RESEARCH ARTICLE

WILEY

Individual differences in representational similarity of first and second languages in the bilingual brain

Emily S. Nichols^{1,2} | Yue Gao³ | Sofia Fregni⁴ | Li Liu³ | Marc F. Joanisse^{2,5}

¹Department of Applied Psychology, Faculty of Education, The University of Western Ontario, London, Canada

²Brain and Mind Institute, The University of Western Ontario, London, Canada

³State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing, China

⁴Faculty of Psychology, Dresden University of Technology, Dresden, Germany

⁵Department of Psychology, The University of Western Ontario, London, Canada

Correspondence

Emily S. Nichols, Department of Applied Psychology, Faculty of Education, The University of Western Ontario, 1137 Western Road, London, ON N6A 5C2, Canada. Email: enicho4@uwo.ca

Li Liu, State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, No.19, Xinjiekou Wai St., Haidian District, Beijing 100875, China. Email: lilyliu@bnu.edu.cn

Funding information

National Natural Science Foundation of China. Grant/Award Number: 31970977. National Key Laboratory of Cognitive Neuroscience and Learning Open-Project; Natural Sciences and Engineering Research Council of Canada

Abstract

Current theories of bilingualism disagree on the extent to which separate brain regions are used to maintain or process one's first and second language. The present study took a novel multivariate approach to address this question. We examined whether bilinguals maintain distinct neural representations of two languages; specifically, we tested whether brain areas that are involved in processing word meaning in either language are reliably representing each language differently, and whether language representation is influenced by individual differences in proficiency level and age of acquisition (AoA) of L2. Thirty-one English-Mandarin bilingual adults performed a picture-word matching task in both languages. We then used representational similarity analysis to examine which brain regions reliably showed different patterns of activity for each language. We found that both proficiency and AoA predicted dissimilarity between language representations in several brain areas within the language network as well as several regions of the ventral visual pathway, demonstrating that top-down language knowledge and individual language experience shapes concept representation in this processing stream. The results support the model of an integrated language system in bilinguals, along with a novel description of how representations for each language change with proficiency level and L2 AoA.

KEYWORDS

bilingualism, individual differences, representational similarity analysis, word recognition

1 INTRODUCTION

Current theories of bilingual language processing hold that bilingual speakers coactivate their two languages during speech, and that they maintain similar, overlapping representations for both (Goldrick, Putnam, & Schwarz, 2016; Pyers & Emmorey, 2008; Spalek, Hoshino, Wu, Damian, & Thierry, 2014; Starreveld, De Groot, Rossmark, & Van Hell, 2014). In addition, past neuroimaging research has provided much evidence that a second language (L2) is processed similarly to the speaker's first language (Cao, Tao, Liu, Perfetti, & Booth, 2013;

Indefrey, 2006; Perani et al., 2003; Sun et al., 2015; Wang et al., 2011). Even when L1-L2 differences exist, such as more extensive activity in L2 (Lucas, McKhann, & Ojemann, 2004; Nichols & Joanisse, 2016), there remains extensive overlap (Indefrey, 2006). This suggests that similar underlying language networks are engaged regardless of which language is being used. The concept of language coactivation in bilinguals is widely accepted, as is that of a single, integrated lexicon (van Heuven & Dijkstra, 2010; Zeng, Branigan, & Pickering, 2020). Proponents of the BIA+/BIA-d framework also propose that there is an L1/L2 language "node," which determines which

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes. © 2021 The Authors. Human Brain Mapping published by Wiley Periodicals LLC.

language will be accessed. While this model accounts for crosslanguage priming and interference (Ando, Matsuki, Sheridan, & Jared, 2015; Jared & Szucs, 2002; Jouravlev, Lupker, & Jared, 2014; Midgley, Holcomb, van Heuven, & Grainger, 2008; Smits, Martensen, Dijkstra, & Sandra, 2006), the mechanism of the language node remains unclear at the neurobiological level. While neuroimaging provides much support for an integrated lexicon through activation of similar structures, the separation of patterns of activity within the shared L1/L2 brain areas may provide evidence for some degree of distinction of how the lexicon is accessed between L1 and L2. That is, these separable representational patterns may reflect the action of a regulating 'language node' that allows access to language-specific semantic information within shared brain regions.

Proponents of the various current models of bilingual word recognition generally agree that individual differences such as proficiency and age of acquisition (AoA) influence bilingual lexico-semantic processing based on the strength of the associations between phonology, orthography, and semantics. For example, within the BIA+/BIA-d framework, in unbalanced bilinguals resting activation levels (i.e., the parameter assigned to word nodes within the model, reflecting the frequency of their usage) are lower in the nondominant language (often L2) leading to slower word recognition. However, as bilinguals become balanced in proficiency, resting activation levels become similar between languages, leading to symmetrical priming effects across languages. Similarly, within the Multilink framework (Diikstra et al., 2019), a computational model of bilingual word recognition, word forms are characterized by a frequency-dependent resting-level activation. As bilinguals with different L2-proficiency have used L2 words more or less frequently, this implies differences in the resting level activation for L2 words. In addition, task demands are assumed to be distributed throughout the processing pathway; that is, different sets of elementary processing operations are activated depending on the task requirements (Dijkstra & van Heuven, 2002). It is possible then, that differences in proficiency and AoA would place different task demands on speakers, in turn leading to greater separation within the areas responsible for task demands. With more similar resting activation levels (i.e., at higher proficiencies and earlier AoAs), task demands become more similar, potentially leading to more overlap in these regions. It is important to note that both models are based on reading; however, it has been assumed that they are also valid for bilingual auditory word recognition (Dijkstra & van Heuven, 2002).

Despite L1 and L2 sharing a network of structures, traditional univariate contrasts cannot tell us how languages are being represented in those areas, and while there is extensive overlap in brain areas that represent L1 and L2 (Chee, Tan, & Thiel, 1999; Indefrey, 2006; Perani et al., 2003; Wang et al., 2011), how the languages are represented may vary. That is, regions coding for language-specific information, such as spoken codes (e.g., left superior temporal gyrus and left inferior frontal gyrus) may represent each language differently. In contrast, regions involved in executive and attentional control (e.g., dorsolateral prefrontal cortex and insula) are likely to show less differentiation in how each language is represented as the function of these regions should not differ qualitatively from one language to

another. Individual differences in language ability and experience also play an important role in bilingual language processing (Newman, Tremblay, Nichols, Neville, & Ullman, 2012; Nichols & Joanisse, 2016, 2017) and may affect the integration of the neural representation of each language. Previous research indicates that low proficiency speakers and late L2 learners have greater separation of their two languages' conceptual knowledge (Van Hell & Tanner, 2012), and this separation may also be reflected in the neural representation of words and concepts within co-activated brain areas.

Representational similarity analysis (RSA) is one of several multivariate functional magnetic resonance imaging (fMRI) analysis techniques relying on reproducible spatial patterns of activity that correlate with distinct experimental conditions (Kriegeskorte, Mur, & Bandettini, 2008). RSA has been used to reveal differences between conditions within individual brain regions that were previously undetectable using standard univariate methods; it reveals cortical patterns sensitive to differences in stimuli even when the degree of activation is similar (Connolly et al., 2012; Eiaz, Hamada, & Diedrichsen, 2015; Fabbri, Stubbs, Cusack, & Culham, 2016; Joanisse & DeSouza, 2014). For example, this approach has been used to identify how regions differentiate between languages during reading (Xu, Baldauf, Chang, Desimone, & Tan, 2017), supporting the view that during visual word recognition, brain regions that are similarly active for both may nevertheless maintain representationally distinct patterns for them. Similar studies of bilingual reading have found that high proficiency readers showed more similarity in the reading network than low proficiency readers (Li et al., 2019; Qu et al., 2019). However, others have found that AoA, rather than proficiency, predicted degree of similarity within the reading network, with more dissimilarity in left inferior and middle frontal regions in earlier AoAs (Ou, Li, Yang, Wang, & Xu, 2020). While these studies have demonstrated the effect of individual differences in visual word recognition, it is much less clear how this relates to language representation within the auditory word recognition pathway, how this pertains to theories of access to a shared bilingual lexicon, and the effects of proficiency and AoA on these representational differences. Considering that much of language occurs within the spoken domain, the many differences between speech and reading (Guediche, Baart, & Samuel, 2020), and the assumption that the tenets of the BIA+ hold for spoken word recognition, it is important to investigate these questions. In the absence of a reading task, RSA may be particularly relevant to describing bilingual word processing, as it has the potential to identify differences between languages that were previously thought to not exist. RSA allows us to examine possible language-processing differences in areas that are assumed to be engaged similarly for both languages, suggesting that they are representing L1 and L2 differently. In addition, by measuring individual differences in bilingual experience, it is possible to determine how the neural representation of each language changes with these measures.

1.1 | Rationale for the present study

The present study examined whether brain areas involved in both L1 and L2 representationally distinguish the two languages during

bilingual auditory word recognition. We recruited a unique sample of L1 English, L2 Mandarin adults living in Beijing, whose AoA and proficiency levels naturally varied (Oh et al., 2019). Participants performed a lexico-semantic recognition task in each language, and we examined whether brain regions showed reliably different patterns of activity for each language within regions that significantly activated to both. We predicted that, consistent with models of an integrated bilingual lexicon, representational similarity would increase with increasing proficiency and earlier ages of L2 AoA due to increasingly similar resting activation levels. In contrast, areas involved in domain general cognitive processes, such as executive function, were not expected to show language-selective patterns.

2 | MATERIAL AND METHODS

2.1 | Participants

Thirty-two (13 female) neurologically healthy right-handed native speakers of English were recruited via posters and word of mouth in Beijing, China. All participants were second-language learners of Mandarin, aged 18–37 (M = 23.84, SD = 4.59), and had begun learning Mandarin between the ages of 0 and 28 years (M = 18.09, SD = 7.10). This study was approved by the Beijing Normal University research ethics board and all participants gave informed consent prior

TABLE 1	Participant	demographic and	l language in	Iformation
---------	-------------	-----------------	---------------	------------

N32Sex13 female, 19 maleAge (years)23.84 (4.59)Age of L2 acquisition18.90 (7.10)Time spent speaking Mandarin (years)5.75 (5.55)Country of origin (n)5.75 (5.55)United States16United Kingdom9Canada3India1Japan1New Zealand1Singapore1English88.93 (5.88)Mandarin38.54 (18.15)Function time (ms)1,203.60 (202.21)Mandarin1,203.60 (202.21)Mandarin1,607.88 (231.78)		
Sex13 female, 19 maleAge (years)23.84 (4.59)Age of L2 acquisition18.90 (7.10)Time spent speaking Mandarin (years)5.75 (5.55)Country of origin (n)1United States16United Kingdom9Canada3India1Japan1New Zealand1Singapore1Proficiency (%)88.93 (5.88)English88.93 (5.88)Mandarin38.54 (18.15)Reaction time (ms)1,203.60 (202.21)Mandarin1,607.88 (231.78)	Measure	M (SD)
Age (years)23.84 (4.59)Age of L2 acquisition18.90 (7.10)Time spent speaking Mandarin (years)5.75 (5.55)Country of origin (n)1United States16United Kingdom9Canada3India1Japan1New Zealand1Singapore1English88.93 (5.88)Mandarin38.54 (18.15)Reaction time (ms)1,203.60 (202.21)Mandarin1,607.88 (231.78)	N	32
Age of L2 acquisition18.90 (7.10)Time spent speaking Mandarin (years)5.75 (5.55)Country of origin (n)1United States16United Kingdom9Canada3India1Japan1New Zealand1Singapore1Proficiency (%)1English88.93 (5.88)Mandarin38.54 (18.15)Reaction time (ms)1,203.60 (202.21)Mandarin1,607.88 (231.78)	Sex	13 female, 19 male
Time spent speaking Mandarin (years)5.75 (5.55)Country of origin (n)1United States16United Kingdom9Canada3India1Japan1New Zealand1Singapore1Proficiency (%)1English88.93 (5.88)Mandarin38.54 (18.15)Reaction time (ms)1,203.60 (202.21)Mandarin1,607.88 (231.78)	Age (years)	23.84 (4.59)
Country of origin (n)16United States16United Kingdom9Canada3India1Japan1New Zealand1Singapore1Proficiency (%)1English88.93 (5.88)Mandarin38.54 (18.15)Reaction time (ms)1,203.60 (202.21)Mandarin1,607.88 (231.78)	Age of L2 acquisition	18.90 (7.10)
United States16United Kingdom9United Kingdom3Canada3India1Japan1New Zealand1New Zealand1Forficiency (%)1English88.93 (5.88)Mandarin38.54 (18.15)English1,203.60 (202.21)Mandarin1,203.60 (202.21)Mandarin1,607.88 (231.78)	Time spent speaking Mandarin (years)	5.75 (5.55)
United Kingdom9Canada3Canada3India1Japan1New Zealand1Singapore1Proficiency (%)1English88.93 (5.88)Mandarin38.54 (18.15)Reaction time (ms)1,203.60 (202.21)Inglish1,203.60 (202.21)Mandarin1,607.88 (231.78)	Country of origin (n)	
Canada 3 India 1 Japan 1 New Zealand 1 Singapore 1 Proficiency (%) English 88.93 (5.88) Mandarin 38.54 (18.15) Reaction time (ms) English 1,203.60 (202.21) Mandarin 1,607.88 (231.78)	United States	16
India 1 Japan 1 New Zealand 1 Singapore 1 Proficiency (%) 1 English 88.93 (5.88) Mandarin 38.54 (18.15) Reaction time (ms) 1,203.60 (202.21) Mandarin 1,607.88 (231.78)	United Kingdom	9
Japan1New Zealand1New Zealand1Singapore1Proficiency (%)1English88.93 (5.88)Mandarin38.54 (18.15)Reaction time (ms)1,203.60 (202.21)English1,203.60 (202.21)Mandarin1,607.88 (231.78)	Canada	3
New Zealand1Singapore1Proficiency (%)1English88.93 (5.88)Mandarin38.54 (18.15)Reaction time (ms)1,203.60 (202.21)English1,607.88 (231.78)	India	1
Singapore 1 Proficiency (%) 88.93 (5.88) Anadarin 38.54 (18.15) Reaction time (ms) 1,203.60 (202.21) Mandarin 1,607.88 (231.78)	Japan	1
Proficiency (%) 88.93 (5.88) English 88.93 (5.88) Mandarin 38.54 (18.15) Reaction time (ms) 1,203.60 (202.21) Mandarin 1,607.88 (231.78)	New Zealand	1
English 88.93 (5.88) Mandarin 38.54 (18.15) Reaction time (ms) 1,203.60 (202.21) Mandarin 1,607.88 (231.78)	Singapore	1
Mandarin 38.54 (18.15) Reaction time (ms) 1,203.60 (202.21) English 1,607.88 (231.78)	Proficiency (%)	
Reaction time (ms) 1,203.60 (202.21) Mandarin 1,607.88 (231.78)	English	88.93 (5.88)
English 1,203.60 (202.21) Mandarin 1,607.88 (231.78)	Mandarin	38.54 (18.15)
Mandarin 1,607.88 (231.78)	Reaction time (ms)	
	English	1,203.60 (202.21)
Accuracy (9/)	Mandarin	1,607.88 (231.78)
Accuracy (76)	Accuracy (%)	
English 94.17 (4.21)	English	94.17 (4.21)
Mandarin 83.07 (10.35)	Mandarin	83.07 (10.35)

to participation. Demographic and language information is summarized in Table 1.

2.2 | Behavioral tests

L1 English and L2 Mandarin proficiency levels were assessed prior to scanning using a subset of 48 questions from the Test of English as a Second Language (ETS, Princeton, NJ) and 48 questions from the Hanyu Shuiping Kaoshi measure of Mandarin (HSK Centre, Beijing, China), respectively. Both tests consisted of three sections, grammar, reading comprehension, and vocabulary, which were combined to give a final score for each language, representing overall proficiency in these three domains.

AoA was obtained by self-report, defined as the age at which individuals first began learning Mandarin. To verify handedness, participants completed an abridged version of the Edinburgh Handedness Inventory (Oldfield, 1971). Behavioral measures, informed consent and task instructions were administered in English, aside from the Mandarin proficiency test, which was administered in Mandarin.

2.3 | fMRI task

Participants completed a picture-word matching task during scanning, in alternating runs of English and Mandarin. This task has been used extensively in the past to study lexical knowledge (Nichols & Joanisse, 2016; Weniger, Crelier, Alkadhi, & Kollias, 2000; Breining et al., 2014; Dräger et al., 2004), and was chosen in order to examine lexical-semantic processing. Pictures were presented via LCD projector to the center of a screen mounted at the head of the scanner bore, which was viewed through a mirror placed above the head coil. At the same time, a word was played binaurally through insert earphones (Sensimetrics Corporation, Malden, MA). Participants were required to indicate as guickly as possible with a button press whether the picture and word matched. Each picture was visible for 2.5 s. They viewed a fixation crosshair between trials as baseline. Stimulus presentation and response recording was controlled with E-Prime software (Psychology Software Tools, Inc., Sharpsburg, PA) and a Windows laptop.

The scanning session was divided into eight alternating English and Mandarin runs. Four English runs were interleaved with four Mandarin runs, with starting language counterbalanced, so that a run in the first language was always followed by a run in the other language. Four orderings were produced: one version starting with English, one version starting with Mandarin, and an additional version of each in which runs were presented in the reverse order. Each run began with an image reminding participants of which buttons to respond with, and the language in which the next run would be performed. Each run consisted of 20 trials for a total of 160 trials (80 in each language, with 40 matching and 40 mismatching). A short break was provided between each 3.5-min scanning run. Each image appeared twice during the experiment, once in a matching pair and once in a semantically unrelated mismatching pair, with order counterbalanced so matching and unrelated trials occurred equally often in either order. Each trial was 2.5 s in duration, with intertrial interval jittered between 2.5 and 12.5 s in 2.5 s increments, to optimize the deconvolution of the blood oxygen-level-dependent signal.

Stimulus words consisted of 40 common single-word concepts, retrieved using Google Image Search, with the constraint that they are expressed as single two-syllable words in both English and Mandarin, and have frequencies greater than 40 per million in both languages (English: CELEX Lexical Database (Baayen, Piepenbrock, & Gulikers, 1995) and Mandarin: SUBTLEX-CH (Cai & Brysbaert, 2010)). In a separate pilot study involving different participants (42 native speakers of English and 33 native speakers of Mandarin), we asked groups of native speakers of English or Mandarin to rate the imageability and familiarity of the stimulus words, as well as the correspondence of the pictures to target words, on a Likert scale of 1–7. Both groups showed equally high ratings on familiarity ($M_{\text{Mandarin}} = 5.78$, $M_{\text{English}} = 5.48$) and picture/word correspondence ($M_{\text{Mandarin}} = 6.08$, $M_{\text{English}} = 5.95$).

2.4 | Data acquisition and processing

Imaging was conducted on a Siemens Magnetom TIM Trio wholebody 3 Tesla scanner with a 32-channel head coil. T2*-weighted functional scans were acquired in the transverse plane with 45 slices per volume (TR = 2.5 s; TE = 38 ms; flip angle = 80°; FOV = 192 × 192 mm; voxel size $3 × 3 × 3 mm^3$) using an iPAT parallel acquisition sequence (generalized autocalibrating partially parallel acquisition [GRAPPA]; acceleration factor = 2), providing full coverage of the cerebrum and the superior portion of the cerebellum. A total of 576 functional scans were acquired for each participant over 8 runs (3.5 min per run). After the final functional run, a whole-head high-resolution 3D anatomical scan was acquired in the sagittal plane, using a 3D pulse sequence weighted for T1 contrast (MPRAGE; TR = 2.3 s; TE = 2.98 ms; FOV = 256×256 mm; voxel size = 1 mm³; 176 slices; GRAPPA acceleration factor = 2).

Raw data were converted from DICOM to BIDS format and preprocessed using FMRIPREP version 1.0.0 (Gorgolewski et al., 2018) a Nipype (Gorgolewski et al., 2011, 2018) based tool. Each T1-weighted volume was corrected for bias field using N4BiasFieldCorrection v2.1.0 (Tustison et al., 2010) and skull-stripped using antsBrainExtraction.sh v2.1.0 (using OASIS template). Cortical surface was estimated using FreeSurfer v6.0.0 (Dale, Fischl, & Sereno, 1999). The skull-stripped T1w volume was coregistered to skull-stripped ICBM 152 Nonlinear Asymmetrical template version 2009c (Fonov, Evans, McKinstry, Almli, & Collins, 2009) using nonlinear transformation implemented in ANTs v2.1.0 (Avants, Epstein, Grossman, & Gee, 2008).

Functional data were slice time corrected using AFNI (Cox, 1996) and motion corrected using MCFLIRT v5.0.9 (Jenkinson, Bannister, Brady, & Smith, 2002). This was followed by co-registration to the corresponding T1-weighted volume using boundary-based registration with 9 degrees of freedom—implemented in FreeSurfer v6.0.0 (Greve & Fischl, 2009). Motion-correcting transformations, T1-weighted transformation and MNI template warp were applied in a single step using antsApplyTransformations v2.1.0 with Lanczos interpolation.

Three tissue classes were extracted from T1w images using FSL FAST v5.0.9 (Zhang, Brady, & Smith, 2001). Voxels from cerebrospinal fluid and white matter were used to create a mask which was in turn used to extract physiological noise regressors using aCompCor (Behzadi, Restom, Liau, & Liu, 2007). The mask was eroded and limited to subcortical regions to limit overlap with gray matter, and six principal components were estimated. Frame-wise displacement (Power, Schlaggar, & Petersen, 2014) was calculated for each functional run using Nipype implementation. For more details of the pipeline, see https://fmriprep.readthedocs.io/en/latest/workflows.html.

2.5 | First- and second-level statistics

Single-subject statistical maps were formed in the context of the general linear model using the AFNI 3dDeconvolve function. Linear trends in the functional data were removed, and first-level analysis was conducted by modeling all English trials together and all Mandarin trials together. The statistical maps were formed in the context of the general linear model using AFNI 3dDeconvolve function. Additional regressors were included for the six motion parameters, an estimate of physiological noise from the preprocessing step, and trial-wise response times. This yielded one English and one Mandarin statistical map per subject that we used to compute the second-level (crosssubject) univariate contrasts. One sample t tests against zero were computed for each language (AFNI 3dttest++, results shown in Figure S1 and Table S1) and a conjunction analysis (AFNI 3dcalc) was performed to identify areas that significantly activated for both English and Mandarin thresholded at 2.596 (p = 0.01 uncorrected). Note a relatively liberal threshold was used at this stage in order to include as many areas in the multivariate search space as possible. A brain mask was then created using the results of this conjunction analysis. Finally, first-level single-subject statistics were recomputed for English and Mandarin, this time creating separate models for even and odd runs. In addition, results of a between language t tests are shown in Figure S2 and Table S2.

Only correct trials were included in both first-level analyses, with accuracy ranging from 81.25% to 100% correct on the English task and from 61.25% to 96.25% correct on the Mandarin task.

2.6 | Split-half correlation searchlight analysis

Searchlight RSA was then performed to identify regions in which the representations of L1 and L2 were reliably different, regardless of groupwise differences in activation levels. The search space for the analysis was constrained to regions within the English–Mandarin conjunction mask, shown in Figure 1. A split-half correlation searchlight

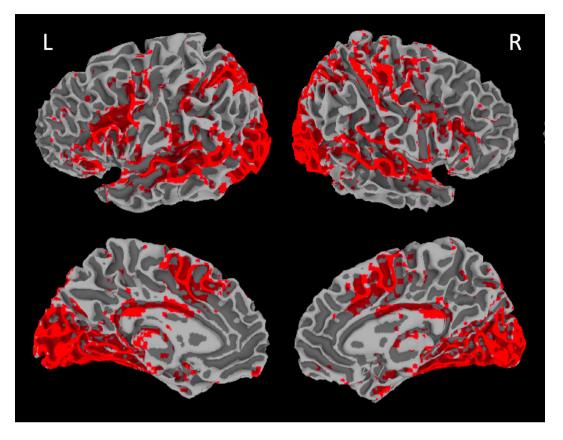


FIGURE 1 Areas that significantly activated for both L1 English and L2 Mandarin at p = .01 uncorrected. Results are overlaid on a stereotaxic brain in MNI space. L = left, R = right

was performed within the CoSMoMVPA Matlab toolbox (Oosterhof, Connolly, & Haxby, 2016), using a search sphere radius of three voxels (Connolly et al., 2012). Within each searchlight sphere Pearson correlations were performed for activity patterns between even and odd runs, within-language (English-English and Mandarin-Mandarin) and between-language (English-Mandarin), yielding a 2×2 similarity matrix for each individual at each point of the searchlight. Next, the degree of dissimilarity of between-language versus within-language patterns (on-diagonal versus off-diagonal) was computed using a pairwise t test based on the difference of Fisher-transformed mean correlations (Haxby et al., 2001). Significant differences in an area within the searchlight sphere indicated this region differentially encodes L1 and L2. The center of the searchlight was then moved to the next location of the search space, and the statistical analysis was repeated, ultimately yielding a statistical map of all voxels falling within the conjunction map. Analyses were performed using subject-wise coefficient maps in MNI space. Once single-subject searchlight results were computed, a group statistic was created via a one-sample t test, which identified voxels showing significantly greater representational similarity withinlanguage than between-languages, across all subjects. Next, we computed random-effect cluster statistics corrected for multiple comparison (cosmo_montecarlo_cluster_stat) with a mean of zero under the null hypothesis and 10,000 iterations, and significant clusters were converted to z scores.

2.7 | Regression with proficiency and AoA

We then conducted a linear regression to examine whether AoA and the difference in proficiency level between L1 and L2 predicted the degree of representational dissimilarity within-subject. Two linear models were constructed, the first with the difference in proficiency scores between L1 and L2 as a continuous regressor and adjusting for AoA, the second with AoA as a continuous regressor and adjusting for the difference in proficiency scores. The minimum cluster-size threshold was determined in two steps. First, we estimated the smoothness of the residuals for each subject output by 3dDeconvolve using the autocorrelation function (ACF) option (AFNI 3dFWHMx), and the mean smoothness level was calculated. Next, minimum cluster size was determined using a 10,000 iteration Monte Carlo simulation (AFNI 3dClustSim) at a voxelwise alpha level of p = .01, using bi-sided thresholding and first-nearest neighbor clustering. Correction for multiple comparisons at p = .01 was achieved by setting a minimum cluster size of 7 voxels.

3 | RESULTS

3.1 | Behavioral

Performance on the L1 (English) proficiency test ranged from 72.92 to 100%, and performance on the L2 (Mandarin) proficiency test ranged

from 12.5 to 77.08%. Analysis of the proficiency test data acquired prior to scanning indicated that L2 proficiency was significantly lower than L1 proficiency (M = 88.93%, SD = 5.88, M = 38.54%, SD = 18.15, respectively; t[31] = -15.93, p < .001, 95% CI [43.94, 56.84]). L2 proficiency did not significantly correlate with L2 AoA (r[30] = -0.21, p = .255). Participants responded faster on English trials than Mandarin trials (M = 1,203.60 ms, SD = 202.21,SD = 231.78, M = 1.607.88 ms. respectively; t[31] = -14.67, p < .001, 95% CI [-460.48, -348.09]) and were more accurate on English trials than Mandarin trials (M = 94.17%, SD = 4.21,M = 83.07%, SD = 10.35; t[31] = 6.84, p < .001,95% CI [7.78, 14,40]).

3.2 | Conjunction analysis

Results of the conjunction analysis are shown in Figure 1 and Table 2. Both L1 English and L2 Mandarin produced significant activation at a voxelwise *p* value of 0.01 (uncorrected) in an extensive network of bilateral brain regions including the Heschl's gyrus, superior temporal gyrus (STG), inferior frontal gyrus (IFG), fusiform and lingual gyri, and occipital and parietal cortices.

TABLE 2Areas of common activation revealed by a conjunctionof English and Mandarin

		MNI coordinates			
Reg	Region		у	z	Voxels
L	Lingual gyrus	-3	-60	5	9,969
R	Planum temporale	56	-14	4	671
R	Premotor cortex	1	3	46	536
L	Middle frontal gyrus	-45	10	35	461
R	Putamen	27	1	-3	113
R	Cerebellum	19	-41	-45	30
L	Temporal fusiform cortex	-32	-7	-35	20
R	Insula	40	-2	15	12
R	Parietal operculum cortex	48	-32	25	11
L	Planum Polare	-45	-17	-2	6
R	Entorhinal cortex	31	-8	-36	5
L	Brainstem	0	-17	-17	5
L	Precentral gyrus	-59	-23	50	5
L	Insula	-37	0	7	4
R	Insula	38	7	5	4
L	Parietal operculum cortex	-43	-37	16	4
R	Brainstem	14	-30	-27	3
L	Pars triangularis	-57	33	3	3
R	Anterior intraparietal sulcus	39	-42	47	3
R	Premotor cortex	15	-12	81	3

Note: Coordinates denote the center of mass. L/R = left/right.

3.3 | Searchlight with split-half correlation analysis

3.3.1 | Group-level RSA searchlight

As a group, no regions showed significantly greater representational similarity within-language (Mandarin–Mandarin and English–English) compared to between-language (Mandarin–English).

3.3.2 | Regression with proficiency and AoA

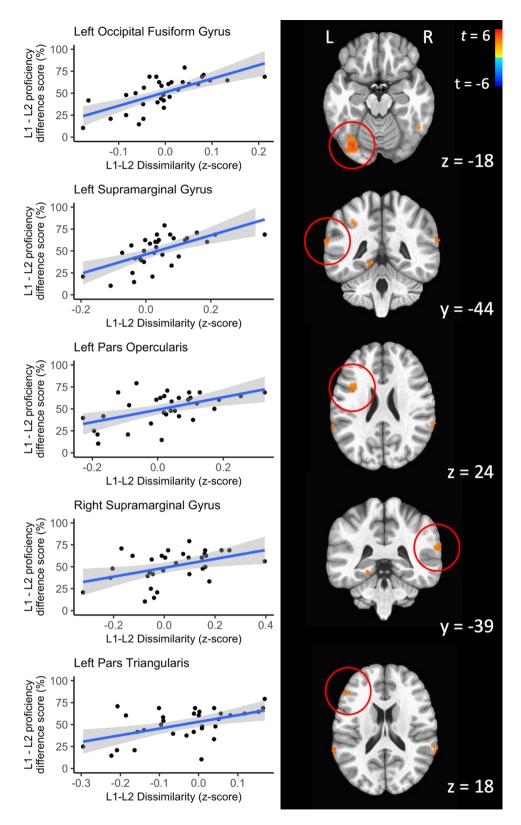
In order to determine whether proficiency or AoA predicted the degree of difference in representational similarity within- and between-language, subject-wise searchlight maps were next submitted to linear regression analysis. L1–L2 proficiency score difference predicted greater within-language representational similarity than between-language similarity in several areas including the left fusiform, IFG, bilateral STG, and right lingual gyrus, shown in Figure 2 and Table 3. All areas showed a positive relationship, indicating that as the difference in proficiency between languages increased, so did the degree of difference in representation between English and Mandarin.

The relationship between AoA and representational similarity is shown in Figure 3 and Table 3. AoA positively predicted greater within-language than between-language representational similarity in the left middle temporal gyrus and right inferior occipital gyrus, indicating that later AoAs were associated with larger differences between L1 and L2 in these areas. In contrast, AoA showed a negative correlation with the left inferior parietal lobe and right insula and calcarine sulcus, indicating that earlier AoAs were associated with smaller L1–L2 representational differences in these areas.

4 | DISCUSSION

The present study investigated the hypothesis that bilinguals maintain similar, overlapping lexical representations for both of their languages. Using a lexico-semantic recognition task, we found both similarity and dissimilarity in the representation of bilinguals' two languages within the bilingual word recognition network. There were no regions that significantly differed in their representation of English and Mandarin at the group level, however both proficiency and AoA predicted the degree of representational similarity in several areas. That is, individual differences predicted differentiation in the representation of bilinguals' two languages in areas that were significantly activated during the word recognition task in both Mandarin and English. These results extend behavioral and event-related potential findings that bilinguals have a single, integrated lexicon (Ando et al., 2015; Jouravlev et al., 2014; Midgley et al., 2008; van Heuven & Dijkstra, 2010), demonstrating how the neural representations within activated regions change with language experience. While prior meta-analyses and reviews have argued this on the basis of relative intensity of fMRI activity (Indefrey, 2006; van Heuven & Dijkstra, 2010), degree of

FIGURE 2 The relationship between difference in L1 - L2proficiency scores (%) and L1 - L2similarity. *z*-Score values represent the mean across the entire region of interest (ROI). Higher *z*-scores indicate greater differences between correlation values between-language versus withinlanguage. Statistical maps are thresholded at *p* = .01, overlaid on an MNI brain atlas. L = left, R = right. Cluster locations and sizes are reported in Table 3



activation cannot tell us about how each language is being represented. It can also be difficult to interpret the meaning of greater activity: increased fMRI signal may represent a greater specialization of a region to a certain task, or it might alternatively indicate increased neural effort required due to weaker familiar with that task. Here, we reconceptualize regional activation in terms of degree of language differentiation, focusing on regions that do not show clear specialization for one language or the other.

Consistent with our hypotheses, several regions of the language network showed patterns of representation that differentiated

TABLE 3	Regions where p	roficiency or age	of acquisition (Ac	oA) significantly	predicted z score

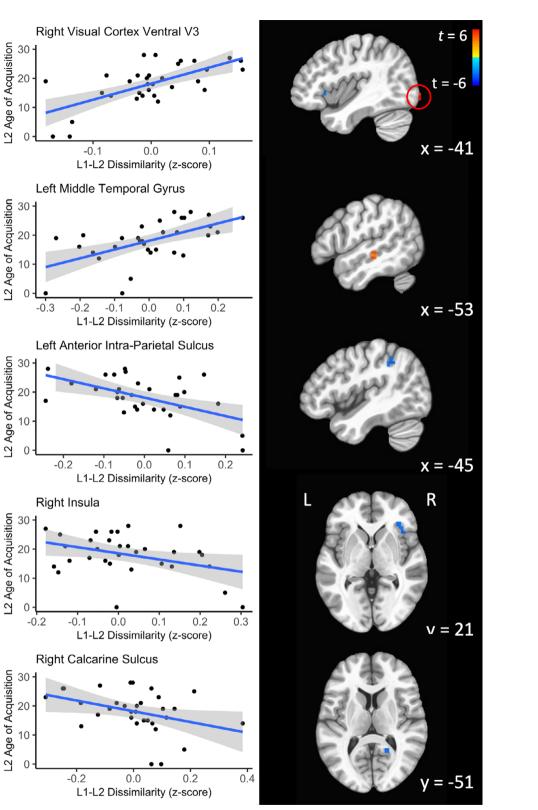
			м	MNI coordinates				
Predictor	Region		x	у	z	Voxels	t	p
L1–L2 proficiency	R	Cerebellum	6	-81	-30	35	5.23	<.001
	L	Occipital fusiform gyrus	-33	-75	-18	96	4.72	<.001
	L	Supramarginal gyrus	-66	-45	21	13	4.20	<.001
	L	Precentral gyrus	-33	-9	66	12	4.10	<.001
	L	Pars opercularis	-39	3	24	20	4.07	<.001
	R	Cerebellum	33	-66	-48	25	4.03	<.001
	R	Middle occipital gyrus	51	-81	0	9	3.97	<.001
	L	Anterior intra-parietal sulcus	-36	-48	42	9	3.90	.001
	R	Primary visual cortex	18	-60	9	26	3.88	.001
	R	Inferior temporal gyrus	48	-51	-24	12	3.76	.001
	L	Lingual gyrus	-15	-45	-9	13	3.71	.001
	R	Supramarginal gyrus	66	-45	24	17	3.70	.001
	R	Orbitofrontal cortex	33	33	-3	10	3.63	.001
	L	Pars triangularis	-51	33	18	8	3.61	.001
	R	Visual cortex ventral V3	21	-78	-6	8	3.51	.001
	R	Cerebellum	3	-57	-45	7	3.31	.003
AoA	R	Visual cortex ventral V3	42	-93	-6	8	5.09	<.001
	L	Middle temporal gyrus	-54	-24	-9	9	4.34	<.001
	L	Anterior intraparietal sulcus	-39	-45	48	15	-3.50	.002
	R	Insula	39	21	0	16	-3.46	.002
	R	Calcarine sulcus	18	-51	9	8	-3.32	.002

Note: Coordinates denote the location of peak activation. L/R = Left/Right. P values have been cluster-size corrected to p < .05.

languages depending on individual differences. For example, one of these regions was the left IFG (including both the pars opercularis and the pars triangularis), an area engaged in representing and planning articulatory codes for speech and tone (Broca, 1865; Fedorenko, Fillmore, Smith, Bonilha, & Fridriksson, 2015; Gao, Guo, Liu, Mo, & Wang, 2020; Wise, Greene, Buchel, & Scott, 1999). Indeed, these features differ between English and Mandarin in that each language has phonological features that are not present in the other (e.g., tone in Mandarin, consonant clusters in English). The left IFG showed greater representational similarity between languages when the difference between L1 and L2 proficiency was smaller, suggesting that as bilinguals become more matched in proficiency across their two languages, the phonological representations become more integrated. Similarly, language similarity within the bilateral supramarginal gyrus was greater with smaller proficiency differences, an area important for auditory-motor integration during word recognition (Catani, Jones, & Ffytche, 2005).

One notable result was that of representational dissimilarity in lower L2 proficiency and later AoA speakers throughout the ventral visual stream, a cortical pathway responsible for object recognition and concept representation (Martin, Douglas, Newsome, Man, & Barense, 2018). The language differentiation in visual areas is especially interesting as participants in the present study saw the same images in each language; the manipulation here was only the language in which they heard the names of these objects. As a result, languagedependent differences in this region suggest a top-down modulation of high-level visual processing by the linguistic input. Although visual processing of the same images may appear to be a domain-general process, support for it being language-specific comes from the labelfeedback hypothesis, which suggests that language modulates ongoing cognitive and perceptual processing (Lupyan, 2012). In line with this hypothesis, each language's verbal label for the paired image influences the perception of that image. Thus, while the image remains the same, the top-down influence of the language is producing separable representations in high-level visual areas, distinguishing between the visual perception of the spoken word *table* versus that of the spoken word $\frac{1}{R}$ (the Mandarin word for *table*) (Jared, Poh, & Paivio, 2013).

In addition to areas showing a positive relationship between AoA and representational similarity, three regions showed greater dissimilarity at earlier AoAs. The right insula has been implicated in inhibitory control (Cai et al., 2014), and larger differences in neural representation within this area may reflect differences in how inhibition of the other language is performed. One tenet of the BIA-d Model is that once conceptual connections are in place, inhibitory connections between translation equivalents develop, allowing for improved processing (Grainger et al., 2010). Thus, these inhibitory connections, more likely to have had time to develop in earlier bilinguals, may be controlled though the right insula. Interestingly, the left anterior **FIGURE 3** The relationship between L2 age of acquisition (AoA) and L1 – L2 dissimilarity. z-Score values represent the mean across the entire region of interest (ROI). Higher *z*-scores indicate greater differences between correlation values betweenlanguage versus within-language. Statistical maps are thresholded at p = .01, overlaid on an MNI brain atlas. L = left, R = right. Cluster locations and sizes are reported in Table 3



intraparietal sulcus, another area that showed a negative relationship between representational dissimilarity and AoA, is important in the planning and control of fine finger movement, and has strong connections to the bilateral insula (Uddin et al., 2010). The third region, the area prostriata of the calcarine sulcus, has been shown to have cortical connections to the cingulate motor cortex in monkeys (Morecraft, Rockland, & Van Hoesen, 2000). While the reason for these links with AoA is less clear, it is possible that the process of initiating a response, done through a button press, was more separable for participants with greater inhibitory connections between 5442 WILEY-

languages. Future research should aim to further elucidate the role of these areas in bilingual auditory word recognition, including their relationship with AoA.

Finally, although it may seem surprising that no regions showed higher within-language representational similarity, this result is likely due to the high degree of variability in AoA and proficiency in our sample. Based on our predictions that individual differences in these factors will predict degree of similarity, it then logically follows that when considering everyone together, no consistent pattern would emerge. Even the external properties of the stimuli that differ between languages, such as the phonology of tone that exists in Mandarin and English, have been shown to be affected by individual differences (e.g., Yu et al., 2019), perhaps explaining why we still did not see higher within-language representational similarity within-language than between-language.

There have been numerous studies showing activation differences between L1 and L2, showing greater activation in language areas for one language versus another (Chee, Hon, Lee, & Soon, 2001: Ding et al., 2003; Perani et al., 2003), or showing additional areas recruited for L2 processing versus L1 processing (Wang et al., 2011). These differences have largely been attributed to later acquisition of L2, differences in proficiency, or other external factors affecting how L2 was acquired (Chee et al., 2001; De Bleser et al., 2003; Indefrey, 2006). In contrast, matched bilinguals tend to show overlapping activity in language regions, with little or no differentiation between languages at the univariate level (Hernandez, Dapretto, Mazziotta. & Bookheimer. 2001: Hernandez. Martinez. З Kohnert, 2000; Rodriguez-Fornells et al., 2005). L2 speakers in the present study showed experience-dependent representational differences between L1 and L2 in both the language network as well as throughout the ventral visual stream, providing further evidence for integration of bilinguals' two languages but only when speakers are matched in ability across those two languages. This represents an important but underexplored perspective on how neuroplasticity is expressed in bilingualism.

5 | CONCLUSION

We investigated first and second language representation in English-Mandarin bilinguals. Using RSA, we identified both regions in which individual differences predicted differentiation in representation between English and Mandarin. Experience-modulated withinlanguage representational similarity was present in language-network areas (e.g., portions of the left IFG) as well as several regions of the ventral visual pathway. The results thus support a model in which the degree to which bilinguals maintain separable representations of their two languages varies by brain region, and that the strength of such effects also varies appreciably as a function of both maturational and experiential factors.

A logical extension of present study is the examination of representational differences in different types of second language processing. For instance, results may differ when comparing two languages that are more similar than English and Mandarin, such as Spanish and French, or when using items that vary in similarity, such as cognates and noncognates. In addition, word processing does not involve grammatical processing, which is also an important aspect of bilingual language processing that can differ greatly between L1 and L2. Univariate approaches that contrast degree of brain activation may miss important differences in this regard. The multivariate approach used here may thus provide a way forward in our ability to fully discern how L1 and L2 are represented in the brain.

ACKNOWLEDGMENTS

We are grateful to Suzanne Witt and BrainsCAN for help with the RSA analysis. This work was supported by an NSERC Discovery Grant to Marc F. Joanisse, a National Key Laboratory of Cognitive Neuroscience and Learning Open-Project Grant to Marc F. Joanisse and Li Liu, and a China NSF Grant (No. 31970977) to Li Liu.

CONFLICT OF INTEREST

The authors declare no potential conflicts of interest.

ETHICS STATEMENT

The study was conducted according to the guidelines of the Declaration of Helsinki, and approved by the Beijing Normal University research ethics board. All participants gave written informed consent prior to participation.

DATA AVAILABILITY STATEMENT

Due to ethics restrictions, data cannot be made publicly available. However, data can be shared through a formal data sharing agreement by contacting the corresponding authors.

ORCID

Emily S. Nichols D https://orcid.org/0000-0003-0541-9233

REFERENCES

- Ando, E., Matsuki, K., Sheridan, H., & Jared, D. (2015). The locus of Katakana-English masked phonological priming effects. *Bilingualism: Language and Cognition*, 18(1), 101–117. https://doi.org/10.1017/ S1366728914000121
- Avants, B. B., Epstein, C. L., Grossman, M., & Gee, J. C. (2008). Symmetric diffeomorphic image registration with cross-correlation: Evaluating automated labeling of elderly and neurodegenerative brain. *Medical Image Analysis*, 12(1), 26–41. https://doi.org/10.1016/j.media.2007. 06.004
- Baayen, R. H., Piepenbrock, R., & Gulikers, L. (1995). The CELEX lexical database [webcelex]. Philadelphia, PA: University of Pennsylvania Linguistic Data Consortium.
- Behzadi, Y., Restom, K., Liau, J., & Liu, T. T. (2007). A component based noise correction method (CompCor) for BOLD and perfusion based fMRI. *NeuroImage*, 37(1), 90–101. https://doi.org/10.1016/j. neuroimage.2007.04.042
- Breining, B., Faria, A., & Argye, H. (2014). Neural regions supporting lexical processing of objects and actions: A case series analysis. *Frontiers in Psychology*. https://doi.org/10.3389/conf.fpsyg.2014.64. 00030
- Broca, P. (1865). Sur le siège de la faculté du langage articulé. Bulletins de La Société d'Anthropologie de Paris, 6, 377–393.

- Cai, Q., & Brysbaert, M. (2010). SUBTLEX-CH: Chinese word and character frequencies based on film subtitles. *PLoS One*, 5(6), e10729. https:// doi.org/10.1371/journal.pone.0010729
- Cai, W., Ryali, S., Chen, T., Li, X. C. R., & Menon, V. (2014). Dissociable roles of right inferior frontal cortex and anterior insula in inhibitory control: Evidence from intrinsic and task-related functional parcellation, connectivity, and response profile analyses across multiple datasets. *The Journal of Neuroscience*, 34(44), 14652–14667. https://doi.org/10.1523/JNEUROSCI.3048-14.2014
- Cao, F., Tao, R., Liu, L., Perfetti, C. A., & Booth, J. R. (2013). High proficiency in a second language is characterized by greater involvement of the first language network: Evidence from Chinese learners of English. *Journal of Cognitive Neuroscience*, 25(10), 1649–1663. https://doi.org/10.1162/jocn
- Catani, M., Jones, D. K., & Ffytche, D. H. (2005). Perisylvian language networks of the human brain. Annals of Neurology, 57(1), 8–16. https:// doi.org/10.1002/ana.20319
- Chee, M. W. L., Hon, N., Lee, H. L., & Soon, C. S. (2001). Relative language proficiency modulates BOLD signal change when bilinguals perform semantic judgments. *NeuroImage*, 13(6), 1155–1163. https://doi.org/ 10.1006/nimg.2001.0781
- Chee, M. W. L., Tan, E. W. L., & Thiel, T. (1999). Mandarin and English single word processing studied with functional magnetic resonance imaging. *Journal of Neuroscience*, 19(8), 3050–3056.
- Connolly, A. C., Guntupalli, J. S., Gors, J., Hanke, M., Halchenko, Y. O., Wu, Y.-C., ... Haxby, J. V. (2012). The representation of biological classes in the human brain. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 32(8), 2608–2618. https://doi.org/10. 1523/JNEUROSCI.5547-11.2012
- Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance Neuroimages. *Computers and Biomedical Research*, 29(3), 162–173. https://doi.org/10.1006/cbmr.1996.0014
- Dale, A. M., Fischl, B., & Sereno, M. I. (1999). Cortical surface-based analysis. I. Segmentation and surface reconstruction. *NeuroImage*, 9(2), 179–194. https://doi.org/10.1006/nimg.1998.0395
- De Bleser, R., Dupont, P., Postler, J., Bormans, G., Speelman, D., Mortelmans, L., & Debrock, M. (2003). The organisation of the bilingual lexicon: A PET study. *Journal of Neurolinguistics*, 16(4–5), 439– 456. https://doi.org/10.1016/S0911-6044(03)00022-8
- Dijkstra, T., & van Heuven, W. J. B. (2002). The architecture of the bilingual word recognition system: From identification to decision. *Bilingualism: Language and Cognition*, 5(03), 175–197. https://doi.org/10. 1017/S1366728902003012
- Dijkstra, T., Wahl, A., Buytenhuijs, F., Van Halem, N., Al-Jibouri, Z., De Korte, M., & Rekké, S. (2019). Multilink: A computational model for bilingual word recognition and word translation. *Bilingualism*, 22(4), 657–679. https://doi.org/10.1017/S1366728918000287
- Ding, G., Perry, C., Peng, D., Ma, L., Li, D., Xu, S., ... Yang, J. (2003). Neural mechanisms underlying semantic and orthographic processing in Chinese–English bilinguals. *Neuroreport*, 14(12), 1557–1562. https:// doi.org/10.1097/01.wnr.0000087906.78892.8e
- Dräger, B., Breitenstein, C., Helmke, U., Kamping, S., & Knecht, S. (2004). Specific and nonspecific effects of transcranial magnetic stimulation on picture-word verification. *European Journal of Neuroscience*, 20(6), 1681–1687. https://doi.org/10.1111/j.1460-9568.2004.03623.x
- Ejaz, N., Hamada, M., & Diedrichsen, J. (2015). Hand use predicts the structure of representations in sensorimotor cortex. *Nature Neurosci*ence, 103(June), 1–10. https://doi.org/10.1038/nn.4038
- Fabbri, S., Stubbs, K. M., Cusack, R., & Culham, J. C. (2016). Disentangling representations of object and grasp properties in the human brain. The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 36(29), 7648–7662. https://doi.org/10.1523/JNEUROSCI.0313-16.2016
- Fedorenko, E., Fillmore, P., Smith, K., Bonilha, L., & Fridriksson, J. (2015). The superior precentral gyrus of the insula does not appear to be

functionally specialized for articulation. *Journal of Neurophysiology*, 113(7), 2376–2382. https://doi.org/10.1152/jn.00214.2014

- Fonov, V. S., Evans, A. C., McKinstry, R. C., Almli, C. R., & Collins, D. L. (2009). Unbiased nonlinear average age-appropriate brain templates from birth to adulthood. *NeuroImage*, 47, S102. https://doi.org/10. 1016/S1053-8119(09)70884-5
- Gao, Z., Guo, X., Liu, C., Mo, Y., & Wang, J. (2020). Right inferior frontal gyrus: An integrative hub in tonal bilinguals. *Human Brain Mapping*, 41(8), 2152–2159. https://doi.org/10.1002/hbm.24936
- Goldrick, M., Putnam, M., & Schwarz, L. (2016). Coactivation in bilingual grammars: A computational account of code mixing. *Bilingualism: Language and Cognition, FirstView*, 19, 857–876. https://doi.org/10.1017/ S1366728915000802
- Gorgolewski, K. J., Burns, C., Madison, C., Clark, D., Halchenko, Y., Waskom, M., & Ghosh, S. (2011). Nipype: A flexible, lightweight and extensible neuroimaging data processing framework in python. Frontiers in Neuroinformatics, 5, 13. https://doi.org/10.3389/fninf.2011. 00013
- Gorgolewski, K. J., Esteban, O., Ellis, D. G., Notter, M. P., Ziegler, E., Johnson, H., ... Ghosh, S. (2018). *Nipype*. Retrieved from https:// zenodo.org/record/4035081#.YR0UD80zbIU
- Grainger, J., Midgley, K. J., & Holcomb, P. J. (2010). Re-thinking the bilingual interactive-activation model from a developmental perspective (BIA-d). In M. Kail & M. Hickmann (Eds.), *Language Acquisition across Linguistic and Cognitive Systems* (pp. 267–283). New York, NY: John Benjamins. https://doi.org/10.1075/lald.52.18gra
- Greve, D. N., & Fischl, B. (2009). Accurate and robust brain image alignment using boundary-based registration. *NeuroImage*, 48(1), 63–72. https://doi.org/10.1016/j.neuroimage.2009.06.060
- Guediche, S., Baart, M., & Samuel, A. G. (2020). Semantic priming effects can be modulated by crosslinguistic interactions during second-language auditory word recognition. *Bilingualism: Language and Cognition*, 23(5), 1082–1092. https://doi.org/10.1017/S136672892 0000164
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, 293, 2425–2430.
- Hernandez, A. E., Dapretto, M., Mazziotta, J., & Bookheimer, S. (2001). Language switching and language representation in Spanish-English bilinguals: An fMRI study. *NeuroImage*, 14(2), 510–520. https://doi. org/10.1006/nimg.2001.0810
- Hernandez, A. E., Martinez, A., & Kohnert, K. (2000). In search of the language switch: An fMRI study of picture naming in Spanish-English bilinguals. *Brain and Language*, 73(3), 421–431. https://doi.org/10. 1006/brln.1999.2278
- Indefrey, P. (2006). A meta-analysis of hemodynamic studies on first and second language processing: Which suggested differences can we trust and what do they mean? *Language Learning*, *56*, 279–304. https://doi.org/10.1111/j.1467-9922.2006.00365.x
- Jared, D., Poh, R. P. Y., & Paivio, A. (2013). L1 and L2 picture naming in Mandarin–English bilinguals: A test of bilingual dual coding theory. *Bilingualism: Language and Cognition*, 16(2), 383–396. https://doi.org/ 10.1017/S1366728912000685
- Jared, D., & Szucs, C. (2002). Phonological activation in bilinguals: Evidence from interlingual homograph naming. *Bilingualism: Language* and Cognition, 5, 225–239. https://doi.org/10.1017/S13667289020 03024
- Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved optimization for the robust and accurate linear registration and motion correction of brain images. *NeuroImage*, 17(2), 825–841. https://doi. org/10.1006/nimg.2002.1132
- Joanisse, M. F., & DeSouza, D. D. (2014). Sensitivity of human auditory cortex to rapid frequency modulation revealed by multivariate representational similarity analysis. *Frontiers in Neuroscience*, 8, 1–10. https://doi.org/10.3389/fnins.2014.00306

5444 WILEY-

- Jouravlev, O., Lupker, S. J., & Jared, D. (2014). Cross-language phonological activation: Evidence from masked onset priming and ERPs. *Brain* and Language, 134, 11–22. https://doi.org/10.1016/j.bandl.2014. 04.003
- Kriegeskorte, N., Mur, M., & Bandettini, P. (2008). Representational similarity analysis—connecting the branches of systems neuroscience. *Frontiers in Systems Neuroscience*, 2, 4. https://doi.org/10.3389/neuro. 06.004.2008
- Li, H., Qu, J., Chen, C., Chen, Y., Xue, G., Zhang, L., ... Mei, L. (2019). Lexical learning in a new language leads to neural pattern similarity with word reading in native language. *Human Brain Mapping*, 40(1), 98–109. https://doi.org/10.1002/hbm.24357
- Lucas, T. H., McKhann, G. M., & Ojemann, G. (2004). Functional separation of languages in the bilingual brain: A comparison of electrical stimulation language mapping in 25 bilingual patients and 117 monolingual control patients. *Journal of Neurosurgery*, 101, 449–457. https://doi. org/10.3171/jns.2004.101.3.0449
- Lupyan, G. (2012). Linguistically modulated perception and cognition: The label-feedback hypothesis. *Frontiers in Psychology*, *3*, 1–13. https://doi. org/10.3389/fpsyg.2012.000154
- Martin, C. B., Douglas, D., Newsome, R. N., Man, L. L. Y., & Barense, M. D. (2018). Integrative and distinctive coding of perceptual and conceptual object features in the ventral visual stream. *eLife*, 7, e31873. https:// doi.org/10.7554/eLife.31873
- Midgley, K. J., Holcomb, P. J., van Heuven, W. J. B., & Grainger, J. (2008). An electrophysiological investigation of cross-language effects of orthographic neighborhood. *Brain Research*, 1246, 123–135. https:// doi.org/10.1016/j.brainres.2008.09.078
- Morecraft, R. J., Rockland, K. S., & Van Hoesen, G. W. (2000). Localization of area prostriata and its projection to the cingulate motor cortex in the rhesus monkey. *Cerebral Cortex*, 10, 192–203. https://doi.org/10. 1093/cercor/10.2.192
- Newman, A. J., Tremblay, A., Nichols, E. S., Neville, H. J. H. J., & Ullman, M. T. M. T. (2012). The influence of language proficiency on lexical semantic processing in native and late learners of English. *Journal of Cognitive Neuroscience*, 24(5), 1205–1223. https://doi.org/10. 1162/jocn_a_00143
- Nichols, E. S., & Joanisse, M. F. (2016). Functional activity and white matter microstructure reveal the independent effects of age of acquisition and proficiency on second-language learning. *NeuroImage*, 143, 15–25. https://doi.org/10.1016/j.neuroimage.2016. 08.053
- Nichols, E. S., & Joanisse, M. F. (2017). Individual differences predict ERP signatures of second language learning of novel grammatical rules. *Bilingualism: Language and Cognition*, 22, 1–15. https://doi.org/10. 1017/S1366728917000566
- Oh, T. M., Graham, S., Ng, P., Yeh, I. B., Chan, B. P. L., & Edwards, A. M. (2019). Age and proficiency in the bilingual brain revisited: Activation patterns across different L2-learner types. *Frontiers in Communication*, 4, 1–14. https://doi.org/10.3389/fcomm.2019.00039
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113. https://doi.org/ 10.1016/0028-3932(71)90067-4
- Oosterhof, N. N., Connolly, A. C., & Haxby, J. V. (2016). CoSMoMVPA: Multi-modal multivariate pattern analysis of neuroimaging data in Matlab/GNU Octave. Frontiers in Neuroinformatics, 10, 1–27. https:// doi.org/10.3389/fninf.2016.00027
- Ou, J., Li, W., Yang, Y., Wang, N., & Xu, M. (2020). Earlier second language acquisition is associated with greater neural pattern dissimilarity between the first and second languages. *Brain and Language*, 203, 104740. https://doi.org/10.1016/j.bandl.2019. 104740
- Perani, D., Abutalebi, J., Paulesu, E., Brambati, S., Scifo, P., Cappa, S. F., & Fazio, F. (2003). The role of age of acquisition and language usage in early, high-proficient bilinguals: An fMRI study during verbal fluency.

Human Brain Mapping, 19(3), 170-182. https://doi.org/10.1002/hbm. 10110

- Power, J. D., Schlaggar, B. L., & Petersen, S. E. (2014). Studying brain organization via spontaneous fMRI signal. *Neuron*, 84(4), 681–696. https:// doi.org/10.1016/j.neuron.2014.09.007
- Pyers, E., & Emmorey, K. (2008). The face of bimodal bilingualism. *Psychological Science*, 19(6), 531–536. https://doi.org/10.1111/j.1467-9280. 2008.02119.x
- Qu, J., Zhang, L., Chen, C., Xie, P., Li, H., Liu, X., & Mei, L. (2019). Crosslanguage pattern similarity in the bilateral fusiform cortex is associated with reading proficiency in second language. *Neuroscience*, 410, 254– 263. https://doi.org/10.1016/j.neuroscience.2019.05.019
- Rodriguez-Fornells, A., van der Lugt, A., Rotte, M., Britti, B., Heinze, H. J., & Munte, T. F. (2005). Second language interferes with word production in fluent bilinguals: Brain potential and functional imaging evidence. *Journal of Cognitive Neuroscience*, 17(3), 422–433. https://doi.org/10.1162/0898929053279559
- Smits, E., Martensen, H., Dijkstra, T., & Sandra, D. (2006). Naming interlingual homographs: Variable competition and the role of the decision system. *Bilingualism*, 9(03), 281–297. https://doi.org/10.1017/S13667 2890600263X
- Spalek, K., Hoshino, N., Wu, Y. J., Damian, M., & Thierry, G. (2014). Speaking two languages at once: Unconscious native word form access in second language production. *Cognition*, 133(1), 226–231. https://doi. org/10.1016/j.cognition.2014.06.016
- Starreveld, P. A., De Groot, A. M. B., Rossmark, B. M. M., & Van Hell, J. G. (2014). Parallel language activation during word processing in bilinguals: Evidence from word production in sentence context. *Bilingualism: Language and Cognition*, 17(02), 1–19. https://doi.org/10.1017/ S1366728913000308
- Sun, Y., Peng, D., Ding, G., Qi, T., Desroches, A. S., & Liu, L. (2015). The dynamic nature of assimilation and accommodation procedures in the brains of Chinese–English and English–Chinese bilinguals. *Human Brain Mapping*, 36, 4144–4157. https://doi.org/10.1002/hbm.22904
- Tustison, N. J., Avants, B. B., Cook, P. A., Zheng, Y., Egan, A., Yushkevich, P. A., & Gee, J. C. (2010). N4ITK: Improved N3 bias correction. *IEEE Transactions on Medical Imaging*, 29(6), 1310–1320. https://doi.org/10.1109/TMI.2010.2046908
- Uddin, L. Q., Supekar, K., Amin, H., Rykhlevskaia, E., Nguyen, D. A., & Greicius, M. D. (2010). Dissociable connectivity within human angular gyrus and intraparietal sulcus: evidence from functional and structural connectivity. *Cerebral cortex*, 20(11), 2636–2646. https://doi.org/10. 1093/cercor/bhq011
- Van Hell, J. G., & Tanner, D. (2012). Second language proficiency and cross-language lexical activation. *Language Learning*, 62(2), 148–171.
- van Heuven, W. J. B., & Dijkstra, T. (2010). Language comprehension in the bilingual brain: fMRI and ERP support for psycholinguistic models. *Brain Research Reviews*, 64(1), 104–122. https://doi.org/10.1016/j. brainresrev.2010.03.002
- Wang, Y., Xiang, J., Vannest, J., Holroyd, T., Narmoneva, D., Horn, P., ... Holland, S. (2011). Neuromagnetic measures of word processing in bilinguals and monolinguals. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, 122(9), 1706– 1717. https://doi.org/10.1016/j.clinph.2011.02.008
- Weniger, D., Crelier, G. R., Alkadhi, H., & Kollias, S. S. (2000). Picture-word matching as a paradigm in determining regions of language processing: An fMRI study. *NeuroImage*, 11(5), S314. https://doi.org/10.1016/ S1053-8119(00)91246-1
- Wise, R. J., Greene, J., Buchel, C., & Scott, S. K. (1999). Brain regions involved in articulation. *Lancet*, 353(9158), 1057–1061. https://doi. org/10.1016/S0140-6736(98)07491-1
- Xu, M., Baldauf, D., Chang, C. Q., Desimone, R., & Tan, L. H. (2017). Distinct distributed patterns of neural activity are associated with two languages in the bilingual brain. *Science Advances*, 3(7), e1603309. https://doi.org/10.1126/sciadv.1603309

- Yu, K., Li, L., Chen, Y., Zhou, Y., Wang, R., Zhang, Y., & Li, P. (2019). Effects of native language experience on Mandarin lexical tone processing in proficient second language learners. *Psychophysiology*, 56(11), 1–20. https://doi.org/10.1111/psyp.13448
- Zeng, T., Branigan, H. P., & Pickering, M. J. (2020). Do bilinguals represent between-language relationships beyond the word level in their lexicon? *Journal of Neurolinguistics*, 55, 100892. https://doi.org/10.1016/ j.jneuroling.2020.100892
- Zhang, Y., Brady, M., & Smith, S. (2001). Segmentation of brain MR images through a hidden Markov random field model and the expectationmaximization algorithm. *IEEE Transactions on Medical Imaging*, 20(1), 45–57. https://doi.org/10.1109/42.906424

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Nichols, E. S., Gao, Y., Fregni, S., Liu, L., & Joanisse, M. F. (2021). Individual differences in representational similarity of first and second languages in the bilingual brain. *Human Brain Mapping*, *42*(16), 5433–5445. https://doi.org/10.1002/hbm.25633