# Bilingual language processing relies on shared semantic representations that are modulated by each language

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**Abstract**

Billions of people throughout the world are bilingual and can extract meaning from multiple languages. While some evidence suggests that there is a shared system in the human brain for processing semantic information from different languages, other evidence suggests that semantic processing is to some degree distinct between languages. We conducted a study to determine how semantic representations in the brains of bilinguals can support both shared and distinct processing for different languages. Functional magnetic resonance imaging (fMRI) was used to record brain responses while participants who are fluent in both English and Chinese read several hours of natural narratives in each language. These data were then used to specifically and comprehensively compare semantic representations between the two languages. First, we show that semantic representations are largely shared between languages. Second, we show that there are finer-grained differences that systematically alter how the same meaning is represented between different languages. Our results suggest that for bilinguals, semantic brain representations are shared across languages but modulated by each language. These results reconcile current competing theories of bilingual language processing.

## Introduction

Over four billion people throughout the world are bilingual and can understand the meaning of words in both their native and non-native languages[1]. However, there is conflicting evidence about how bilinguals process the meanings of words from different languages. Some behavioral studies have shown knowledge of one language can interfere with semantic processing in another. For example, prior work has shown that second language acquisition can increase processing times for false cognates[2–4], and can change how speakers describe concepts in their native language[5]. This interference suggests that the human brain has one shared system that processes semantic information from different languages. However, other behavioral evidence indicates that semantic processing is to some extent different between languages. For example, emotional intensity can be experienced more strongly in native as compared to non-native languages[6,7], and the language of a conversation can bias what memories are recalled by a bilingual speaker[8]. From behavioral evidence alone, it remains unclear how a single shared semantic system in the brain can also encode differences in semantic representations between languages.

Prior neuroimaging work has studied which brain regions respond to different languages. These studies suggest that similar brain regions are used to process different languages[9–13] (although a few studies have reported anatomical differences[14–16]). However, those studies had three key limitations. First, they identified the brain regions that are activated during language comprehension, but did not show how brain activity within these regions encodes the meaning of words[10–16]. Thus, it is unclear whether functional patterns that encode word meaning (i.e., semantic representations) are similar or different between languages. Second, many prior studies

did not perform within-participant comparisons between languages[14,17–19]. Thus, individual differences in brain function and anatomy[20] prevented spatially fine-grained, voxel-level comparison of semantic representations. Third, many prior studies used controlled stimuli[10–12,14,21]. Thus, it was unclear whether reported results generalize to naturalistic settings[22]. In sum, prior neuroimaging studies have been insufficient to determine how the brains of bilinguals represent semantic information from different languages.

Prior neuroimaging studies of English language comprehension offer a new hypothesis for how a shared semantic system in the brain can also encode differences in semantic representations between languages. These studies showed that, for English, semantic information in language is represented in a network of brain regions that are each tuned towards different word meanings[23]. Recent evidence has shown that semantic representations can be modulated by different task conditions[24,25]. Between different task conditions semantic representations remain largely similar, but the semantic tuning of each brain region can shift to emphasize task-relevant concepts. Based on this evidence, we hypothesized that in the brains of bilinguals semantic representations remain largely similar between languages, but that semantic tuning is systematically modulated by each language to encode differences in semantic representations between languages (Figure 1A).

To test this hypothesis we designed a study to investigate how the brains of bilinguals encode the meanings of words in different languages. Six native Chinese speakers who are also fluent in English read natural narratives for over two hours in each language while functional magnetic resonance imaging (fMRI) was used to record brain responses. Voxelwise modeling was used to estimate semantic representations for each language separately. Semantic representations were compared between the two languages for each individual participant. Our results support the hypothesis that semantic brain representations are shared between languages and that these shared representations are modulated by each language.

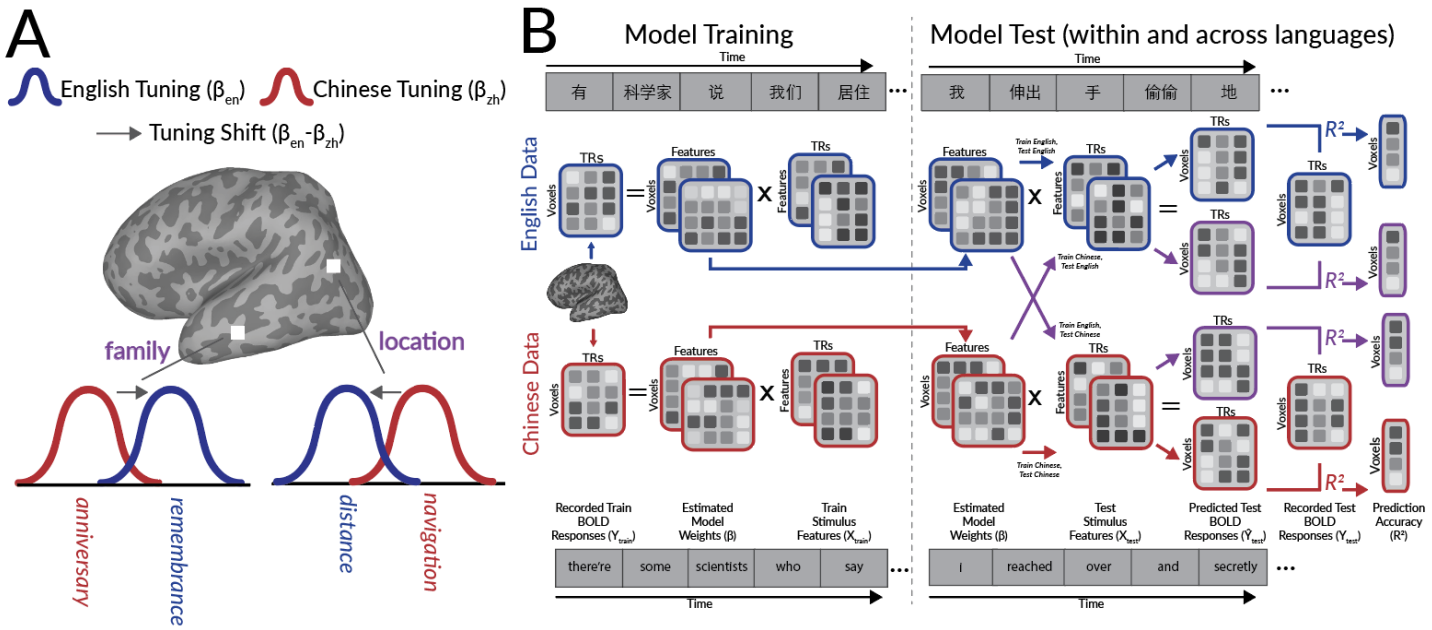


**Figure 1. Hypothesis and experimental procedure.**
**A.** Schematic illustrating hypothesized semantic representation shifts. The semantic tuning of a voxel describes how it responds to word meaning. Shifts in semantic representations were quantified as the change in semantic tuning between languages. For each voxel, blue and red curves respectively denote semantic tuning in English and Chinese. Arrows represent semantic tuning shifts from Chinese to English. The hypothetical voxel in the parietal cortex responds to location-related words in both languages, but emphasizes number-related aspects ("distance") in English, and action-related aspects ("navigation") in Chinese. The hypothetical voxel in temporal cortex responds to family-related words in both languages,

but emphasizes emotion-related aspects ("remembrance") in English, and number-related aspects ("anniversary") in Chinese. **B.** Experiment and modeling procedure. Six fluent Chinese-English bilingual participants read over two hours of narratives in each language while BOLD responses were measured using fMRI. Semantic stimulus features were constructed by projecting each stimulus word into a 300-dimensional word embedding space[26]. Ridge regression was used to estimate encoding models that describe voxelwise semantic tuning for each participant and language. Estimated model weights were used to predict BOLD responses to held-out narratives not used for model estimation. Model weights estimated in one language were used to predict BOLD responses to the same language (red and blue arrows; *within-language*) and to the other language (purple arrows; *across-language*). Prediction accuracy was quantified as the coefficient of determination (CD; $R^2$) between predicted and recorded BOLD responses.

## Results

Six Chinese-English bilinguals read natural narratives while fMRI was used to record blood oxygen level dependent (BOLD) responses. Each narrative was presented in both English and Chinese as written text. Words were presented one at a time at a natural reading rate. Each participant read narratives for over two hours per language. Semantic stimulus features were extracted by projecting each word into a distributional word embedding space (fastText[26,27]) in which words in different languages with similar meanings project to nearby vectors. Regularized regression was used to estimate voxelwise encoding models that describe how the semantic stimulus features are encoded in brain responses. Models were estimated separately for each participant and language (Figure 1B). Nuisance features such as word rate and spatiotemporal visual features were regressed out of BOLD responses prior to model estimation. The estimated model weights describe the semantic tuning of each individual voxel, for each language separately. Estimated model weights were compared between English and Chinese to examine whether and how semantic representations differ between languages. To ensure the generalizability of the results and to prevent overfitting, the estimated model weights were evaluated on BOLD responses to a held-out story that was not used for model estimation. To ensure generalization to new participants, models were estimated and evaluated separately for each participant and the results were replicated in each individual participant, and data for two participants (P5 and P6) were not analyzed until the entire analysis pipeline was finalized.

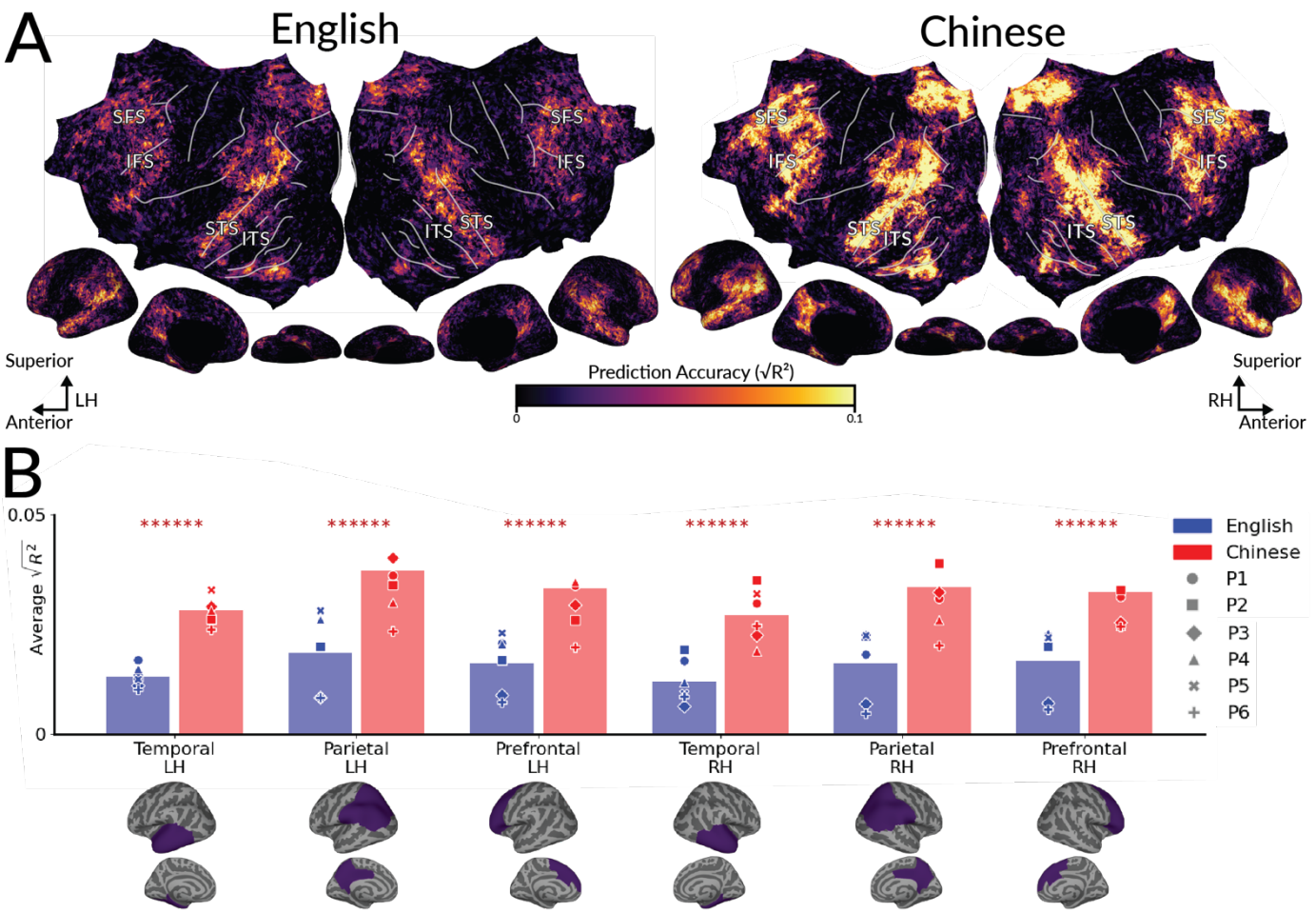


**Figure 2. Cortical distribution of semantic representations for each language.** To determine where semantic information is represented for each language, voxelwise models estimated for each language were used to predict held-out data for the same language. Prediction accuracy was computed as the CD ($R^2$) between predicted and recorded BOLD responses. **A.** Group-level prediction accuracy. Results are shown for each language on the flattened cortical surface of the template space. For both languages, prediction accuracy is highest in the bilateral temporal, parietal, and prefrontal cortices. Prediction accuracy in these regions is statistically significant for each participant (Figure S6). The same brain regions are well-predicted for both languages. (SFS=superior frontal sulcus; IFS=inferior frontal sulcus; STS=superior temporal sulcus; ITS=inferior temporal sulcus, LH=left hemisphere; RH=right hemisphere) **B.** Prediction accuracy by cortical region. For each brain region and participant, blue and red markers show the mean prediction accuracy over voxels for English and Chinese respectively. Bars show the mean across participants. Red asterisks denote the number of participants for which prediction accuracy is significantly higher in Chinese than in English (one-sided p<.05 by a permutation test). While the same brain regions are well-predicted for both languages, the semantic model explains more variability in brain responses for Chinese than for English.

The hypothesis that semantic representations are similar between languages presents two predictions. First, the same brain regions should represent semantic information for both languages. Second, within these regions the same word meaning should activate a similar set of voxels across languages. To study the first prediction, we examined the prediction accuracy of the estimated semantic model weights. If a voxel represents semantic information in one language, then estimated semantic model weights for that language will accurately predict held-out test data for that language. Prediction accuracy was computed as the coefficient of determination (CD;

$R^2$) between predicted and recorded BOLD responses for each voxel, participant, and language separately. Group-level results were computed by projecting voxelwise accuracies for each participant to a template space (fsAverage[28]), and then averaging the projected values across participants for each vertex and language separately. Figure 2A shows vertexwise group-level prediction accuracy for each language separately. Results for each participant are similar to group-level results (Figure S5 and S6). For each language, prediction accuracy is highest within bilateral temporal, parietal, and prefrontal cortices, regions that together comprise the *semantic system*[23,29]. These results show that the same brain regions represent semantic information for both languages.

While the same brain regions are well-predicted for both languages, visual inspection of Figure 2A indicates that prediction accuracy in these participants is overall higher in Chinese than in English. To quantify this difference for each brain region in the semantic system, we identified the set of voxels in the temporal, parietal, and prefrontal regions for each participant using the Desikan-Killiany atlas[30]. We then computed the average prediction accuracy separately for each language and region. Figure 2B shows the average prediction accuracy for each language, region, and participant. Prediction accuracy within these regions is significantly greater in Chinese than in English (one-sided $p<.05$ by a permutation test for all brain regions and participants).

There are two potential explanations for why prediction accuracy is higher in Chinese (L1) than in English (L2) in this experiment. One possibility is that the recorded brain responses simply have a higher signal-to-noise ratio (SNR) in Chinese than in English. This could happen if, for example, the participants paid more attention when the stories were presented in Chinese than in English. To test this possibility, we examined voxelwise explainable variance (EV). EV estimates the SNR of each voxel by measuring the repeatable signal over multiple repetitions of the same stimulus[31–33]. If the SNR is higher for Chinese than for English, then EV will be higher in Chinese than in English. Across participants, EV was not higher in Chinese than in English (Figure S7), suggesting that SNR is not higher in Chinese than in English.

A second possibility is that SNR is comparable between languages, but semantic processing more strongly influences brain representations for Chinese as compared to English. Brain representations reflect not only semantic processes, but also other processes such as sentence-level syntactic parsing, working memory load, or high-level control. The semantic model weights can only predict how the brain represents information captured by the word embeddings, and the word embeddings do not capture extra-linguistic processes such as working memory load. Aspects of language processing that are not reflected in the word embeddings contribute to variance in the repeatable signal that is not explained by the semantic model weights. To test for this possibility, we examined voxelwise noise-ceiling corrected prediction accuracy. Noise-ceiling corrected prediction accuracy measures how well a model predicts brain responses, relative to the maximum possible accuracy of a model given the noise in the data[31–33]. If semantic processing more strongly influences brain representations for Chinese, then the noise-ceiling corrected prediction accuracy will be higher for Chinese than for English. Across participants, the noise-ceiling corrected prediction accuracy was significantly higher for Chinese than for English (Figure S8), suggesting that semantic processes more strongly influence brain representations for Chinese as compared to English.

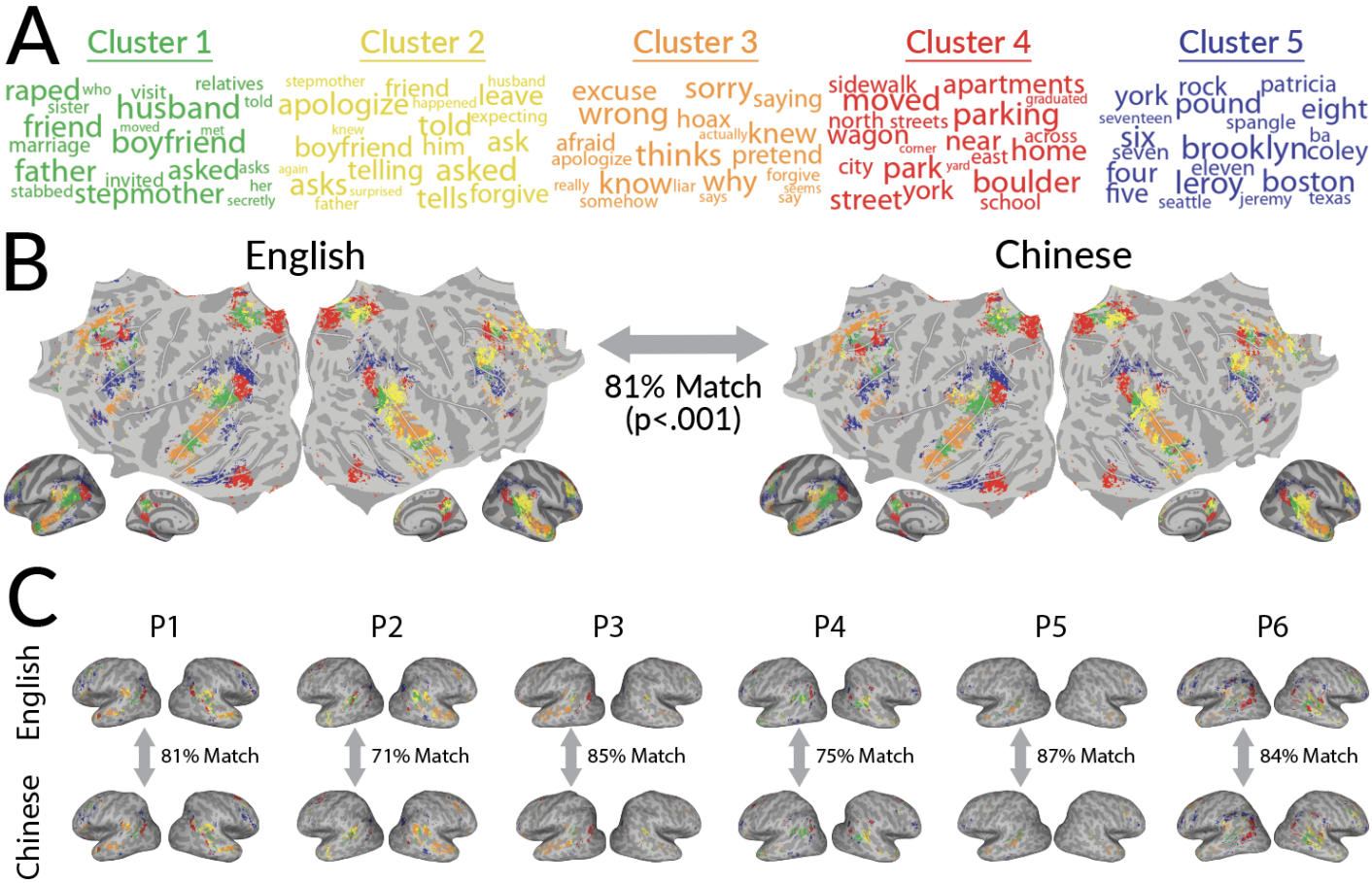


**Figure 3. Shared semantic representations between languages.** Hierarchical clustering on estimated semantic model weights was used to categorize voxels based on their semantic tuning in each language. **A.** Words closest to each cluster. The five semantic clusters are respectively related to family (Cluster 1, green), communication (Cluster 2, yellow), cognition (Cluster 3, orange), locations (Cluster 4, red), and numbers/names (Cluster 5, blue). **B**. Cortical distribution of semantic clusters, group-level. Group-level results are shown for each language. Vertex color reflects the assigned semantic cluster. Vertices that are poorly-predicted by the semantic model are shown in grey. Cluster assignments are the same between languages in 81% of well-predicted vertices. **C**. Cortical distribution of semantic clusters in individual participants. Voxel color reflects the assigned semantic cluster, following the same color scheme as in B. For each participant, cluster assignments are the same between languages in over 70% of well-predicted voxels. Thus, semantic representations are largely shared between languages in individual participant and group-level.

Figure 2 shows that between languages semantic information is represented in the same brain regions. The hypothesis that semantic representations are similar between languages additionally predicts that within these brain regions, the same word meaning should activate a similar set of voxels across languages. This means that each voxel should be tuned towards similar word meanings between languages. Alternatively, a voxel that represents semantic information for both languages might be tuned towards different word meanings in different languages. For example, a voxel might be tuned towards emotion-related words in one language and location-related words in the other. Although such a voxel would represent semantic information in both languages, its semantic tuning would differ between languages. To examine whether the semantic tuning of each voxel is similar between languages, we classified voxels into semantic clusters based on semantic tuning in each language, and then evaluated whether voxelwise cluster assignments are similar between languages.

First, we used a cross-validated clustering approach (*model connectivity*[34]) to identify semantic clusters from the estimated semantic model weights. Five clusters best summarized the distribution of semantic model weights across participants and languages (Figure S9). To interpret each cluster, we identified the English stimulus words that are closest to each cluster. Distance between a word and a cluster was computed as the Pearson correlation between the word embedding and the cluster centroid. Figure 3A lists the closest words to each cluster. The clusters categorize voxels that are tuned towards words related to family (Cluster 1), communication (Cluster 2), cognition (Cluster 3), locations (Cluster 4), and numbers/names (Cluster 5). Then each voxel was assigned to the semantic cluster with the lowest Euclidean distance between the cluster centroid and the vector of semantic model weights for that voxel. Cluster assignments were performed for each participant and language separately. To summarize results across participants, we projected semantic model weights of each participant and language to the template space. Then for each vertex of the template space and for each language separately, we computed the mean model weights across participants, and used the mean model weights to assign each vertex to one of the five clusters.

Figure 3B shows semantic cluster assignments for each language at the group-level. Semantic cluster assignments are shown for vertices that were well-predicted in both languages ($\sqrt{R^2} > 0.1$) in at least one participant. To quantify whether the cluster assignments are consistent between languages, we computed the confusion matrix between cluster assignments in English and Chinese. For 81% of well-predicted vertices semantic cluster assignments are the same between languages ($p<.001$ by a permutation test). Figure 3C shows semantic cluster assignments for each language in individual subjects. For each participant, cluster assignments are the same between languages for over 70% of well-predicted voxels ($p<.001$ by a permutation test). The consistency of semantic cluster assignments suggests that semantic tuning is similar between languages. As a converging test, we measured whether model weights estimated in one language could predict voxel responses to the other language (across-language prediction accuracy). Models estimated for English accurately predicted brain responses to Chinese and vice versa throughout bilateral temporal, parietal, and prefrontal cortices (Figures S6, S11). Overall, these results show that semantic representations are similar between languages.

One potential limitation of the results in Figure 3, which shows that semantic representations are similar between languages, is the cultural homogeneity in the stimulus narratives. Our original experiment used stimulus narratives from a similar cultural context (US-American), and Figure 3 shows that semantic representations are similar after a change in the stimulus language itself. However, culture-specific variations in stimulus content could lead to differences in semantic representations. To test whether semantic representations are similar even with culturally diverse stimuli, we used fMRI to record brain responses while one participant (P1) read a second set of eight narratives with varied cultural contexts. We then used this dataset to estimate voxelwise semantic tuning for each language separately, and then for each language we assigned each voxel to one of the five clusters shown in Figure 3A. Cluster assignments are the same between languages for 71% of well-predicted voxels ($p<.001$ by a permutation test). This suggests that the results shown in Figure 3 are not unique to narratives from a specific cultural context (Figure S12).

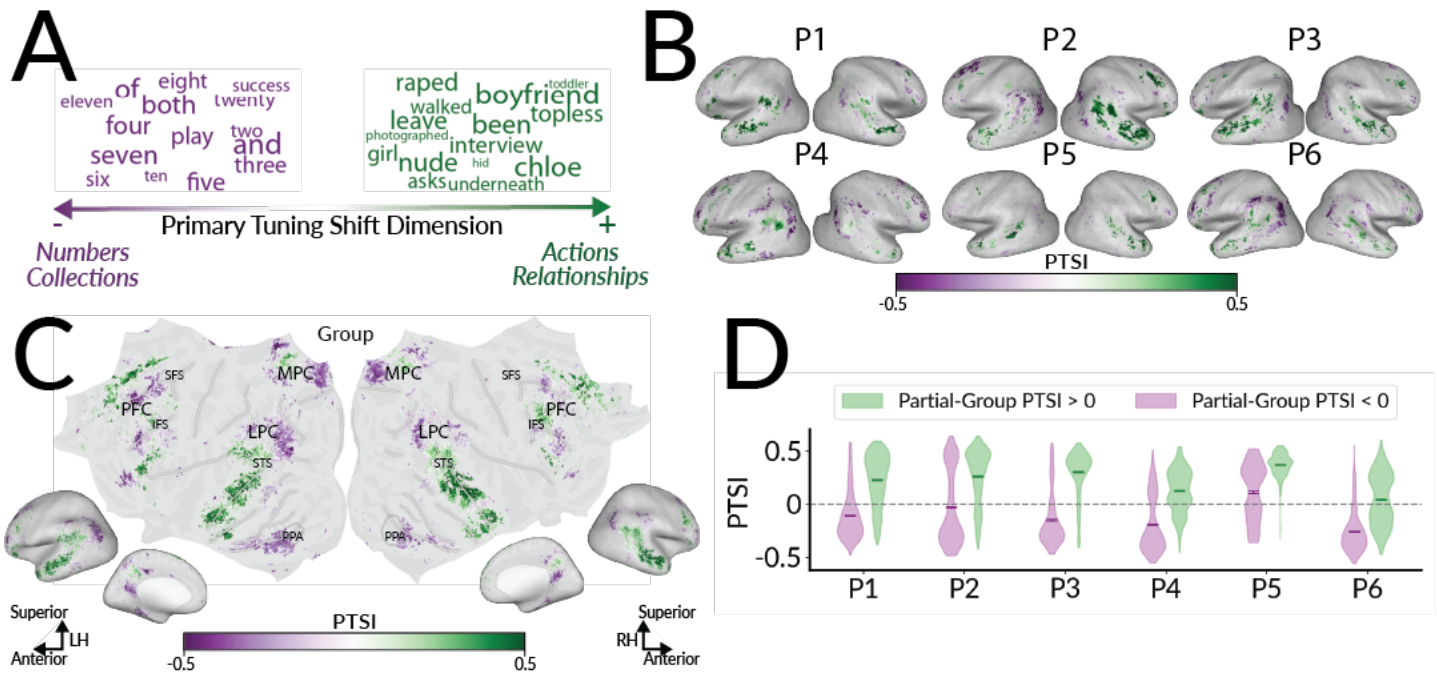


**Figure 4. Cortical distribution of semantic tuning shifts between languages.** Voxelwise *semantic tuning shift* was defined as the change in model weights between English and Chinese: $semantic_tuning_shift = \frac{\beta_{en}}{||\beta_{en}||_2} - \frac{\beta_{zh}}{||\beta_{zh}||_2}$. For each voxel, the semantic tuning shift describes how the semantic tuning differs between the two languages. These shifts in semantic tuning serve to increase the voxel's sensitivity to certain word meanings. The primary dimensions of voxelwise semantic tuning shifts were identified using principal component analysis (PCA). The first semantic tuning shift PC reliably explains variance in semantic tuning shifts across voxels and participants (Figure S13). **A.** Interpretation of the first PC. Words closest to one end of the PC are shown in purple. Words closest to the other end of the PC are shown in green. One end emphasizes number- and collection-related semantics (purple), while the other end emphasizes action- and relationship-related semantics (green). **B.** Cortical distribution of semantic tuning shifts for each participant. The direction of voxelwise semantic tuning shifts was summarized with the *primary tuning shift index* (PTSI), which is the Pearson correlation between a voxel's semantic tuning shift and the first semantic tuning shift PC. The color of each voxel reflects its PTSI. Voxels shown in purple shift towards the negative end of the PC. Voxels shown in green shift towards the positive end of the PC. Poorly predicted vertices are shown in grey. The cortical distribution of PTSI appears to be consistent across participants. **C.** Cortical distribution of semantic tuning shifts at the group-level. Group-level PTSI is shown on the flattened cortical surface of the template space. The color of each vertex reflects group-level PTSI, according to the same colormap as in B. The cortical distribution of group-level PTSI appears to be consistent with results for each individual participant. **D.** Consistency of PTSI between participants. For each participant, the other five participants were used to compute a partial-group estimate of vertexwise PTSI. Violinplots show the distribution of vertexwise PTSI for each participant, separately for vertices in which PTSI is negative (purple violinplots) and positive (green violinplots) in the partial-group. Vertices with positive PTSI in the partial-group also have positive PTSI in the participant ($p<.05$ by a one-sided t-test after Fisher z-transformation), and vertices with negative PTSI in the partial-group also have negative PTSI in the participant ($p<.05$ by a one-sided t-test after Fisher z-transformation; except P5). Overall, these results show that there are systematic shifts in semantic tuning between languages.

Based on prior behavioral evidence that semantic processing is to some extent different between languages[6–8] we hypothesized that semantic representations in the brain are modulated by each language (Figure 1A). Modulation of semantic representations could be observed as a shift in the exact semantic tuning of each voxel.

For example, a voxel might respond to the same semantic clusters (location-related words) in both languages (Figure 2 and 3), but the semantic tuning of the voxel may subtly shift towards words associated with actions ("navigation") in English, and towards words associated with numbers ("distance") in Chinese. These shifts in semantic tuning would serve to increase the voxel's sensitivity to action-related words in English, or to number-related words in Chinese.

To determine whether the semantic tuning of each voxel shifts between languages, we investigated the change in estimated model weights between languages $\frac{\beta_{en}}{\|\beta_{en}\|_2} - \frac{\beta_{zh}}{\|\beta_{zh}\|_2}$, which we refer to as the voxelwise *semantic tuning shift*. The semantic tuning shift for each voxel describes which word meanings are emphasized in each language relative to the other language. To identify dimensions of semantic tuning shifts that are reliable across voxels and participants, we used a leave-one-participant-out procedure. For each of the six participants, we concatenated voxelwise semantic tuning shifts from the other five participants and then used principal component analysis (PCA) to obtain 300 orthogonal axes (principal components; PCs). Then we evaluated how well each PC explains variance in semantic tuning shifts for the left-out participant. The chance rate was defined as the variance explained by the PCs of semantic model weights within each language. The first semantic tuning shift PC, which is the main dimension along which semantic representations shift between languages, reliably explains more variance than chance (Figure S13, by a 95% bootstrap confidence interval). To obtain an estimate of the first semantic tuning shift PC that incorporates data from all six participants, we applied PCA to voxelwise semantic tuning shifts concatenated over all six participants.

The first semantic tuning shift PC reveals the primary dimension in the word embedding space along which voxelwise semantic tuning tends to shift. However, dimensions of the word embedding space are not constructed in terms of classical semantic dimensions. Therefore this dimension alone does not reveal which word meanings each voxel shifts towards or away from. To understand what a shift toward either end of the PC means in terms of the word meanings that activate each voxel, we inspected the set of words that are closest to each end of the PC. These words were identified by finding the word embeddings with the highest Pearson correlation with each end of the PC. Figure 4A shows the English stimulus words that are closest to each end of the PC. (The Chinese stimulus words closest to each end of the PC are similar and are shown in Figure S15). The words closest to one end of the PC (colored in purple) are related to numbers and collections (e.g., "three", "both"). The words closest to the other end (colored in green) are related to actions and human relationships (e.g., "leave", "boyfriend"). A shift along the PC may reflect not only higher sensitivity to the meanings of words from certain semantic categories, but also to the meanings of words from certain grammatical categories. For example, between the two ends of the PC one end (colored in purple) includes relatively more quantifiers, while the other end (colored in green) includes relatively more verbs, suggesting that semantic tuning shifts may be tied to the meanings of words in different grammatical categories. For brevity, we intuitively describe a semantic tuning shift towards the one end of the PC as an emphasis on number and collection-related word meanings, and shifts towards the other end as an emphasis on action- and relationship-related word meanings.

To determine whether semantic tuning shifts are consistent across participants, we mapped the direction of semantic tuning shifts onto the cortical surface of each subject. For each voxel we computed the Pearson correlation between the voxel's semantic tuning shift vector and the first semantic tuning shift PC. We refer to this correlation as the *primary tuning shift index* (PTSI). Because the orientation of PCs are arbitrary, the sign of the PTSI (positive or negative) is also arbitrary. We use the terms "positive" and "negative" simply to distinguish between shifts towards the two ends of the PC. Figure 4B shows voxelwise PTSI for each individual participant. Group-level results are shown in Figure 4C. Voxels with negative PTSI (shown in purple) emphasize number and collection-related words in English, or action and relationship-related words in Chinese. Negative PTSI is found in bilateral lateral parietal cortex (LPC), fusiform gyrus and near parahippocampal place area (PPA), superior and inferior medial parietal cortex (MPC), and middle frontal cortex (FC). Voxels with positive PTSI (shown in green) emphasize action and relationship-related words in English, or number and collection-related words in Chinese. Positive PTSI is found in bilateral STS, LPC, middle MPC, superior frontal

gyrus (SFG), and inferior frontal gyrus (IFG). Visual inspection suggests that the PTSI of each participant is consistent with the rest of the group. To quantify this consistency, we projected voxelwise PTSI of each participant onto the template space, and then compared PTSI between participants in the template space. Figure 4D shows the distribution of PTSI for each individual participant, separately for vertices in which PTSI is negative and positive in the rest of the group. (For each participant we only include vertices that were well-predicted in both languages; $\sqrt{R^2} > 0.1$). Vertices with positive PTSI in the rest of the group also have positive PTSI for each individual participant ($p<.05$, by a one-sample, one-sided t-test after Fisher z-transformation). Vertices with negative PTSI in the rest of the group also have negative PTSI for each individual participant ($p<.05$, by a one-sample, one-sided t-test after Fisher z-transformation; except P6). The distribution of PTSI is consistent between participants, suggesting that semantic tuning shifts are consistent across individuals. Overall, these results show that there are systematic shifts in semantic tuning between languages and that these shifts are consistent across participants.

There are several potential confounds that could affect the results described in Figure 4. First, the idiosyncrasies of one particular word embedding space (fastText embeddings) could bias the estimated semantic tuning shifts. To examine this possibility, we replicated our analyses with a separate semantic embedding space based on a multilingual language model (mBERT[35]) that differs from fastText in its training objectives, training data, and embedding dimensionality. Semantic models estimated with mBERT produced similar results to those estimated with fastText (Figures S1-S4), suggesting that our results are not confounded by the choice of embedding space.

Second, the estimated semantic tuning shifts could reflect imperfections in word embedding alignments between languages. Because of non-isometry between embedding spaces of different languages and limitations to multilingual alignment procedures, embedding spaces are not perfectly aligned between languages[36]. Thus, it could be that estimated semantic tuning shifts merely reflect imperfect alignments. To examine this possibility, we used English-Chinese translation pairs, and for each pair words computed the difference between the embeddings of the two words. We refer to these differences as *misalignments*. Then we computed the PCs of these misalignments, and examined how well the misalignment PCs explain variance in the estimated semantic tuning shifts. Figure S13 shows that the misalignment PCs do not explain more variance in the estimated semantic tuning shifts than chance (by a 95% bootstrap confidence interval), suggesting that our results are not confounded by imperfections in word embedding alignments.

Third, the estimated semantic tuning shifts could reflect differences caused by reading translated stimuli (each narrative was originally written in English and later translated into Chinese). To examine this possibility, we performed a new analysis in which we compared semantic representations between two groups of participants: the L2 English speakers in our original experiment, and a separate group of L1 English speakers. Crucially, for this analysis we used brain responses to English narratives to estimate semantic representations for each group of participants. Both groups of participants read the same stimuli, and none of the stimuli were translated from a different language. Therefore any observed semantic tuning shifts between the two groups must not be the result of reading translated stimuli. For each participant we used brain responses to the English narratives to compute voxelwise semantic tuning, and projected voxelwise semantic tuning to the template space. Then, we computed group-averaged model weights for each vertex of the template space, separately for L1 speakers ($\beta_{L1}$) and for L2 speakers ($\beta_{L2}$). Finally, for each vertex we computed semantic tuning shifts between these two sets of group-averaged model weights ($\frac{\beta_{L2}}{\|\beta_{L2}\|_2} - \frac{\beta_{L1}}{\|\beta_{L1}\|_2}$), and the direction of semantic tuning shifts (PTSI). Figure S14 shows vertexwise PTSI between the L1 and L2 speakers who read the same English stimuli. The PTSI shown in Figure S14 are significantly correlated with those shown in Figure 4C ($r=.63$; $p<.001$ by a one-sided permutation test). The consistency between the two sets of PTSI suggests that the semantic tuning shifts shown in Figure 4 are due to differences between semantic representations, and do not reflect differences caused by reading translated stimuli.

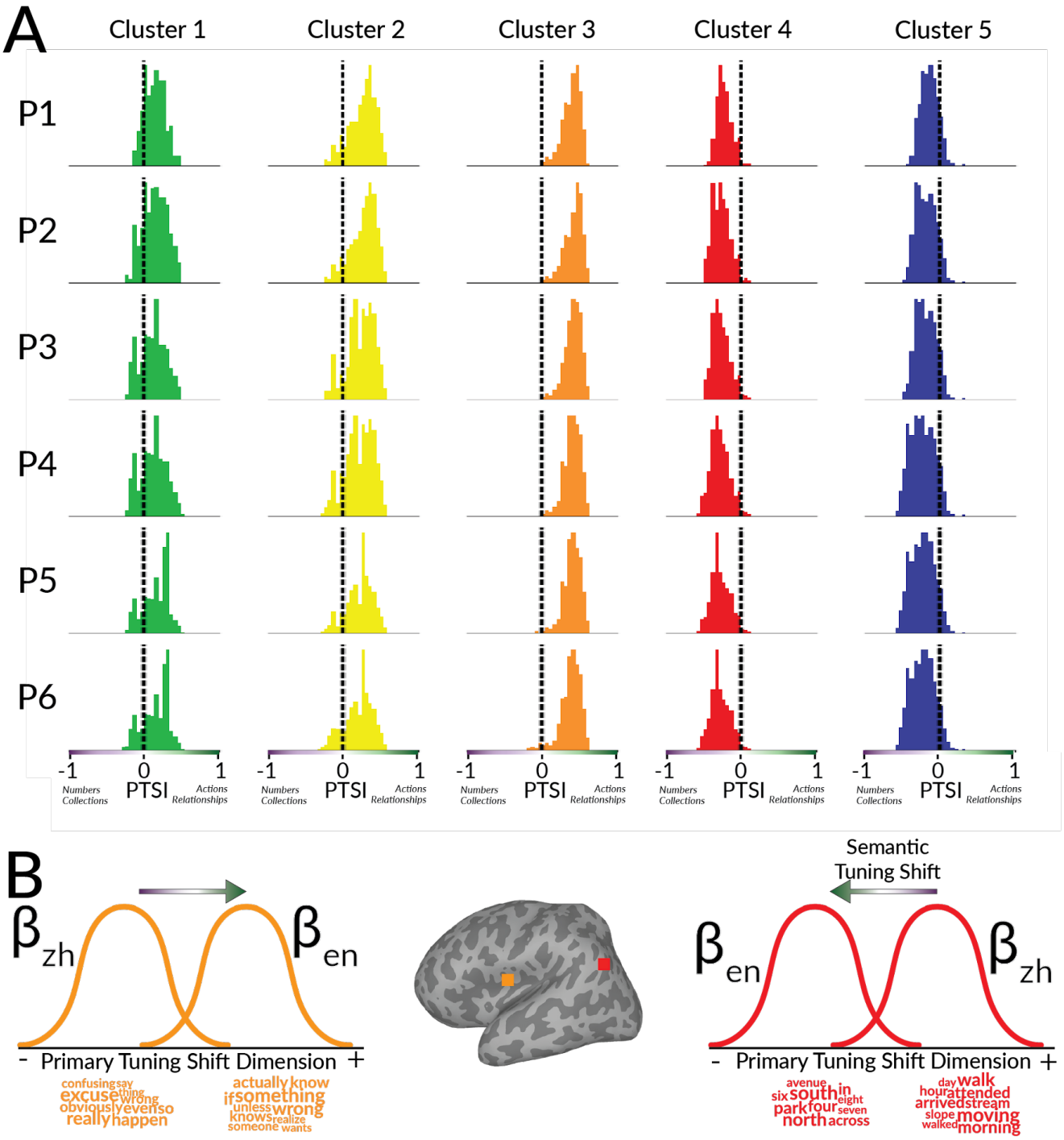


**Figure 5. Semantic tuning shifts for different semantic clusters.** Voxels were categorized into the semantic clusters shown in Figure 3. The distribution of semantic tuning shifts was examined for each semantic cluster. **A**. Semantic tuning shifts for each cluster. Histograms show the distribution of voxelwise PTSI for each cluster and participant separately. Voxels in the family-, communication-, and cognition-related clusters (Clusters 1, 2, and 3) have positive PTSI ($p<.05$ by a two-sided t-test after Fisher z-transformation). Thus, representations of family-, communication-, and cognition-related clusters shift to emphasize action- and relationship-related semantics in English, or number- and collection-related semantics in Chinese. Voxels in the location- and number/name-related clusters (Cluster 4 and 5) have negative PTSI ($p<.05$ by a two-sided t-test after Fisher z-transformation). Thus, representations of location- and name-number-related clusters shift to emphasize number- and collection-related semantics in English, or action- and relationship-related semantics in Chinese. **B**. Semantic tuning shift for two

selected voxels. The voxel in frontal cortex (colored in orange) has positive PTSI. This voxel is tuned towards words related to cognition (Cluster 3) in both languages, but emphasizes action- and relationship-related aspects in English (e.g., "know") compared to Chinese (e.g., "really"). The voxel in parietal cortex (colored in red) voxel has negative PTSI. This voxel is tuned towards words related to locations (Cluster 4) in both languages, but emphasizes number- and collection-related aspects in English (e.g., "four") and action- and relationship-related semantics in Chinese (e.g., "moving"). These two examples illustrate how semantic tuning is modulated between languages.

There are multiple ways in which the semantic tuning shifts shown in Figure 4 could modulate semantic representations between different languages. One possibility is that these semantic tuning shifts systematically modulate semantic representations, such that voxels that are tuned towards similar word meanings shift in a consistent direction. Alternatively, there could be no correspondence between the semantic tuning of a voxel and the direction in which the semantic tuning shifts between languages. To distinguish between these two possibilities, for each voxel we used the English model weights to assign the voxel into one of the five semantic clusters shown in Figure 3A. (Results are consistent when semantic clusters are identified using Chinese model weights; Figure S16). Then we examined the direction of semantic tuning shifts for voxels in each cluster. Figure 5A shows the PTSI for each cluster and participant. For voxels in Clusters 1, 2, and 3 PTSI is positive in all participants ($p<.05$ for each cluster by a two-sided t-test after Fisher z-transformation). Thus, representations of family, communication, and cognition-related clusters emphasize action- and relationship-related aspects of those clusters in English and number- and collection-related aspects in Chinese. For voxels in Clusters 4 and 5 PTSI is negative in all participants ($p<.05$ for each cluster by a two-sided t-test after Fisher z-transformation). Thus, representations of location- and number- and name-related clusters emphasize number- and collection-related aspects in English, or action- and relationship-related aspects in Chinese.

One limitation of the analysis shown in Figure 5 is that projecting semantic tuning shifts for all five semantic clusters onto the first semantic tuning shift PC may mask directions of semantic tuning shifts that are unique to each cluster. To perform a detailed examination of the directions of semantic tuning shifts, we computed the direction of semantic tuning shifts separately for each semantic cluster. We find that the direction of semantic tuning shifts for voxels in each cluster is consistent across participants ($p<.001$, by a two-sided t-test for independent samples). This per-cluster analysis shows the direction of semantic tuning shifts for each cluster is consistent across participants.

To provide two specific examples of how semantic tuning shifts systematically modulate semantic representations, we show the effect of semantic tuning shifts for two selected voxels (Figure 5B). One voxel was selected from Cluster 3 and has positive PTSI. This voxel is tuned towards cognition-related word meanings in both languages, but emphasizes action- and relationship-related aspects in English (e.g., "know") compared to Chinese (e.g., "really"). The other voxel was selected from Cluster 4 and has negative PTSI. This voxel is tuned towards location-related word meanings in both languages, but emphasizes numeric aspects in English (e.g., "four") compared to Chinese (e.g., "moving"). These two examples show that a voxel can represent the same semantic category between languages, yet also exhibit semantic tuning shifts between languages. Overall, the results in Figure 5 show that each language systematically modulates semantic representations.

**Discussion**

This study provides three unique lines of evidence for how in the brains of bilinguals, a single shared semantic system can encode differences between languages. First, the same brain regions represent semantic information for both languages. Second, within these brain regions the specific voxels that are activated by a word meaning are similar between languages. Third, there are systematic, finer-grained shifts between languages in the semantic tuning of each voxel. We replicate these results in each individual participant. Our results generalize across participants, including the two held-out participants. Taken together, these results suggest that in the

brains of bilinguals, semantic representations remain largely similar between languages, but semantic tuning is systematically modulated by each language to encode differences between languages.

Prior neuroimaging studies showed that similar brain regions are activated by different languages[9–13]. These regions could nevertheless represent semantic information differently, if voxelwise semantic tuning varies between languages. Understanding how semantic information is represented between different languages requires not only comparing regions of brain activation, but also the functional semantic representations within these regions. A handful of prior studies have compared functional representations between languages. One such study compared timecourses of brain representations between participants who listened to the same narrative in different languages[17]. This work reported similar brain responses between languages in regions such as the STS and middle frontal gyrus (MFG), and reported statistically significant differences in other regions such as superior temporal gyrus (STG) and right inferior frontal gyrus (IFG). Our study showed that throughout the semantic system, including in STG and IFG, semantic representations are largely similar between languages. The influence of non-semantic representations in the brain may have accounted for the differences observed in STG and IFG. Brain responses reflect not only semantic representations, but also representations from other processes such as pragmatic inference and working memory. Because that work did not explicitly model semantic representations, it remains unclear whether the reported similarities and differences reflect semantic representations. One study explicitly modeled semantic representations in the brain[37], and showed that brain responses to sentences in one language can predict brain responses to sentences in a different language. However, this study focused on brain responses to isolated sentence stimuli, which may not generalize to how the brain represents language in naturalistic contexts[22]. Furthermore, this study did not examine differences between languages, and therefore did not show how semantic representations in the brain can encode language-specific information. Our results add to these prior studies by explicitly modeling semantic representations of naturalistic stimuli, and providing fine-grained, voxel-level comparison of semantic tuning between languages.

Our results inform three lines of prior observations about bilingual language processing. Some studies showed that words in one language can semantically prime words in another language[2], and that words in one language can activate translation equivalents in another language[38]. Our results show that semantic words in one language elicit patterns of brain responses that are similar to those in the other language, suggesting a process that could lead to semantic priming and activation of translation equivalents. Other studies showed that knowledge of one language can interfere with semantic processing in another[2–4]. Our results show that semantic tuning is largely shared between languages, suggesting that learning a new language may influence semantic representations activated by the other language and vice versa. Finally, behavioral studies have shown that the same word meaning can evoke different emotional intensities between native and non-native language comprehension[6,7]. Our results show that there are systematic shifts in voxelwise semantic tuning between languages. These tuning shifts suggest how a single shared semantic system can encode word meanings distinctly for different languages.

Many psycholinguistic theories explicitly differentiate between lexical and conceptual semantic representations. However, in naturalistic stimuli lexical and conceptual semantic representations are likely co-activated in the brain. This co-activation makes it impractical to distinguish between lexical and contextual semantics in a naturalistic experimental paradigm. Thus, in this work we do not explicitly differentiate between these two levels of representation. The semantic representations that we model include representations of meaning that are associated with lexical entries as well as those that are stored in conceptual memory. Nevertheless, our results can inform how psycholinguistic theories might connect to representations in the brain. For example, existing theories suggest that in proficient bilinguals, L1 and L2 have distinct lexical representations, but that both languages are connected to the same conceptual representations[39]. In our study we observed shared semantic representations throughout all brain regions in which the semantic model predicts well. Thus, it is unlikely that lexical representations are anatomically separate at either the lexical or conceptual level. Instead, our results suggest that distinctions between L1 and L2 manifest as modulations of semantic tuning throughout the semantic system.

In this study distributional word embeddings were used to operationalize the meaning of each word. One potential confound is that these embeddings reflect not only the meaning of each word, but also to some extent reflect other word properties such as word frequency and grammatical class. To test for this confound, we created nuisance feature spaces for word frequency and grammatical class, and re-analyzed our data with these nuisance feature spaces. The conclusions of our study were not affected by including these additional nuisance feature spaces (Figure S18). It is impossible to account for all possible non-semantic features that may be reflected in word embeddings, and there could be other non-semantic features in the word embeddings that influence the estimated semantic model weights. Nevertheless, given the robustness of our effects across different word embeddings, and across different brain regions, we do not expect that other non-semantic features would qualitatively change our results.

One limitation of our semantic tuning shift results is that all the participants in our main study were native (L1) Chinese speakers and non-native (L2) English speakers. Therefore the semantic tuning shifts could be due to differences between L1 versus L2 language comprehension, or to differences between English versus Chinese. To address this limitation, we performed an additional experiment in which we used English stimuli to compare semantic tuning between native (L1) and non-native (L2) English speakers. Crucially, this experiment kept the stimulus language the same, but varied whether participants were L1 or L2 speakers. We found that semantic tuning shifts between L1 and L2 English speakers were similar to the semantic tuning shifts shown in the main experiment between L1 Chinese and L2 English comprehension (Figure S14). This suggests that semantic tuning shifts are driven by native (L1) vs. non-native (L2) language processing. A second limitation of our study is that the bilingual participants were sampled from a specific population (L1 Chinese, L2 English participants who are students at a US academic institution). Thus, the results presented here may not reflect semantic representations in the brains of all bilinguals. We speculate that the exact direction and magnitude of semantic tuning shift may depend on factors such as the specific languages spoken by each person, the order in which languages were learned, and the cultural context of language learning. Future studies can use the results and methodology presented here to characterize semantic tuning shifts across additional languages and populations.

While our study does not allow us to draw conclusions about the source of the observed semantic tuning shifts between languages, prior studies offer some possibilities. Prior studies of the human visual system have shown that semantic tuning shifts can be triggered by top-down attention[24]. Furthermore, non-native languages may elicit increased attention and working memory load compared to native languages. Thus, we hypothesize that differences in extra-linguistic processes such as attention and working memory load may modulate semantic representations between different languages. Future studies that combine controlled tasks with the naturalistic bilingual language comprehension paradigm presented here can test this hypothesis.

Our results demonstrate for the first time that the language of a stimulus can elicit systematic shifts in semantic tuning in bilinguals. Moreover, our results demonstrate a new experimental paradigm and analysis method which will enable researchers to examine semantic representations in a broader range of bilingual populations.

## Methods

### Stimuli

*Narrative transcription, translation, and preprocessing*

The stimuli consisted of eleven 10- to 15 min narratives from *The Moth Radio Hour* which have been used in previous studies[23,40–42]. In each narrative, a speaker tells an autobiographical story in front of a live audience. The selected narratives cover a wide range of topics. They include both concrete and abstract words, and include words from a range of grammatical categories (See Figure S19 for details). The audio recording of each narrative was manually transcribed, and the written transcription was aligned to the audio recording. (Details of audio transcription and alignment are described in prior work[42]).

The original narratives were performed verbally in English. To construct matched Chinese stimuli, each of the English narratives was translated into Chinese by a professional translation service. To obtain word presentation times that correspond to natural speech, each translated narrative was read aloud by a professional voice actor. Then the written translations were aligned to these audio recordings. Chinese stimuli were presented with simplified Chinese characters (简化字).

*Stimulus train and test split*

Ten train narratives were used for model estimation, and one held-out test narrative was used for model evaluation. The same test narrative was used for both languages. To obtain noise-ceiling estimates, the test narrative was played to each participant four times in each language. (For P1, the test narrative was played only twice in Chinese due to a change in stimulus design after the first collected sessions.)

*Stimulus presentation format*

The words of each narrative were presented one-by-one at the center of the screen using a Rapid Serial Visual Presentation (RSVP) procedure[43]. Each word was presented for a duration equal to the duration of that word in the spoken version of the narrative.

Each word was presented at the center of the screen in isolation, and a white fixation cross was present at the center of the display throughout the experiment. Participants were asked to fixate on a center cross while reading the narrative. Participants' eye movements were monitored at 60 Hz throughout the scanning sessions using a custom-built camera system equipped with an infrared source (Avotec) and the View-Point EyeTracker software suite (Arrington Research). The eye tracker was calibrated at the end of each run of data acquisition.

Functional MRI data were collected during four 3-hour scanning sessions that were performed on different days. Each scanning session consisted of seven functional runs. Two of these runs presented the test narrative in a single language. The remaining five runs presented five different training narratives. The language of the training narratives was interleaved across runs.

All participants read all the narratives in both English and Chinese. Narrative presentation order was balanced between languages and across participants.

To verify that participants comprehended the narratives and paid attention to the narratives, participants were asked to recount the contents of each narrative to the experimenter at the end of each session and eye movements were manually monitored throughout the scan.

*Experiment with culturally diverse narratives*

For one participant (P1), culturally diverse narratives were used to collect an additional set of functional data. The stimuli for this separate dataset comprised selections from seven written narratives: "Twenty Years After"

(originally published in France; *Vingt ans après*), "The Happy Prince and Other Tales" (originally published in the UK); "The Paper Menagerie" (originally published in the US), "Boy in the Twilight" (originally published in China; *黄昏里的男孩*), "Harry Potter" (originally published in the UK), "Alice in Wonderland" (originally published in the UK), and "The Little Prince" (originally published in France; *Le Petit Prince*). Each narrative was presented in both English and Chinese. Stimulus words were presented in the same RSVP format as the *Moth* narratives.

fMRI data acquisition

Whole-brain MRI data were collected on a 3T siemens TIM trio scanner at the UC Berkeley Brain Imaging Center. A 32-channel Siemens volume coil was used. Functional scans were collected using a T2*-weighted gradient-echo EPI with repetition time (TR) 2.0045s, echo time (TE) 35ms, flip angle 74°, voxel size 2.24x2.24x4.1 mm (slice thickness 3.5mm with 18% slice gap), matrix size 100x100, and field of view 224x224 mm. Thirty axial slices were prescribed to cover the entire cortex and were scanned in interleaved order. A custom-modified bipolar water excitation radiofrequency (RF) pulse was used to prevent contamination from fat signals. Anatomical data were collected using a T1-weighted multi-echo MP-RAGE sequence on the same 3T scanner.

To stabilize head motion during scanning sessions, participants wore a personalized head case that precisely fit the shape of each participant's head[44,45].

fMRI data pre-processing

Each functional run was motion-corrected using the FMRIB Linear Image Registration Tool (FLIRT) from FSL[46]. All volumes in the run were averaged across time to obtain a high quality template volume. FLIRT was used to automatically align the template volume for each run to the overall template, which was chosen to be the temporal average of the first functional run for each participant. These automatic alignments were manually checked and adjusted as necessary to improve accuracy. The cross-run transformation matrix was then concatenated to the motion-correction transformation matrices obtained using MCFLIRT, and the concatenated transformation was used to resample the original data directly into the overall template space. Noise from motion, respiratory, and cardiac signals were removed with a component-based detrending method (CompCor[47]). Responses were z-scored separately for each voxel and narrative. During z-scoring, the mean response across time was subtracted and the remaining response was scaled to have unit variance. Before data analysis, 10 TRs from the beginning and 10 TRs at the end of each narrative were discarded in order to account for the 10 seconds of silence at the beginning and end of each scan and to account for non-stationarity in brain responses at the beginning and end of each scan.

Cortical surface reconstruction and visualization

Cortical surface meshes were generated from the T1-weighted anatomical scans using FreeSurfer software[32]. Before surface reconstruction, anatomical surface segmentations were carefully hand-checked and corrected using Blender software and pycortex[48,49]. Relaxation cuts were made into the surface of each hemisphere. Blender and pycortex were used to remove the surface crossing the corpus callosum. The calcarine sulcus cut was made at the horizontal meridian in V1 using retinotopic mapping data as a guide.

Functional images were aligned to the cortical surface using pycortex. Functional data were projected onto the surface for visualization and analysis using the line-nearest scheme in pycortex. This projection scheme samples the functional data at 32 evenly spaced intervals between the inner (white matter) and outer (pial) surfaces of the cortex and then averages together the samples. Samples are taken using nearest-neighbor interpolation, wherein each sample is given the value of its enclosing voxels.

Cortical parcellation

FreeSurfer ROIs were used to anatomically localize the temporal, parietal, and prefrontal regions for each participant. ROIs were based on the Desikan-Killiany atlas[30]. The ROIs used for the temporal region were *"bankssts", "inferiortemporal", "middletemporal", "superiortemporal", "temporalpole", "transversetemporal", "fusiform", "entorhinal", "parahippocampal"*. The ROIs used for the parietal region were *"inferiorparietal", "superiorparietal", "supramarginal", "precuneus", "isthmuscingulate", "posteriorcingulate"*. The ROIs used for the prefrontal region were *"caudalmiddlefrontal", "parsopercularis", "parsorbitalis", "parstriangularis", "rostralmiddlefrontal", "superiorfrontal", "frontalpole", "caudalanteriorcingulate"*.

Localizers for known ROIs

Known ROIs were localized separately in each participant using a visual category localizer and a retinotopic localizer[50,51]. Details of localizer experiments are provided in prior work[23,42].

Participants

Functional data were collected from six bilingual participants who were fluent in both Mandarin Chinese (native) and English (non-native): P1 (29F), P2 (25M), P3 (25F), P4 (25M), P5 (24F), P6 (26M). Participant P1 was an author of this paper. Language proficiency of each participant was evaluated by the Language Experience and Proficiency Questionnaire (LEAP-Q)[52] and the Language History Questionnaire (LHQ3)[53]. Participants began English language acquisition between the ages of 2 and 11, and spent between 5 and 12 years in a country where English is spoken. At the time of the experiment, participants primarily used Chinese in interactions with family, English in interactions at school/work, and a mix of the two languages in interactions with friends. Please see Table S1 for additional details of participants' use of each language.

All participants were healthy and had normal or corrected-to-normal vision. All subjects were right handed or ambidextrous according to the Edinburgh handedness inventory (laterality quotient of -100: entirely left-handed, +100: entirely right-handed)[54]. Laterality scores were +5, 0, +90, +100, +65, +65 for P1-6 respectively.

A separate set of functional data were collected from six participants between the ages of 24 and 31 who were native English speakers. Data for P7-P12 were originally collected for separate studies[42,55].

Statistical analysis

Voxelwise modeling (VM) was used to model BOLD responses[56,57]. In the VM framework, stimulus and task parameters are nonlinearly transformed into sets of features (also called feature spaces) that are hypothesized to be represented in brain responses. Linearized regression is used to estimate a separate encoding model for each voxel and feature space. Each encoding model describes how a feature space is represented in the BOLD response of a voxel. A held-out dataset that was not used for model estimation is used to evaluate model prediction accuracy and to determine the significance of the model prediction accuracy. Encoding models were estimated and evaluated separately for each participant.

All model fitting and analysis was performed using custom software written in Python, making heavy use of NumPy[58], SciPy[59], Matplotlib[60], Himalaya[61], and Pycortex[49].

*Construction of semantic feature spaces*

To capture the semantic content of the stimulus narratives, each word of the stimulus narrative was projected to a 300-dimensional embedding space[26]. Embedding spaces were constructed separately for English and for

Chinese. The embedding spaces were orthogonally transformed to align the English and Chinese embedding spaces, such that there is a high correlation between embeddings of words in different languages that have similar meanings[27]. This orthogonal transformation was necessary to ensure that reported similarities and differences in model weights are indeed due to underlying brain responses, rather than differences between the embedding space of each language. Furthermore, the estimated semantic models are invariant to orthogonal rotation of the feature spaces because encoding models linearly map from the feature space to brain responses. Given a (num_embedding_dimensions x num_timesteps) feature space matrix $X$ and a (num_timesteps) voxel response vector $y$, we estimate a (num_embedding_dimensions) vector of weights $\beta$ such that $y \approx \beta X$. The estimated weights $\beta$ reflect the semantic tuning of the voxel: the estimated activation of the voxel in response to a word with embedding $v$ is $\beta^T v$. If $X$ is orthogonally rotated with the matrix $M$, the estimated weights would become $M\beta$. But the embedding of each word would also have been rotated by $M$, so the orthogonal rotation of the feature space would not change the estimated tuning of each voxel: with the rotated embedding space, the estimated activation in response to the same word would be $(M\beta)^T(Mv) = \beta^T M^T M v = \beta^T v$, which was the same as the model estimated before orthogonally rotating the embedding space.

Because of non-isometry between embedding spaces of different languages and limitations to multilingual alignment procedures[36], embedding spaces are not perfectly aligned between languages (e.g., "table" and "桌子" [table] may not project to exactly the same vector). To ensure that results are not specific to the idiosyncrasies of a particular embedding space or a particular imperfection in cross-lingual embedding alignments, all analyses were replicated with a different embedding space, multilingual BERT (mBERT, *bert-base-multilingual-cased*[35]). mBERT is a twelve-layer contextual language model that was jointly trained on text from 104 languages. No explicit cross-lingual alignment object was included during the training of mBERT, but embeddings in some layers are implicitly aligned over the course of training[62]. To obtain word embeddings from mBERT, each sentence of the stimulus narratives was provided as input to mBERT and then the 768-dimensional activation of layer nine was used as an embedding of each word. Layer 9 was chosen because it produces the best aligned embeddings (Figure S20), and because intermediate layers of contextual language models have been shown to produce the most accurate predictions of brain responses[41,63–66].

*Construction of low-level feature spaces*

Seven low-level feature spaces were constructed to account for the effects of low-level stimulus information on BOLD responses. For both languages, models were fit with feature spaces that reflect visual spatial and motion features (motion energy)[67–69], word count, single phonemes, diphones, triphones[70], and intermediate level features that capture orthographic similarities by measuring the pixelwise overlap between words[71]. For English, an additional low-level feature space reflected letter count. For Chinese, an additional low-level feature space reflected character count.

*Stimulus feature space preprocessing*

Before voxelwise modeling, each stimulus feature was truncated, downsampled, z-scored, and delayed. Data for the first 10 TRs and the last 10 TRs of each scan were truncated to account for the 10 seconds of silence at the beginning and end of each scan and to account for non-stationarity in brain responses at the beginning and end of each scan. An anti-aliasing, 3-lobe Lanczos filter with cut-off frequency set to the fMRI Nyquist rate (0.25 Hz) was used to resample the stimulus features to match the sampling rate of the fMRI recordings. Then the stimulus features were each z-scored in order to account for z-scoring performed on the MRI data (For details see *MRI data collection*). In the z-scoring procedure, the value of each feature channel was separately normalized by subtracting the mean value of the feature channel across time and then dividing by the standard deviation of the feature channel across time. Lastly, finite impulse response (FIR) temporal filters were used to delay the features in order to model the hemodynamic response function of each voxel. The FIR filters were

implemented by concatenating feature vectors that had been delayed by 2, 4, 6, and 8 seconds (following prior work[23,42,72]). A separate FIR filter was fit for each feature, participant, and language.

*Voxelwise encoding model fitting*

Voxelwise encoding models were estimated in order to determine which features are represented in each voxel. Each model consists of a set of regression weights that describes BOLD responses in a single voxel as a linear combination of the features in a particular feature space. Regression weights were estimated using banded ridge regression[73]. Unlike standard ridge regression, which assigns the same regularization parameter to all feature spaces, banded ridge regression assigns a separate regularization hyperparameter to each feature space. Banded ridge regression thereby avoids biases in estimated model weights that could otherwise be caused by differences in feature space distributions. Mathematically, for a train dataset with $v$ voxels and $n$ TRs, the $m$ delayed feature spaces $F_i(X), i \in \{1, \dots, m\}$ (each dimension $p_i$) were concatenated to form a feature matrix $F'(X)$ (dimension $\sum_i^m \quad p_i \times n$). Then banded ridge regression was used to estimate a mapping $B$ (dimension $v \times \sum_i^m \quad p_i$) from $F'(X)$ to the matrix of voxel responses $Y$ (dimension $v \times n$). $B$ is estimated according to $\hat{B} = argmin_B \left|\left|Y - BF'(X)\right|\right|_2^2 + \lambda \left|\left|CB\right|\right|_2^2$. The diagonal matrix $C$ of regularization hyperparameters for each feature space and each voxel is optimized over 10-fold cross-validation. See *Regularization hyperparameter selection* for details.

*Stepwise regression procedure*

To remove confounds from stimulus correlations between semantics and low-level sensory stimulus features, a stepwise regression procedure was used. First banded ridge regression was used to jointly estimate encoding models that predict BOLD responses from the seven low-level stimulus features. Only data from the train narratives was used to estimate models. Then, the low-level models were used to predict BOLD responses to the train and test narratives. The predicted BOLD responses $\hat{Y}_{lowlevel,train}$ and $\hat{Y}_{lowlevel,test}$ were subtracted from the true BOLD responses $Y_{train}, Y_{test}$. The residual BOLD responses $Y_{train} - \hat{Y}_{lowlevel,train}$ , $Y_{test} - \hat{Y}_{lowlevel,test}$ were zscored. During z-scoring, for each voxel separately the mean response across time was subtracted and the remaining response was scaled to have unit variance. The z-scored residual BOLD responses were used to estimate encoding models that predict BOLD responses from semantic stimulus features.

*Regularization hyperparameter selection*

Five-fold cross-validation was used to find the optimal regularization hyperparameters for each feature space and voxel. Hyperparameter candidates were chosen with a random search procedure[74]: 1000 normalized hyperparameter candidates were randomly sampled from a dirichlet distribution and were then scaled by 21 log-spaced values ranging from $10^{-10}$ to $10^{10}$. The regularization hyperparameters for each feature space and voxel were selected as the hyperparameters that produced the minimum squared error (L2) loss between the predicted voxel responses and the recorded voxel responses ($argmin_{hyperparameters} \left|\left|\hat{y} - y\right|\right|_2^2$). Regularization hyperparameters were chosen separately for each participant and language. Hyperparameter search was performed using the Himalaya Python package[61].

*Model estimation and evaluation*

The selected regularization hyperparameters were used to estimate model weights that map from the semantic feature space to voxel BOLD responses. Model weights were estimated separately for each voxel, language, and participant. The model weights for each voxel and language reflect the semantic tuning of the voxel in that language.

The test dataset was not used to select hyperparameters or to estimate regression weights. The prediction accuracy $R^2$of the feature spaces was computed per voxel as the coefficient of determination (CD) between the predicted voxel responses and the recorded voxel responses on the test dataset. To determine which voxels represent semantic information in each language, prediction accuracy was computed for within-language predictions (train and test on the same language). To determine how well model weights estimated for one language generalize to the other language, prediction accuracy was also computed for across-language predictions (train on one language, and test on a different language).

A permutation test with 1000 iterations was used to compute the statistical significance of prediction accuracy. In each permutation, the test responses were shuffled in blocks of 10 TRs[41,42,65,75–79]. Shuffling was performed in blocks of 10 TRs in order to preserve autocorrelations in voxel responses. Then the prediction accuracy ($R^2$) was computed between the predicted responses and the permuted test responses. The distribution of test accuracies over permutation iterations was used as a null distribution to compute the p-value of prediction accuracy for each voxel. A Benjamini-Hochberg correction for multiple comparisons was applied to the voxelwise p-values[80]. Permutation tests were performed separately for each voxel, language, and participant.

Noise-ceiling correction was performed by normalizing the prediction accuracy of each voxel $R^2$ by the maximum possible prediction accuracy (*noise-ceiling*)[31–33]. To compute the noise-ceiling, first the maximum explainable variance (*EV*, also referred to as *signal power*) is computed for each voxel. EV measures the consistency of measured BOLD responses over repeated stimulus presentations, and reflects the amount of response variance in the test data that could be explained by a perfect model. Formally, for a test dataset with $N$ repeats of a $T$ TR test narrative, and recorded BOLD responses $y_1 \dots y_N \in R^T$ for a single voxel, EV is defined as follows (each $y_i$ is first zscored across time):

$$\bar{Y} = \frac{1}{N}\sum_{i=1}^{N} y_i$$

$$EV = \frac{1}{N-1}\left(NVar(\bar{Y}) - \frac{1}{N}\sum_{i=1}^{N} Var(Y_i)\right)$$

The noise-ceiling $R^2_{max}$ is obtained by dividing the EV of each voxel by $Var(\bar{Y})$. The noise-ceiling corrected prediction accuracy $R^2_{norm}$ is then obtained for each voxel by dividing the prediction accuracy $R^2$ by the noise-ceiling $R^2_{max}$. For very noisy voxels, the estimated noise-ceiling may be lower than the measured $R^2$ and therefore lead to divergent estimates of $R^2_{norm}$. We used a heuristic to correct for this divergence. We identified the set of voxels where $R^2$ is greater than $R^2_{max}$, selected the maximum $R^2_{max}$over these voxels, and then clipped $R^2_{max}$ to be above this maximum value. Note that this heuristic results in a conservative estimate of the noise-ceiling corrected prediction accuracy.

*Group-level prediction accuracy*

Group-level prediction accuracy was computed by computing prediction accuracy for each participant in the participant's native brain space, and then projecting individual participant results into a template space (fsAverage[28]). Average prediction accuracy across six participants was computed for each fsAverage vertex.

*Generalization to new participants*

To ensure generalization to new participants, two steps were performed. First, the entire analysis was performed at the individual participant level – group-averaged results are shown only as summary statistics. Second, before the final analyses were performed, two out of the six participants were set aside as held-out participants. The data for these participants were not analyzed until the data analysis and interpretation pipeline was finalized[81].

Voxel Selection for Tuning Analyses

To ensure that semantic tuning shift analyses were performed only on voxels that represent semantic information in both English and Chinese, all of the following model weight interpretation analyses were performed only on voxels that were well-predicted ($\sqrt{R^2} > 0.1$) in both English and Chinese.

Semantic Tuning Shifts

The semantic tuning shift of each voxel was used to describe how voxelwise semantic tuning changes between languages. First, the model weights were normalized for each language and voxel by dividing each 300-dimensional vector of model weights by the L2-norm of the vector. Then, the semantic tuning shift of each voxel was computed by subtracting the normalized Chinese model weights from the normalized English model weights. Formally, the semantic tuning shift for a voxel with weights $\beta_{en}$ and $\beta_{zh}$ was defined as $semantic_tuning_shift = \frac{\beta_{en}}{||\beta_{en}||_2} - \frac{\beta_{zh}}{||\beta_{zh}||_2}$.

The semantic tuning shift vector for each voxel describes how semantic tuning changes from Chinese to English. For example, for a voxel that becomes more tuned towards number-related semantics when the stimulus language changes from Chinese to English, the semantic tuning shift vector would point in the direction of number semantics in the embedding space.

Note that defining the semantic tuning shift as the change in tuning from Chinese to English ($\frac{\beta_{zh}}{||\beta_{zh}||_2} - \frac{\beta_{en}}{||\beta_{en}||_2}$) would change the sign of the semantic tuning shift vector but also swap the languages on each end of the vector. Thus, the choice to define semantic tuning shift as the shift from Chinese to English rather than from English to Chinese does not affect the reported results.

*Dimensions of semantic tuning shift*

Principal component analysis (PCA) was used to determine the main directions of semantic tuning shifts. Because model weights accurately describe semantic tuning only for well-predicted voxels, we only investigated semantic tuning shifts for voxels that were well-predicted in both languages (see *Voxel Selection for Tuning Analyses* for details; selecting voxels based on significance instead of prediction accuracy produces similar results as shown in Figure S21). To increase the influence of better-predicted voxels on the estimated principal components (PCs), the semantic tuning shift of each voxel was scaled by the voxel's mean prediction accuracy between languages. The semantic tuning shift vectors were concatenated across participants and languages. PCA was applied to the concatenated semantic tuning shift vectors to find a set of orthogonal axes that best explain variance in voxelwise semantic tuning shift vectors. The PCs that explain the highest variance in voxelwise semantic tuning shift describe the primary semantic dimensions of semantic tuning shifts. We refer to the PC that explains the most variance in voxelwise semantic tuning shifts as the *first semantic tuning shift PC.* To examine whether the semantic tuning shift for each voxel is towards one end of the first semantic tuning shift PC or the other, the Pearson correlation was computed between the semantic tuning shift vector of each voxel and the PC. For each voxel we refer to this correlation as the *primary tuning shift index* (PTSI).

Weight Clustering

A clustering approach was used to separate voxels into groups that have similar semantic tuning[40]. Model weights for each participant and language were projected to a standard template space (fsAverage[32]). Each projected model weight $\beta_{vertex,participant,language} \in R^{300}$ was normalized to have unit L2-norm:

$\beta_{normalized} = \frac{\beta}{||\beta||_2}$. The normalized model weights were averaged across participants and languages, and then hierarchical clustering was performed on the normalized group-averaged model weights. Clustering was only performed on vertices that were well-predicted in both languages (group-averaged $\sqrt{R^2_{en}} > 0.05$ and $\sqrt{R^2_{zh}} > 0.05$). In total, there are 12 sets of model weights across the six participants and two languages. The number of clusters was chosen based on a leave-one-out cross-validation procedure. One of the twelve sets of model weights was held out in each cross-validation fold. The remaining eleven sets of model weights were averaged across participants and languages for each vertex of the template space, and hierarchical clustering was used to obtain $N$ group-level clusters, separately for $N$ ranging from 2 through 25. For each number $N$ of clusters, the group-level model weight clusters were used to predict BOLD responses for the held out participant and language in the template space. The cross-validation accuracy was computed for each vertex as the CD ($R^2$) between the predicted and recorded BOLD responses. Only vertices that were well-predicted in both languages (group-averaged $\sqrt{R^2_{en}} > 0.05$ and $\sqrt{R^2_{zh}} > 0.05$) were included in this analysis. The cross-validation score plateaus around five clusters (Figure S9). Thus, we chose to use five clusters for the analyses shown in Figure 3 and Figure 5. This clustering procedure resulted in five 300-dimensional cluster centroids. These centroids define clusters of voxels that are each tuned towards similar word meanings. Voxels were assigned to clusters based on the Pearson correlation between voxelwise model weights and each of the 300-dimensional cluster centroids. Cluster assignments were performed separately for each participant and language.

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Author contributions: CC, XG, CT, JG and FD conceived and designed the experiments. CT and XG recruited bilingual participants. CC, CT, and XG collected fMRI data. XG generated the stimuli, preprocessed the fMRI data, and performed surface segmentation. CC performed analyses. CC and FD wrote the manuscript. All authors contributed to editing the manuscript. FD and JG directed and supervised all aspects of this project.

Data availability: Data will be made publically available on GIN (https://gin.g-node.org) immediately upon acceptance.

Code availability: Analysis code is available in the CodeOcean capsule linked to this submission, and will be made publically available immediately upon acceptance.

References


1. Bialystok, E. The bilingual adaptation: How minds accommodate experience. *Psychol. Bull.* **143**, 233–262 (2017).
2. Duyck, W. Translation and associative priming with cross-lingual pseudohomophones: evidence for nonselective phonological activation in bilinguals. *J. Exp. Psychol. Learn. Mem. Cogn.* **31**, 1340–1359 (2005).
3. Van Hell, J. G. & Dijkstra, T. Foreign language knowledge can influence native language performance in exclusively native contexts. *Psychon. Bull. Rev.* **9**, 780–789 (2002).
4. Dijkstra, T., Grainger, J. & van Heuven, W. J. B. Recognition of Cognates and Interlingual Homographs: The Neglected Role of Phonology. *J. Mem. Lang.* **41**, 496–518 (1999).
5. Malik-Moraleda, S., Mahowald, K., Conway, B. R. & Gibson, E. Concepts Are Restructured During Language Contact: The Birth of Blue and Other Color Concepts in Tsimane'-Spanish Bilinguals. *Psychol. Sci.* **34**, 1350–1362 (2023).
6. Schrauf, R. W. & Rubin, D. C. 'language' and 'feel' of bilingual memory. *Socioling. Stud.* **5**, 21–39 (2004).
7. Pavlenko, A. Bilingualism and emotions. *Multilingua* **21**, 45–78 (2002).
8. Marian, V. & Neisser, U. Language-dependent recall of autobiographical memories. *J. Exp. Psychol. Gen.* **129**, 361–368 (2000).
9. Abutalebi, J. & Green, D. Bilingual language production: The neurocognition of language representation and control. *J. Neurolinguistics* **20**, 242–275 (2007).
10. Klein, D., Milner, B., Zatorre, R. J., Meyer, E. & Evans, A. C. The neural substrates underlying word generation: a bilingual functional-imaging study. *Proc. Natl. Acad. Sci. U. S. A.* **92**, 2899–2903 (1995).
11. Wagner, A. D. *et al.* A functional MRI study of semantic processing in bilinguals. *Neuroimage* **3**, S465 (1996).
12. Luke, K.-K., Liu, H.-L., Wai, Y.-Y., Wan, Y.-L. & Tan, L. H. Functional anatomy of syntactic and semantic processing in language comprehension. *Hum. Brain Mapp.* **16**, 133–145 (2002).
13. Malik-Moraleda, S. *et al.* An investigation across 45 languages and 12 language families reveals a universal language network. *Nat. Neurosci.* **25**, 1014–1019 (2022).
14. Xu, M., Baldauf, D., Chang, C. Q., Desimone, R. & Tan, L. H. Distinct distributed patterns of neural activity are associated with two languages in the bilingual brain. *Sci Adv* **3**, e1603309 (2017).
15. Kim, K. H., Relkin, N. R., Lee, K. M. & Hirsch, J. Distinct cortical areas associated with native and second languages. *Nature* **388**, 171–174 (1997).
16. Dehaene, S. *et al.* Anatomical variability in the cortical representation of first and second language. *Neuroreport* **8**, 3809–3815 (1997).
17. Honey, C. J., Thompson, C. R., Lerner, Y. & Hasson, U. Not lost in translation: neural responses shared across languages. *J. Neurosci.* **32**, 15277–15283 (2012).
18. Li, J. *et al.* Le Petit Prince multilingual naturalistic fMRI corpus. *Sci Data* **9**, 530 (2022).
19. Dunagan, D. *et al.* Neural correlates of semantic number: A cross-linguistic investigation. *Brain Lang.* **229**, 105110 (2022).
20. Fedorenko, E. & Kanwisher, N. Neuroimaging of language: Why hasn't a clearer picture emerged? *Language and Linguistics Compass* **3**, 839–865 (2009).
21. Buchweitz, A., Shinkareva, S. V., Mason, R. A., Mitchell, T. M. & Just, M. A. Identifying bilingual semantic neural representations across languages. *Brain Lang.* **120**, 282–289 (2012).
22. Hamilton, L. S. & Huth, A. G. The revolution will not be controlled: natural stimuli in speech neuroscience. *Lang Cogn Neurosci* **35**, 573–582 (2020).
23. Huth, A. G., de Heer, W. A., Griffiths, T. L., Theunissen, F. E. & Gallant, J. L. Natural speech reveals the semantic maps that tile human cerebral cortex. *Nature* **532**, 453–458 (2016).
24. Çukur, T., Nishimoto, S., Huth, A. G. & Gallant, J. L. Attention during natural vision warps semantic representation across the human brain. *Nat. Neurosci.* **16**, 763–770 (2013).
25. Deniz, F., Tseng, C., Wehbe, L., Dupré la Tour, T. & Gallant, J. L. Semantic Representations during

Language Comprehension Are Affected by Context. *J. Neurosci.* **43**, 3144–3158 (2023).
26. Bojanowski, P., Grave, E., Joulin, A. & Mikolov, T. Enriching Word Vectors with Subword Information. *Transactions of the Association for Computational Linguistics* **5**, 135–146 (2017).
27. Joulin, A., Bojanowski, P., Mikolov, T., Jegou, H. & Grave, E. Loss in Translation: Learning Bilingual Word Mapping with a Retrieval Criterion. *arXiv [cs.CL]* (2018).
28. Fischl, B., Sereno, M. I., Tootell, R. B. & Dale, A. M. High-resolution intersubject averaging and a coordinate system for the cortical surface. *Hum. Brain Mapp.* **8**, 272–284 (1999).
29. Binder, J. R., Desai, R. H., Graves, W. W. & Conant, L. L. Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb. Cortex* **19**, 2767–2796 (2009).
30. Desikan, R. S. *et al.* An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. *Neuroimage* **31**, 968–980 (2006).
31. Sahani, M. & Linden, J. How Linear are Auditory Cortical Responses? in *Advances in Neural Information Processing Systems* (eds. Becker, S., Thrun, S. & Obermayer, K.) vol. 15 (MIT Press, 2002).
32. Schoppe, O., Harper, N. S., Willmore, B. D. B., King, A. J. & Schnupp, J. W. H. Measuring the Performance of Neural Models. *Front. Comput. Neurosci.* **10**, 10 (2016).
33. Hsu, A., Borst, A. & Theunissen, F. E. Quantifying variability in neural responses and its application for the validation of model predictions. *Network* **15**, 91–109 (2004).
34. Meschke, E. X., Visconti di Oleggio Castello, M., Dupré la Tour, T. & Gallant, J. L. Model connectivity: leveraging the power of encoding models to overcome the limitations of functional connectivity. *bioRxiv* (2023) doi:10.1101/2023.07.17.549356.
35. Devlin, J., Chang, M.-W., Lee, K. & Toutanova, K. BERT: Pre-training of Deep Bidirectional Transformers for Language Understanding. *arXiv [cs.CL]* (2018).
36. Søgaard, A., Ruder, S. & Vulić, I. On the Limitations of Unsupervised Bilingual Dictionary Induction. *arXiv [cs.CL]* (2018).
37. Yang, Y., Wang, J., Bailer, C., Cherkassky, V. & Just, M. A. Commonalities and differences in the neural representations of English, Portuguese, and Mandarin sentences: When knowledge of the brain-language mappings for two languages is better than one. *Brain Lang.* **175**, 77–85 (2017).
38. Thierry, G. & Wu, Y. J. Brain potentials reveal unconscious translation during foreign-language comprehension. *Proc. Natl. Acad. Sci. U. S. A.* **104**, 12530–12535 (2007).
39. Potter, M. C., So, K.-F., Eckardt, B. V. & Feldman, L. B. Lexical and conceptual representation in beginning and proficient bilinguals. *Journal of Verbal Learning and Verbal Behavior* **23**, 23–38 (1984).
40. de Heer, W. A., Huth, A. G., Griffiths, T. L., Gallant, J. L. & Theunissen, F. E. The Hierarchical Cortical Organization of Human Speech Processing. *J. Neurosci.* **37**, 6539–6557 (2017).
41. Chen, C., Dupré la Tour, T., Gallant, J. L., Klein, D. & Deniz, F. The cortical representation of language timescales is shared between reading and listening. *Commun Biol* **7**, 284 (2024).
42. Deniz, F., Nunez-Elizalde, A. O., Huth, A. G. & Gallant, J. L. The Representation of Semantic Information Across Human Cerebral Cortex During Listening Versus Reading Is Invariant to Stimulus Modality. *J. Neurosci.* **39**, 7722–7736 (2019).
43. Forster, K. I. Visual perception of rapidly presented word sequences of varying complexity. *Percept. Psychophys.* **8**, 215–221 (1970).
44. Gao, J. S. fMRI visualization and methods. *by JS Gao · Cited by 3 · 2015by JS Gao · Cited by 3 · 2015* (2015).
45. Power, J. D. *et al.* Customized head molds reduce motion during resting state fMRI scans. *Neuroimage* **189**, 141–149 (2019).
46. Jenkinson, M., Bannister, P., Brady, M. & Smith, S. Improved optimization for the robust and accurate linear registration and motion correction of brain images. *Neuroimage* **17**, 825–841 (2002).
47. Behzadi, Y., Restom, K., Liau, J. & Liu, T. T. A component based noise correction method (CompCor) for BOLD and perfusion based fMRI. *Neuroimage* **37**, 90–101 (2007).
48. Community, B. O. Blender - a 3D modelling and rendering package. Preprint at http://www.blender.org (2018).
49. Gao, J. S., Huth, A. G., Lescroart, M. D. & Gallant, J. L. Pycortex: an interactive surface visualizer for

fMRI. *Front. Neuroinform.* **9**, 23 (2015).
50. Spiridon, M., Fischl, B. & Kanwisher, N. Location and spatial profile of category-specific regions in human extrastriate cortex. *Hum. Brain Mapp.* **27**, 77–89 (2006).
51. Hansen, K. A., Kay, K. N. & Gallant, J. L. Topographic organization in and near human visual area V4. *J. Neurosci.* **27**, 11896–11911 (2007).
52. Kaushanskaya, M., Blumenfeld, H. K. & Marian, V. The Language Experience and Proficiency Questionnaire (LEAP-Q): Ten years later. *Biling.* **23**, 945–950 (2020).
53. Li, P., Zhang, F., Yu, A. & Zhao, X. Language History Questionnaire (LHQ3): An enhanced tool for assessing multilingual experience. *Bilingualism: Language and Cognition* **23**, 938–944 (2020).
54. Oldfield, R. C. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* **9**, 97–113 (1971).
55. Chen, C., Gong, L., Deniz, F., Klein, D. & Gallant, J. Representations of Semantic Relations in the Human Brain During Active Relation Processing. in *Cognitive Computational Neuroscience* (2024).
56. Wu, M. C.-K., David, S. V. & Gallant, J. L. Complete functional characterization of sensory neurons by system identification. *Annu. Rev. Neurosci.* **29**, 477–505 (2006).
57. Naselaris, T., Kay, K. N., Nishimoto, S. & Gallant, J. L. Encoding and decoding in fMRI. *Neuroimage* **56**, 400–410 (2011).
58. Harris, C. R. *et al.* Array programming with NumPy. *Nature* **585**, 357–362 (2020).
59. Virtanen, P. *et al.* SciPy 1.0: fundamental algorithms for scientific computing in Python. *Nat. Methods* **17**, 261–272 (2020).
60. Hunter, J. D. Matplotlib: A 2D Graphics Environment. *Comput. Sci. Eng.* **9**, 90–95 (2007).
61. Dupré la Tour, T., Eickenberg, M., Nunez-Elizalde, A. O. & Gallant, J. L. Feature-space selection with banded ridge regression. *Neuroimage* **264**, 119728 (2022).
62. Pires, T., Schlinger, E. & Garrette, D. How multilingual is Multilingual BERT? *arXiv [cs.CL]* (2019) doi:10.18653/v1/P19-1493.
63. Toneva, M. & Wehbe, L. Interpreting and improving natural-language processing (in machines) with natural language-processing (in the brain). *Adv. Neural Inf. Process. Syst.* (2019).
64. Caucheteux, C. & King, J.-R. Brains and algorithms partially converge in natural language processing. *Commun Biol* **5**, 134 (2022).
65. Lamarre, M., Chen, C. & Deniz, F. Attention weights accurately predict language representations in the brain. in *Findings of the Association for Computational Linguistics: EMNLP 2022* (eds. Goldberg, Y., Kozareva, Z. & Zhang, Y.) 4513–4529 (Association for Computational Linguistics, Abu Dhabi, United Arab Emirates, 2022).
66. Schrimpf, M. *et al.* The neural architecture of language: Integrative modeling converges on predictive processing. *Proc. Natl. Acad. Sci. U. S. A.* **118**, (2021).
67. Adelson, E. H. & Bergen, J. R. Spatiotemporal energy models for the perception of motion. *J. Opt. Soc. Am. A* **2**, 284–299 (1985).
68. Watson, A. B. & Ahumada, A. J., Jr. Model of human visual-motion sensing. *J. Opt. Soc. Am. A* **2**, 322–341 (1985).
69. Nishimoto, S. & Gallant, J. L. A three-dimensional spatiotemporal receptive field model explains responses of area MT neurons to naturalistic movies. *J. Neurosci.* **31**, 14551–14564 (2011).
70. Gong, X. L. *et al.* Phonemic segmentation of narrative speech in human cerebral cortex. *Nat. Commun.* **14**, 4309 (2023).
71. Gong, X. L. Language representation in human cerebral cortex. (UC Berkeley, 2024).
72. Nakai, T., Yamaguchi, H. Q. & Nishimoto, S. Convergence of Modality Invariance and Attention Selectivity in the Cortical Semantic Circuit. *Cereb. Cortex* **31**, 4825–4839 (2021).
73. Nunez-Elizalde, A. O., Huth, A. G. & Gallant, J. L. Voxelwise encoding models with non-spherical multivariate normal priors. *Neuroimage* **197**, 482–492 (2019).
74. Bergstra, J. & Bengio, Y. Random search for hyper-parameter optimization. *J. Mach. Learn. Res.* **13**, 281–305 (2012).
75. LeBel, A. *et al.* A natural language fMRI dataset for voxelwise encoding models. *Sci Data* **10**, 555

(2023).
76. Jain, S. *et al.* Interpretable multi-timescale models for predicting fMRI responses to continuous natural speech. in *Advances in Neural Information Processing Systems* 13738–13749 (2020).
77. Reddy, A. J. & Wehbe, L. Can fMRI reveal the representation of syntactic structure in the brain? *bioRxiv* (2020) doi:10.1101/2020.06.16.155499.
78. Oota, S. R., Marreddy, M., Gupta, M. & Bapi, R. How does the brain process syntactic structure while listening? in *Findings of the Association for Computational Linguistics: ACL 2023* (eds. Rogers, A., Boyd-Graber, J. & Okazaki, N.) 6624–6647 (Association for Computational Linguistics, Toronto, Canada, 2023).
79. Tang, J., Du, M., Vo, V. A., Lal, V. & Huth, A. G. Brain encoding models based on multimodal transformers can transfer across language and vision. in *Proceedings of the 37th International Conference on Neural Information Processing Systems* 29654–29666 (Curran Associates Inc., Red Hook, NY, USA, 2024).
80. Benjamini, Y. & Hochberg, Y. Controlling the false discovery rate: A practical and powerful approach to multiple testing. *J. R. Stat. Soc. Series B Stat. Methodol.* **57**, 289–300 (1995).
81. Popham, S. F. *et al.* Visual and linguistic semantic representations are aligned at the border of human visual cortex. *Nat. Neurosci.* **24**, 1628–1636 (2021).
82. Brysbaert, M., Warriner, A. B. & Kuperman, V. Concreteness ratings for 40 thousand generally known English word lemmas. *Behav. Res. Methods* **46**, 904–911 (2014).
83. Kitaev, N., Cao, S. & Klein, D. Multilingual constituency parsing with self-attention and pre-training. in *Proceedings of the 57th Annual Meeting of the Association for Computational Linguistics* 3499–3505 (Association for Computational Linguistics, Stroudsburg, PA, USA, 2019).