furthermore, the conditions under which L2 recruits additional regions during this early time period are not well characterized.

Later lexico-semantic processing stages have been studied more extensively in bilingual populations. It has been demonstrated behaviorally using lexical decision and other priming paradigms that L1 and L2 are not completely isolated from one another, with both interfering and reinforcing effects having been observed (Costa and Santesteban, 2004; Gollan et al., 2002; Potter et al., 1984; Silverberg and Samuel, 2004; Thierry and Wu, 2007). Yet the existing neuroimaging literature on bilingual lexico-semantic representation is inconclusive and contradictory with respect to how the brain represents the two languages (Indefrey, 2006; Simos et al., 2005). Some studies using functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) have found distinct neural representations for L1 and L2 within the classical left hemisphere language regions (Kim et al., 1997; Marian et al., 2007b; Perani et al., 1998). In studies that specifically examined lexico-semantic processes in bilinguals, in the less proficient language, the left posterior middle frontal gyrus, left inferior frontal gyrus, left anterior cingulate gyrus, and left posterior inferior parietal lobule all show greater activity that is modulated by L2 proficiency (Chee et al., 2001; Xue et al., 2004). In contrast, other studies have found that cortical activation for L1 and L2 is located in identical regions of the left hemisphere (Chee et al., 1999; Illes et al., 1999; Klein et al., 1995; Nakada et al., 2001; Tan et al., 2003).

Though such inconsistencies are likely due in part to different methodologies, subject populations, and tasks being used among studies, it is also the case that the hemodynamic signals (blood flow and oxygenation) that are measured by fMRI and PET indirectly reflect neuronal activity. Because the hemodynamic response is slow (on the order of several seconds), these studies neglect significant information about the temporal dynamics of language processing, which may be critical for isolating brain regions that subserve specific processing stages, including early sensory, visual word encoding, and late lexico-semantic responses.

Other studies have used electroencephalography (EEG) to investigate the temporal dynamics of bilingual lexico-semantic processing, and have found that a negative-going event-related potential (ERP, which is derived from the stimulus-locked EEG signal) known as the N400 is delayed in the less proficient L2 compared to L1 (Alvarez et al., 2003; Ardal et al., 1990; Hahne, 2001; Moreno and Kutas, 2005; Phillips et al., 2006). The N400 (and its magnetic counterpart, N400m) has been used as a measure of linguistic processing, since it has been shown to vary its amplitude and latency in relation to the degree of difficulty of contextual integration, stimulus frequency, and stimulus repetition (Kutas and Federmeier, 2000). The differences in N400 latency that have been found in bilingual populations suggest that at the very least, L1 and L2 are processed on different time scales in the brain. However, the poor spatial resolution inherent to EEG makes it difficult to determine whether these temporal differences are localized within common brain areas or whether longer latency N400 responses are related to the recruitment of additional regions in the less dominant language.

In addition to identifying distinct stages in bilingual language processing, we sought to expand the focus of the late lexico-semantic stage beyond the classical left hemisphere frontal and prefrontal regions. There is reason to suspect that when a speaker is not as proficient in L2 compared to the native language, the locations of all or some of the representations may be different (Perani et al., 1998; Silverberg and Samuel, 2004). In the present study, we hypothesized that in addition to a shared left fronto-temporal substrate, L2 learners would show significant activity in right hemisphere (Dehaene *et al.*, 1997) and other areas in the less proficient second language. It has been suggested previously that the right hemisphere's specialized functions may aid both first and second language learners by providing an additional level of analysis when processing stimuli is more difficult (Goldberg and Costa, 1981; Goldberg et al., 1978; Seliger, 1982). Furthermore, studies of child L1 acquisition have shown that bilateral posterior visual processing areas including lateral and ventral occipitotemporal cortex are more active in children than in adults (Brown *et al.*, 2005; Schlaggar *et al.*, 2002). We sought to examine whether these regions are more active in the non-dominant L2, even though the bilingual individuals in this study had already attained fluency in one language.

The primary aim of this study was to provide a novel perspective on bilingual word processing by examining both early (~150 ms) and late (~400 ms) stages in L1 and L2 with high spatiotemporal accuracy. We used a multimodal imaging approach, which combines magnetoencephalography (MEG) and high-resolution structural MRI to obtain a detailed spatiotemporal picture of dynamic brain activity. MEG is generated principally by the current flows within the apical dendrites of cortical pyramidal cells that result from synaptic and other active transmembrane currents (Cohen and Halgren, 2009). To localize the sources in the cortex, we applied a noise-normalized cortically-constrained minimum norm inverse solution known as dynamic statistical parametric mapping (dSPM) (Dale et al., 2000; Dale and Sereno, 1993). Although source estimation from MEG or EEG is always uncertain, this method has been shown to produce results that are consistent with intracranial recordings of local field potentials during language tasks (Halgren et al., 1994a; Halgren et al., 1994b; Marinkovic, 2004). dSPM provides maps of event-related cortical activity with millisecond temporal resolution and spatial resolution of about a centimeter.

Eleven adult Spanish-English bilingual participants who began acquiring English around age six, but who consider themselves more proficient in their native Spanish, viewed single visually presented concrete nouns in each language and simple line drawings and made size judgments about the stimuli while whole-head high-density MEG signals were recorded. N400m-like responses were evoked using a repetition priming paradigm, in which some of the stimuli were repeated throughout the experiment, and were interspersed with novel stimuli that were seen only once. This classical N400 manipulation allowed us to vary the ease with which subjects processed words in both languages (specifically during lexico-semantic processing), thereby permitting us to examine whether hypothesized differences in right hemisphere and bilateral visual areas related to proficiency in the non-native language.

Materials and Methods

Subjects

Eleven healthy right-handed adults (3 males, age range 18–29 years, mean 21.42 ± 3.00 years) participated in this study. Participants reported no history of psychological or neurological impairment, and all had completed at least some college. All were native Spanish speakers and were sequential L2 English learners, although they began acquiring English early in life when they entered school (mean age of acquisition = 5.83 years, SD = 2.17 years). We selected this group because these subjects are likely to be homogeneous in terms of proficiency, and they have had significant experience with both languages. Therefore, any neural differences are likely to be chronic and fundamental, rather than passing or nonspecific effects of incomplete learning. Language history and proficiency in both languages were assessed by a detailed questionnaire that asked subjects to rate learning sources and degrees of exposure to each language, and their reading, writing, and speaking abilities in each language (adapted from (Marian et al., 2007a). L1 is defined as the language that was acquired first, however these subjects also considered L1 to be the dominant language.

On a scale from 1–10, all subjects rated their abilities in both languages between 7 and 10, so they can be considered proficient speakers in both languages. With one exception, all participants rated their L2 abilities lower than their L1 abilities, which was also confirmed by ten subjects reporting that they would always choose to speak in their native language (Spanish) if given a choice. All but one participant indicated that they began reading in L1 prior to L2, and five subjects rated their L1 reading abilities (mean = 9.0) higher than their L2 reading abilities (mean = 8.6), while two subjects rated L1 and L2 reading skills at the same level, and three subjects rated L2 better than L1 (one subject’s self assessment scores were lost). Seven subjects responded that they would choose to read in L2 at least as often as in L1. All but two subjects reported using L2 more on a daily basis as adults, and every subject indicated that he or she spoke L1 more as a child. In general, these types of self-assessments of language proficiency have been shown to be accurate measures that correspond with more objective assessments (Marian et al., 2007a; Ross, 1998). Participants gave informed, written consent and were paid for their time. This study was approved by the Institutional Review Board at the University of California, San Diego.

Task

Subjects performed a semantic size judgment task for visually presented words and line drawings while MEG was recorded. The task is similar to a previous MEG lexico-semantic language study (Marinkovic *et al.*, 2003) and a concurrent study of monolingual adults and children. All stimuli were concrete, highly imageable objects, and were both high frequency and early-learned words in each language of presentation. Approximately 85% of the stimuli were not cognates in Spanish and English, which helps to control for the overlap between representations across languages at initial levels of processing. The base set of stimuli was taken from a standardized dataset (Snodgrass and Vanderwart, 1980), and was complemented by stimuli from another database that has been standardized across multiple languages (Szekely *et al.*, 2004). The participants were told that they would not see definite or indefinite articles in front of the words, since one potential flaw in studies of Spanish-English bilinguals is that Spanish words presented without an article are unnatural to native speakers and highly proficient L2 learners (Peña, 2007). By setting up an expectation that the nouns would be presented in isolation, we hoped to reduce these effects.

Participants were instructed to lift one finger from a response paddle if the object “fits into a shoebox,” and to lift the other finger if the object was too large to fit into a shoebox. The response hand mappings were counterbalanced across subjects. In addition, subjects were asked to remain still during data acquisition (they were told that they would be given breaks between each 3 minute block), and to respond as quickly as possible. The stimuli were mixed in terms of difficulty for the size judgment task (see Supplementary Table 1 for examples of word and picture stimuli).

Each participant completed four blocks of stimuli in each of L1, L2, and picture conditions (12 blocks total). The first block of each condition was a practice block that was used to set up the repetition priming effect, where subjects were presented with ten stimuli that repeated six times each in a random order. Throughout the next three blocks of that condition, those same 10 stimuli appeared six more times as repeated presentations, interspersed with 60 stimuli that were shown only once (‘novel’ stimuli). Within each participant, different stimuli were presented in each language to ensure that the novel stimuli were truly novel within the task. Stimulus presentation order within each block was randomized, with the only constraint being that there must be at least one intervening novel stimulus between presentations of a particular repeated stimulus. For each trial, a word was presented for 300 ms, followed by a masking fixation cross for 2000–2200 ms, during which subjects made their responses.

To ensure that subjects were processing words in L1 and L2 as if they were in an environment where only one language was being used (i.e., not code switching), all blocks in one language were presented in succession, followed by four blocks with non-verbal pictures, and then four blocks in the other language. The order of the languages was counterbalanced across subjects. All interactions with the subjects and instructions for each block were presented verbally in the language of the subsequent stimuli. Once subjects had completed all blocks of the first language of presentation, the experimenter switched to the other language and informed the subjects that the rest of the experiment would be carried out in that language. This was done to allow us to focus on the organizations of the two lexicons, rather than interactions between languages or mechanisms for language switching (despite the fact that these highly proficient subjects were adept at code switching).

MEG recording

Subjects sat in a magnetically shielded room (IMEDCO-AG, Switzerland) with the head in a Neuromag Vectorview helmet-shaped dewar containing 102 magnetometers and 204 gradiometers (Elekta AB, Helsinki, Finland). Data were collected at a continuous sampling rate of 2000 Hz with minimal filtering (0.1 to 200 Hz). The positions of four non-magnetic coils affixed to the subjects’ heads were digitized along with the main fiduciary points such as the nose, nasion, and preauricular points for subsequent coregistration with high-resolution MRI images. The average 3-dimensional Euclidian distance for head movement from the beginning of the session to the end of the session was 7.97 mm (SD = 4.19 mm). Most of this movement was in the up-down direction, due to the subjects slowly sinking into the cushions. The mean distances (and standard deviations) in each direction were: X = 1.43 mm (1.64), Y = 1.62 mm (2.34), Z = 7.08 mm (4.37).

Anatomically Constrained MEG Analysis

The data were analyzed using a multimodal imaging approach that constrains the activity to the cortical surface as determined by high-resolution structural MRI (Dale and Halgren, 2001; Dale et al., 2000). This noise-normalized linear inverse technique, known as dynamic statistical parametric mapping (dSPM) provides a solution to the inverse problem that also allows the data to be visualized across time on the cortical surface as movies. Note that EEG and MEG are not sufficient for unambiguous current source localization, because any given extracranial electromagnetic field is consistent with an infinite number of possible equivalent current dipole (ECD) configurations in the brain. The dSPM method reduces this ambiguity with the reasonable assumption that sources are located in the cortex, and the solutions in language tasks have been validated by comparison with direct intracranial recordings (Halgren et al., 1994a; Halgren et al., 1994b; Marinkovic, 2004).

The cortical surface was reconstructed in each individual from high-resolution 3D T1-weighted structural MRI (TE = 4.87 ms, TR = 10.7 ms, TI = 1 sec, flip angle = 8 deg, bandwidth = 16.13 KHz, FOV = 25.6 cm, matrix = 256 × 192, slice thickness = 1.0 mm). Proton density-(PD) weighted MRI (TE = 4 ms, TR = 17 ms, TI = 0 sec, flip angle = 5 deg, bandwidth = 31.25 KHz, FOV = 25.6 cm, matrix = 256 × 192, slice thickness = 1.0 mm) was collected for defining the inner skull surface on each subject for a Boundary Element Model forward solution (the expected MEG sensor values based on known activity in the cortex) (Oostendorp and Van Oosterom, 1992).

The cortical surface was then downsampled to ~2500 dipole locations per hemisphere (Dale *et al.*, 1999; Fischl *et al.*, 1999), and the activity of each of these dipoles was estimated at each latency (however, the dipoles at each location were not constrained by their orientations). The noise sensitivity at each dipole location was estimated from the average baseline across all conditions. Significance levels reported on the mean dSPM images were derived by taking the square root of the F-distributed mean activity with 33 degrees of freedom in the numerator (3 dipoles at each location X 11 subjects). The denominator degrees of freedom were 50, derived from the number of time points used to calculate the average noise covariance matrix for each condition. For each individual condition, significance thresholds were set at $p < 10^{-11}$, with a full yellow response indicating $p < 10^{-21}$. The *p*-values in these maps, which do not compare activity between conditions or directly take into account between-subject variance, should be viewed as measures of signal to noise at each point on the cortical surface.

The data were inspected for bad channels (channels with excessive noise, no signal, or unexplained artifacts), which were excluded from all further analyses. Additionally, trials with large (>3000 fT for gradiometers) transients were rejected. Blink artifacts were removed using independent components analysis (ICA; (Delorme and Makeig, 2004) by pairing each MEG channel with the electrooculogram (EOG) channel, and rejecting the independent component that contained the blink. This allowed us to include approximately 55–60 trials per condition for each subject. The data were epoched from −200 ms to 1000 ms relative to stimulus onset, and all valid trials were included in the analysis, regardless of task performance. See Supplementary Figure 4 for a single representative subject's data in sensor space. Individual subject dSPMs were constructed from the averaged data in the 1200 ms epoch for each condition using only data from the gradiometers, and then these data were combined across subjects by taking the mean activity at each vertex on the cortical surface and plotting it on an average brain. Vertices were matched across subjects by morphing the reconstructed cortical surfaces into a common sphere, optimally matching gyral-sulcal patterns and minimizing shear (Fischl et al., 1999; Sereno et al., 1996). All statistical comparisons and ROI analyses were made on these group data, as described in the results.

Results

Reaction Time

Reaction time data was obtained in 10 subjects. One participant’s behavioral responses were lost due to an equipment malfunction. Reaction times were entered into a repeated-measures ANOVA, with stimulus type (L1 vs. L2 vs. pictures) and repetition (novel vs. repeated) as factors. Subjects responded significantly faster to repeated than novel stimuli, F(1,9) = 181.65, $p < 0.0001$ (Table 1). There was also a main effect of stimulus type [F(2,18) = 13.00, $p < 0.0001$], however post-hoc *t*-tests determined that the difference between L1 words and L2 words was not significant. There were significant differences between novel L1 words and pictures [t(9) = 2.99, $p < 0.02$], repeated L1 words and pictures [t(9) = 3.02, $p < 0.02$], novel L2 words and pictures [t(9) = 4.03, $p < 0.004$], and repeated L2 words and pictures [t(9) = 4.05, $p < 0.004$]. The interaction between stimulus type and repetition was not significant.

MEG Estimates

Noise normalized dSPMs were calculated for each subject, and then averaged onto a common space as a group mean of the estimates (see Supplementary Movie 1 and Supplementary Movie 2 for the dynamic activity over the full time course). From the group mean time courses of the activity, temporal windows were selected for statistical analysis in various regions of interest (ROIs). 17 ROIs were selected based on *a priori* hypotheses about the data, combined with information from a grand average of the activity across all subjects and all conditions. In most cases, each ROI was anatomically constrained to part of a single sulcus or gyrus (Supplementary Figure 1). The group average F-values from the time course of the mean activity within each ROI were entered into a repeated-measures ANOVA with language (L1 vs. L2) and repetition (novel vs. repeated) as within-subject factors (pictures were added as a level in the language factor for additional analyses). All reported *p*-values are uncorrected for multiple comparisons.

Early Sensory Processing (~90–110 ms)

To ensure that there were no early perceptual processing differences at ~100 ms post-stimulus onset that could affect downstream cognitive responses, we examined the activity in the primary visual cortex ROI during this time period (Supplementary Figure 2). The only effect during this time window was a marginally significant language by repetition interaction in the right occipital pole [F(1,10) = 4.66, $p = 0.056$], however no post-hoc paired samples *t*-tests were significant.

Early Visual Word Encoding Responses (~126–146 ms)

The group mean dSPM revealed an activity peak in VOT at ~136 ms post-stimulus onset, which lasted until approximately 180 ms. The data were averaged over a 20 ms time window surrounding 136 ms (126–146 ms), and we compared the activity in left and right VOT across conditions. In the left hemisphere, the posterior fusiform ROI did not show any significant effects of either language or repetition (Figure 1). However, the right posterior fusiform demonstrated a significant language by repetition interaction [F(1,10) = 7.09, $p = 0.02$], with novel L2 words > novel L1 words, t(10) = −2.55, $p = 0.03$ (Figure 1 and Figure 2). In L2, repeated words were suppressed relative to novel words, t(10) = 2.59, $p = 0.03$.

Lexico-semantic Responses (~380–420 ms)

Numerous areas in both hemispheres were found to generate significant activity to words in L1 and in L2 during a 40 ms window around 400 ms chosen *a priori* as during the construction of lexico-semantic representations (Figure 3 and Figure 4; see Supplementary Materials and Supplementary Figure 3 for analyses of a slightly earlier peak response time window). During this time window, two regions showed significant main effects of language. The posterior superior temporal sulcus (STS) in the left hemisphere showed a significantly greater response to L2 words than to L1 words, F(1,10) = 6.07, $p < 0.05$. The posterior STS also showed a main effect of repetition, with novel > repeated words, F(1,10) = 5.38, $p < 0.05$. The only other region to show a significant main effect of language at this time was the right hemisphere inferior precentral sulcus, where L2 words elicited a greater response than L1 words, F(1,10) = 6.54, $p < 0.05$. This region also showed a trend toward an interaction between language and repetition, with novel L2 words showing a greater response than novel words in L1, [F(1,10) = 3.90, $p = 0.076$], which was confirmed by a post-hoc paired samples *t*-test, t(10) = −2.84, $p < 0.02$.

Additionally, in a lateral region of ventral occipitotemporal cortex (VOT) in the right hemisphere, at ~400 ms, responses to repeated words were suppressed relative to novel words [F(1,10) = 5.50, $p < 0.05$], and there was a trend toward a significant language by repetition interaction, F(1,10) = 4.03, $p = 0.07$. Post-hoc paired samples *t*-tests confirmed that this interaction was driven by differences between novel words in each language [t(10) = −3.20, $p = 0.01$], and also by a strong repetition effect in L2, t(10) = 3.42, $p < 0.01$.

Several other regions showed significant main effects of repetition at ~400 ms, all with novel > repeated words. In the left hemisphere, these regions included an area of posterior fusiform cortex [F(1,10) = 7.77, $p < 0.05$], and a nearby area of medial VOT, F(1,10) = 5.76, $p < 0.05$. In the right hemisphere, intraparietal sulcus [F(1,10) = 5.50, $p < 0.05$], anterior STS [F(1,10) = 6.95, $p < 0.05$], and posterior STS [F(1,10) = 16.90, $p < 0.005$] all showed novel > repeated effects.

Also in the right hemisphere, a region of lateral occipitotemporal (LOT) cortex showed a similar main effect of repetition, F(1,10) = 11.82, $p < 0.007$. This region also demonstrated a significant interaction [F(1,10) = 6.26, $p < 0.05$], which was driven by an L2 > L1 difference for novel words [t(10) = −3.90, $p < 0.005$] and by a strong repetition effect in L2, t(10) = 3.53, $p = 0.005$.

In left anterior temporal cortex, the mean dSPM images appeared to show strong effects of both language and repetition. While the repetition effect was significant [F(1,10) = 8.59, $p < 0.02$], the apparent language-related effects were not, due to relatively high variability between subjects in these regions.

Words vs. Pictures

Since we hypothesized that L2 would show activity in posterior visual processing regions during lexico-semantic encoding, we compared the activity between words and line drawings of objects. Overall, pictures produced a more bilateral response than words, as we anticipated. At ~400 ms, we found similarities in the mean dSPM images between L2 words and pictures, both of which differed from L1 words (Figure 5). A repeated-measures ANOVA with stimulus type (L1 vs. L2 vs. pictures) and repetition (novel vs. repeated) revealed statistically significant main effects of stimulus type in left posterior STS [F(2,20) = 4.77, $p = 0.02$], right posterior fusiform [F(2,20) = 3.52, $p < 0.05$], right inferior precentral sulcus [F(2,20) = 4.32, $p < 0.03$], right inferior temporal cortex [F(2,20) = 3.47, $p = 0.05$], right lateral VOT [F(2,20) = 4.26, $p < 0.03$], and right anterior temporal cortex, F(2,20) = 3.89, $p < 0.04$. The following left hemisphere regions showed significant main effects of repetition: posterior STS, posterior fusiform, and anterior temporal cortex. Repetition effects were also found in these right hemisphere regions: intraparietal sulcus, anterior STS, posterior STS, and LOT.

Several regions also showed stimulus type by repetition interactions. The only region on the left with such an effect was lateral VOT [F(1,10) = 5.04, $p < 0.02$], although no post-hoc tests were significant. In the right hemisphere, LOT showed a trend toward an interaction [F(1,10) = 2.96, $p = 0.075$], where novel L1 words differed significantly from novel L2 words [t(10) = 3.90, $p < 0.005$] and from novel pictures [t(10) = 2.50, $p = 0.03$] (Figure 6). Lateral VOT and inferior precentral sulcus showed the same pattern of L2 and pictures having similar responses, and both differing from L1.

Peak Latency Effects

An additional hypothesis relates to the timing of peak N400m activity in L1 versus L2. Previous electrophysiological studies have demonstrated a delay in the peak of the N400 response in L2 compared to L1 (or the non-dominant compared to the dominant language). Therefore, we obtained peak response latencies for 9 of the 17 ROIs that appeared to be involved in generating the lexico-semantic responses that we observed in this study (denoted by ** in Supplementary Figure 1). Full 1200 ms epochs (with a 200 ms baseline period) for each of these 9 ROIs were extracted, and then lowpass filtered at 5 Hz (width = 1), so that broad peak latencies could be measured.

In the left hemisphere, the only significant effect was in the posterior STS, which had an earlier peak response to repeated words (repeated: 310 ms, novel: 354 ms), F(1,10) = 16.95, $p < 0.005$. Although this region reached its peak amplitude before the time windows used in other analyses, it remained near this peak until ~450–500 ms.

In the right hemisphere at ~400 ms, the pars opercularis of the inferior frontal gyrus demonstrated a delayed peak for L2 compared to L1 words (L1: 386 ms, L2: 426 ms), F(1,10) = 5.03, $p < 0.05$. Similarly, the right posterior STS showed the same effect of language (L1: 300 ms, L2: 332 ms), F(1,10) = 4.79, $p = 0.05$. Like its left hemisphere counterpart the posterior STS reached its peak magnitude at ~300 ms, however this response was sustained until well after the 400 ms time window that was used in the analyses above.

Additionally, there was a marginally significant effect of language in right LOT at ~300 ms post-stimulus onset, with L2 words peaking later than L1 words (L1: 292 ms, L2: 332 ms), F (1,10) = 4.28, $p = 0.065$. This region was selected for peak latency analysis because it demonstrated a significant effect during the late lexico-semantic time window, with L2 novel words > L1 novel words. Like the effects in posterior STS, the peak response was largely sustained during the 400 ms time window, despite the fact that the region initially reached its peak earlier.

Discussion

In this study, we sought to investigate the neural representations of first and second language word processing using a multimodal imaging approach that affords high spatiotemporal accuracy. We wanted to compare between languages specific processes involved in the language stream that are expected to occur sequentially, such as sensory processing, early visual word encoding, and late lexico-semantic processing. Responses to Spanish (L1) and English (L2) words differentiated as early as ~135 ms after word onset, when word selective activity first occurs. While both languages recruited left posterior fusiform cortex, only L2 novel words additionally evoked strong early activity in the right fusiform. This early bilateral distribution for novel stimuli continued through the language stream to ~400 ms, when L2 showed greater activity than L1 in bilateral posterior and right frontal regions. Strikingly, the responses to simple line drawings and L2 words were similar in these regions, and both differed significantly from L1 words. Additionally, consistent with previous electrophysiological studies, we found that an equally activated frontal region, as well as a posterior temporal area that was more strongly active in L2, showed delays in the timing of the peak lexico-semantic activity for L2 compared to L1. In general, we have shown that the brain distinguishes the language of word presentation early in the language stream, and that throughout the course of processing, L2 recruits a more extended network of regions in posterior visual and right hemisphere areas when the stimuli are less familiar.

It is striking that the brain distinguishes language identity so early, especially since English and Spanish share an orthographic system and the word stimuli used here were high frequency concrete nouns. While left fusiform activity reflecting both orthographic and lexical features is consistently observed during word reading (Fiez and Petersen, 1998; McCandliss et al., 2003), activity in the right fusiform has been observed in a number of studies, especially when encoding is more difficult. Developmental studies of word reading find right VOT activity, which declines as children grow up and become proficient readers (Maurer et al., 2005; Turkeltaub et al., 2003). In monolingual adults, this region may be recruited in a sustained attentionally-based top-down manner when it is initially uncertain if the stimulus is a word, and its activity decreases as lexical certainty increases (Tagamets et al., 2000). Furthermore, when words are embedded in progressively greater amounts of visual noise, right VOT activity as early as ~130 ms increases compared to words without noise (Tarkiainen et al., 1999). Thus, early recruitment of the right hemisphere by English words in native Spanish speakers may reflect a more general propensity for bilateral engagement of VOT when the visual word encoding system is not entirely tuned to the stimuli. The current study provides strong support for this interpretation in that right but not left posterior fusiform activation decreased for L2 words when they were presented repeatedly.

Besides boosting the visual encoding of unfamiliar words, right VOT engagement may route such information to the right hemisphere homologues of anterior language areas that are involved in later lexico-semantic processing. We found that at ~400 ms, the non-native (and non-dominant, though highly proficient) language recruits both the classical left hemisphere language network (Cabeza and Nyberg, 2000; Dhond et al., 2001; Halgren et al., 1994b; Marinkovic et al., 2003) and an additional set of posterior and right hemisphere regions. It has been suggested previously that non-native languages may recruit more right hemisphere regions (Abutalebi et al., 2001; Dehaene et al., 1997; Perani et al., 1998), however this effect tends to appear only in studies that show differential L1/L2 left hemisphere responses (Chee *et al.*, 1999; Klein *et al.*, 1995). It is important to note that although there is a general focus in the literature on left-lateralized N400 generators, intracranial recordings with monolingual subjects have demonstrated right hemisphere generators as well (Halgren et al., 1994a; Halgren et al., 1994b; Smith et al., 1986).

Greater right hemisphere activity in the non-dominant language could be related to a processing strategy wherein the brain recruits regions that may be able to provide supplementary information regarding the nature of the stimuli (Goldberg and Costa, 1981; Goldberg et al., 1978). It is difficult to determine from our data whether such supplementary information (such as coarser analyses of both linguistic and meta-linguistic features) is required due to greater difficulty associated with encoding the stimuli, however the bilateral VOT activity during early visual word encoding could support this hypothesis. Additionally, since many of the areas that show strong activity in L2 are areas that are known to be useful for language processing when the analogous left hemisphere regions are damaged (Hertz-Pannier *et al.*, 2002), it is possible that they are recruited when the language system encounters stimuli that do not fit the mold of the entrenched native language. Although the subjects in the present study considered themselves less proficient in L2, their equal behavioral performance in both languages suggests that this is only achieved by engaging additional cortical areas. Further studies with bilinguals who have highly variable L2 proficiency will be required to determine whether these effects are more strongly influenced by language proficiency, order of acquisition, or other factors.

Additional support for the hypothesis that the right hemisphere is recruited when the brain is presented with stimuli in a less familiar language comes from our analysis of peak latency effects. We have replicated the finding that lexico-semantic responses in L2 are delayed by approximately 40–50 ms compared to L1 (Hahne, 2001). Since the direction of this effect can be reversed if L1 is the non-dominant language (Moreno and Kutas, 2005), it may be a reasonable interpretation to suggest that difficulty and familiarity are factors in right hemisphere recruitment. Although the peak responses in the present study are approximately 80–100 ms earlier than those that have been found with ERP, the similarities between the tasks and processes that are being probed between studies suggests that the delay in our results may be similar to the N400-like effects in other studies. A possible explanation for this timing discrepancy may relate to differences between the N400 as measured by EEG and similar, but not identical MEG responses that have been termed the N400m (Halgren *et al.*, 2002).

In addition to hemispheric and timing differences between L1 and L2 lexico-semantic representations, an anterior-posterior difference emerged in our results. These results are consistent with evidence from object naming deficits due to direct cortical stimulation suggesting that L1/L2 differences are greater in posterior visual areas including LOT, despite the general focus in the literature on left frontal cortex. In one study, posterior sites including posterior STS and occipito-temporo-parietal cortex showed a greater proportion of L2-specific regions than L1-specific regions in some subjects, while left frontal areas had a higher number of L1-specific and shared regions (Lucas *et al.*, 2004). Although the stimulation sites were limited compared to whole-brain techniques such as fMRI and MEG (and the task involved language production rather than comprehension), there is a striking concordance between the L2-specific regions and the areas that we have shown in the present study to have greater activity in L2, providing support for the hypothesis that there are greater posterior differences between L1 and L2 for lexico-semantic representations in some bilinguals. The more extreme posterior differences between languages found in the present study simply may reflect a difference among the various imaging and recording modalities, however in general, the relatively high spatiotemporal resolution of the distributed-source MEG method used here provides a useful link between previous intracranial, EEG, and fMRI results.

The nature of this posterior secondary visual cortex activity during lexico-semantic processing is unclear based solely on the present results. One possibility is that regions such as LOT become active for high-level visualization of lexico-semantic content (Grill-Spector *et al.*, 2001; Malach *et al.*, 1995). Such an interpretation is consistent with the similarities that we observed between pictures and L2 words in these regions. This may be related to a more perceptually-grounded set of representations in the non-dominant L2, similar to what has been observed in children who are in the process of acquiring their native language (Brown et al., 2005; Mandler, 2000; Nelson, 1974; Ojemann et al., 2003; Saltz et al., 1972; Schlaggar et al., 2002). Furthermore, similarities in posterior visual brain activity between children and adult L2 learners could support the hypothesis that sequential L2 learning is similar to native language acquisition during childhood, and that successful L2 acquisition relies on adequate L1 development (Mayberry, 1993, 2007). Alternatively, it may simply be the case that L2 relies more on visual analysis in the size judgment task used in the present study. Future studies will probe the nature of these representations in the second language to determine whether L2 learners do indeed rely more on perceptual features in the second language relative to the high level abstract concepts that form the basis of the L1 lexico-semantic system.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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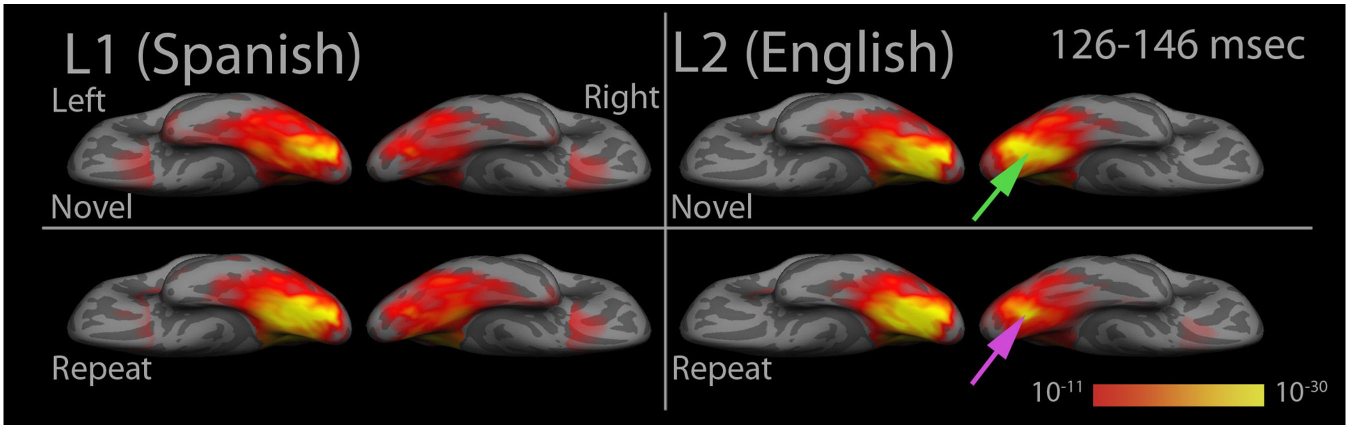

Figure 1. Group dSPM images of the mean activity during early visual word encoding (~136 ms post-stimulus onset) for 11 subjects

Spanish (L1) showed strongly left lateralized activity in VOT. In contrast, English (L2) showed activity in bilateral VOT (green arrow). In addition, right VOT in L2 showed an effect of stimulus repetition (purple arrow). Significance levels (a measure of signal-to-noise) are indicated by the color bar.

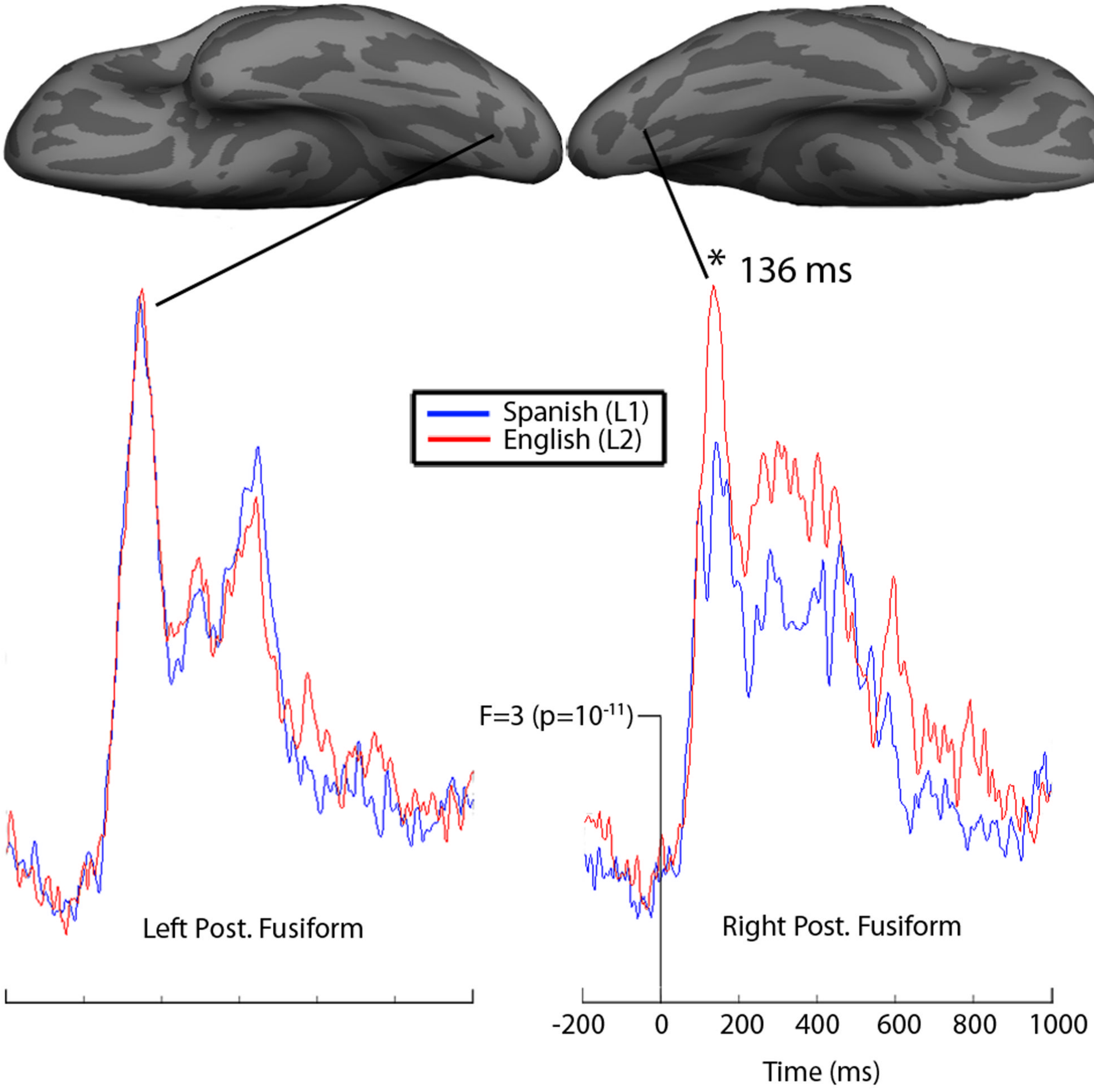

Figure 2. Average time courses for the estimated noise-normalized dipole strength to initial presentation words in Spanish (L1) (blue lines) and English (L2) (red lines) in posterior fusiform cortex

Although there was no difference between languages in left posterior fusiform gyrus, right posterior fusiform showed a L2 > L1 response during an early peak at ~136 ms.

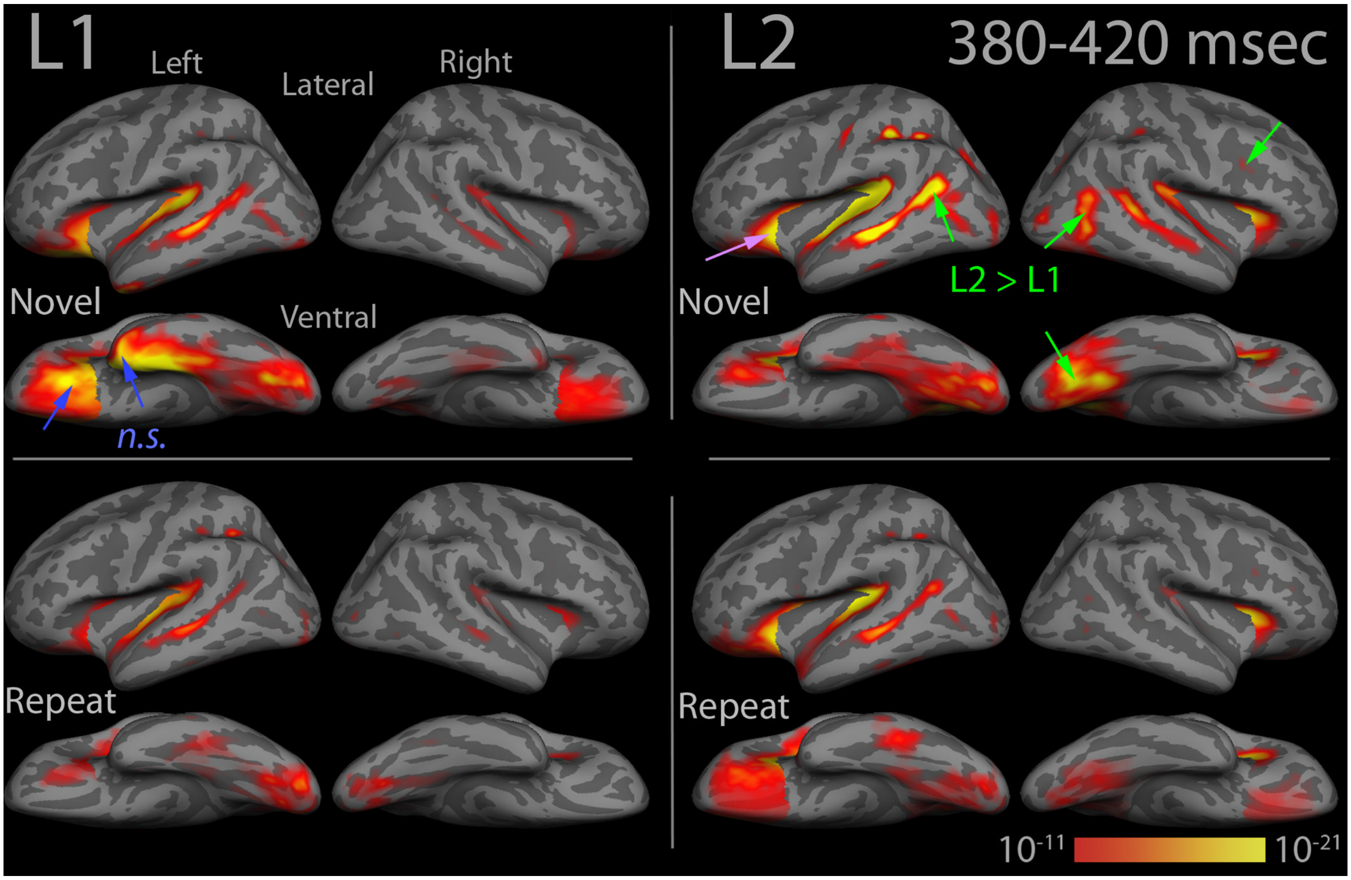

Figure 3. Group dSPM images of the mean activity during the *a priori* lexico-semantic time window (~400 ms) for 11 subjects

L2 showed greater activity than L1 in posterior regions including right LOT, left posterior STS, and right lateral VOT, and in right inferior precentral sulcus (green arrows). Despite differences in the mean maps in left inferior frontal and anterior temporal regions (blue arrows), the between-subject variability was too high for such language differences to reach significance. Stimulus repetition effects were significant for many regions in both hemispheres. The light purple arrow indicates left anterior insula, which showed significant L2 > L1 language effects during the peak time window around ~372 ms. Significance levels (a measure of SNR) are indicated by the color bar.

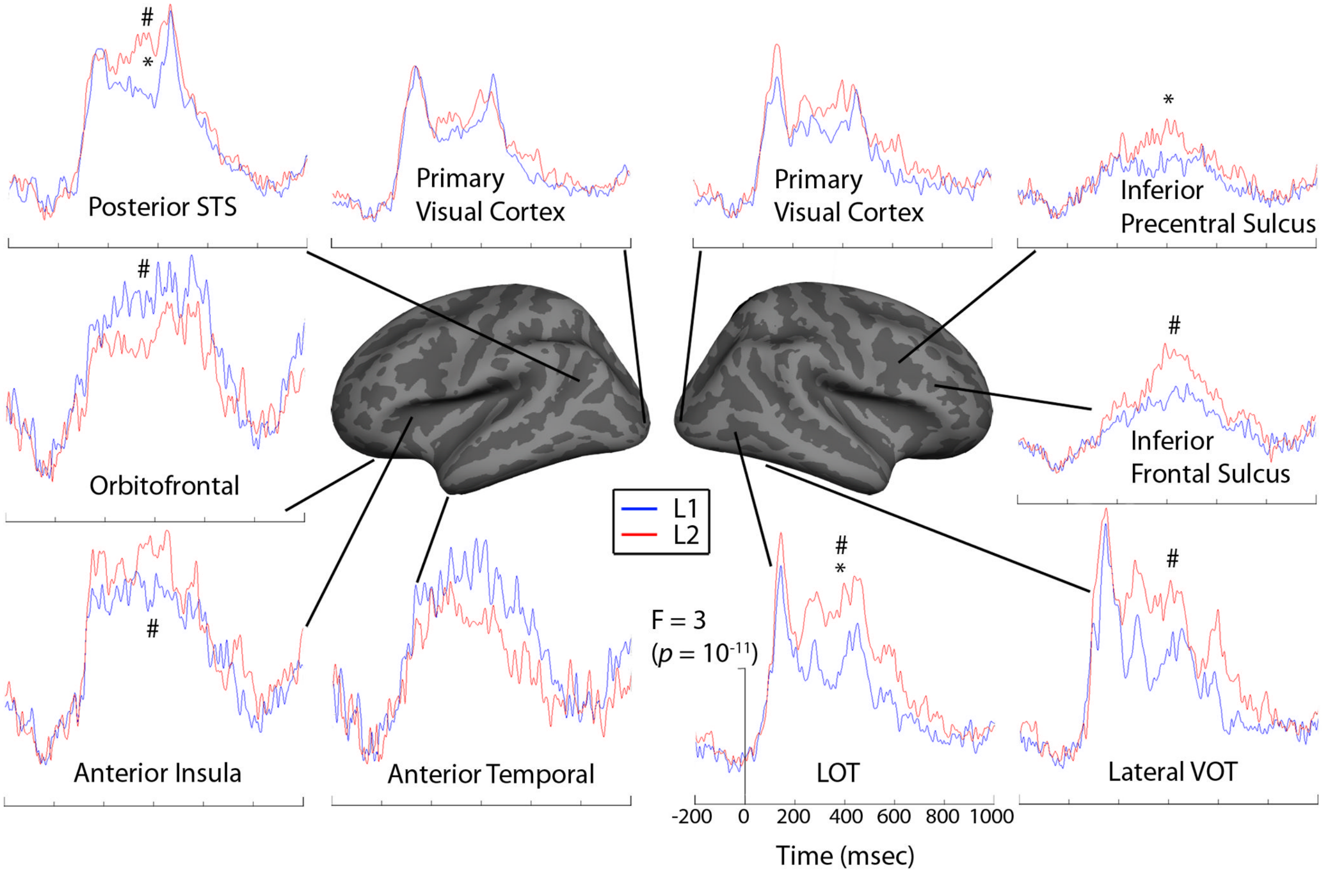

Figure 4. Average time courses for the estimated noise-normalized dipole strength to novel words in L1 (blue lines) and L2 (red lines)

Shown for both hemispheres are a selection of the 17 ROIs that were chosen for statistical analysis. Time courses with a * denote regions with a significant language difference at ~400 ms, while time courses with a # denote additional regions that were significant during the peak window at ~372 ms.

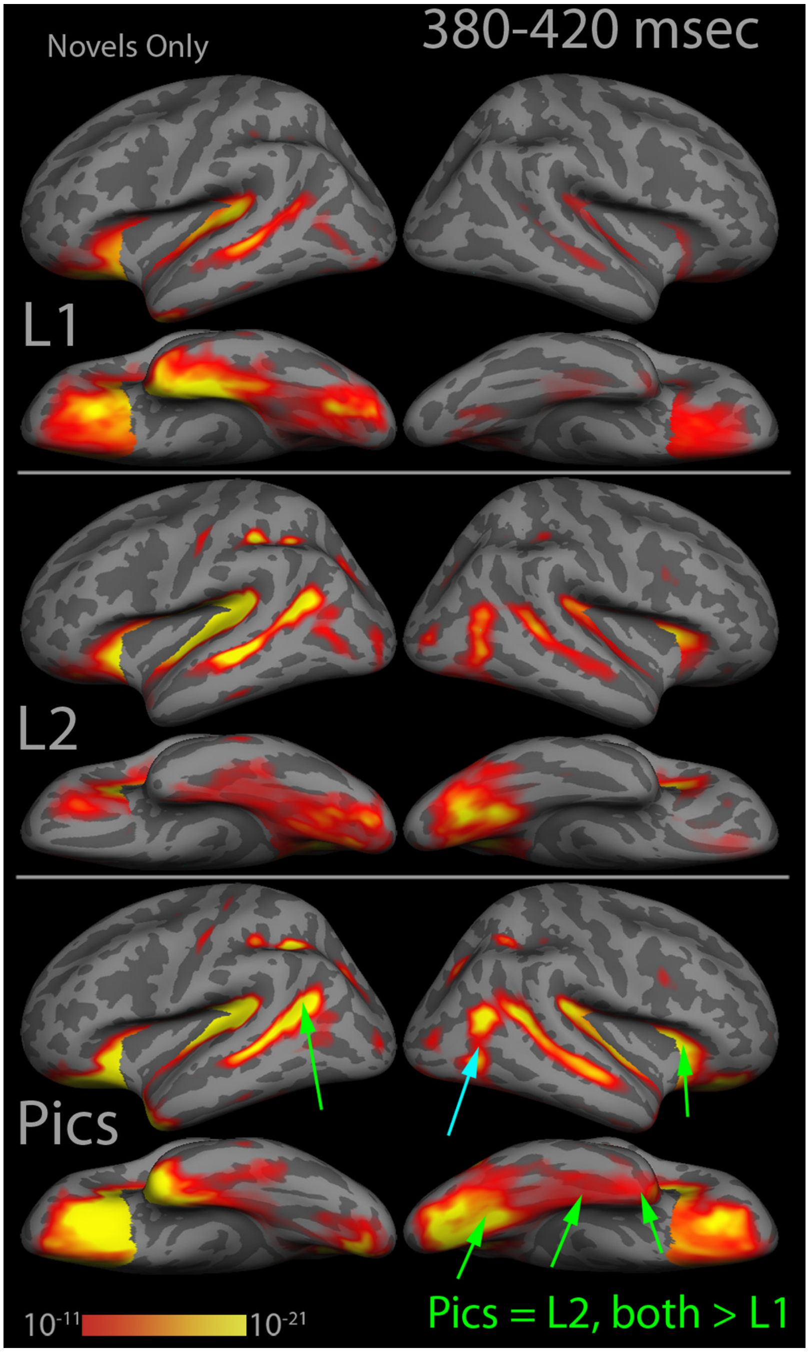

Figure 5. Group dSPM images of the mean activity for novel stimuli ~400 ms for 11 subjects

In several areas, main effects of stimulus type (L1 vs. L2 vs. pictures) were significant such that L2 words and pictures showed similar responses that differed significantly from L1 words (green arrows). One region of particular interest, right LOT, showed an interaction where this pattern emerged only for novel stimuli (cyan arrows), suggesting that LOT processes novel pictures and L2 words similarly, but shows less of a response for L1 words. Significance levels (a measure of SNR) are indicated by the color bar.

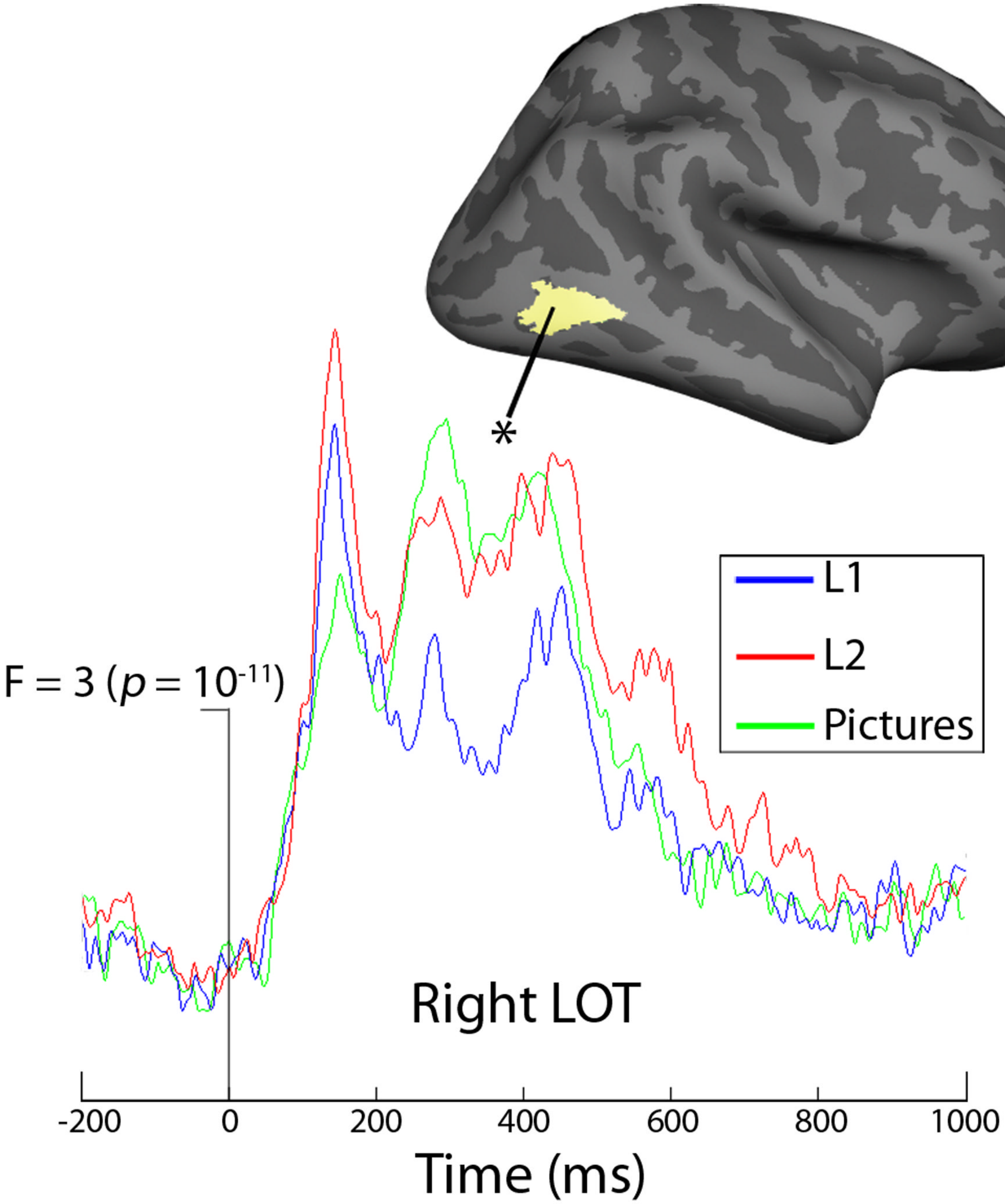

Figure 6. Average time course for the estimated noise-normalized dipole strength to novel stimuli in right LOT for words in L1 (blue line), L2 (red line), and pictures (green line)

At ~400 ms, pictures and L2 words show a similar response that differs significantly from L1 words.

Table 1

Mean reaction times with standard deviations for ten subjects

Subjects responded faster to repeated words in both languages (and for pictures), and did not differ significantly between L1 and L2. The responses to pictures were significantly faster than for both languages.

Condition	Mean (SD) reaction time in ms
L1 Novel	972 (151)
L1 Repeat	760 (131)
L2 Novel	915 (116)
L2 Repeat	753 (142)
Pics Novel	844 (112)
Pics Repeat	642 (67)