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

Emily S. Nichols^a, Yue Gao^b, Sofia Fregni^c, Li Liu^b, Marc F. Joanisse^{d,e}

^aFaculty of Education, the University of Western Ontario, London, Canada

^bState Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing, China

^cFaculty of Psychology, Dresden University of Technology, Dresden, Germany

^dDepartment of Psychology, The University of Western Ontario, London, Canada

^eBrain and Mind Institute, The University of Western Ontario, London, Canada

Corresponding authors:

Emily Nichols

Faculty of Education

University of Western Ontario

London, Ontario, Canada, N6A 5C2

Email: enicho4@uwo.ca

Li Liu

State Key Laboratory of Cognitive Neuroscience and Learning

Beijing Normal University

No.19 Xijiekou Wai St, Haidian District,

Beijing, China, 100875

Email: lilyliu@bnu.edu.cn

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 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. As a group, there were no regions that reliably represented languages distinctly. However, both proficiency and age of acquisition 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 the 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 age of acquisition.

Keywords: bilingualism, word recognition, representational similarity analysis, individual differences

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 both¹⁻⁴. Additionally, past neuroimaging research has provided much evidence that a second language (L2) is processed similarly to the speaker's first language⁵⁻⁹. Even when L1-L2 differences exist, such as more extensive activity in L2^{10,11}, there remains extensive overlap⁶. 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^{12,13}. 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 between L1 and L2 lexicons.

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^{6,7,9,14}, 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^{11,15,16}, 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 knowledge¹⁷, 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 an fMRI analysis technique relying on reproducible spatial patterns of activity that correlate with distinct experimental conditions¹⁸, and has been used in the past to identify regions that differentiate between languages during reading¹⁹. 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^{20–23}. This technique 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. Additionally, by measuring individual differences in bilingual experience, it is possible to determine how the neural representation of each language changes with these measures.

Rationale for the Present Study

The present study examined whether brain areas involved in both L1 and L2 representationally distinguish the two languages. English-Mandarin bilingual adults performed a lexico-semantic recognition task in each language. We then 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 dissimilarity would decrease with increasing proficiency and earlier ages of L2

acquisition (AoA). 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 0-28 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 to participation. Demographic and language information is summarized in Table 1.

Table 1. Participant demographic and language information

Measure	M (SD)
N	32
Sex	13 female, 19 male
Age (years)	23.84 (4.59)
Age of L2 acquisition	18.90 (7.10)
<i>Proficiency (%)</i>	
English	88.93 (5.88)
Mandarin	38.54 (18.15)
<i>Reaction Time (ms)</i>	
English	1203.60 (202.21)
Mandarin	1607.88 (231.78)
<i>Accuracy (%)</i>	
English	94.17 (4.21)
Mandarin	83.07 (10.35)

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 (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.

Age of acquisition 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 ²⁴. 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. 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 quickly 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 8 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-minute scanning run. Each image appeared twice during the experiment, once in a matching pair and once in a semantically unrelated mismatching pair. Each trial was 2.5 s in duration, with inter-trial 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 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 Database²⁵ and Mandarin: SUBTLEX-CH²⁶). In a separate pilot study involving different participants, 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 ($M_{Mandarin} = 5.78$, $M_{English} = 5.48$) and picture/word correspondence ($M_{Mandarin} = 6.08$, $M_{English} = 5.95$).

2.4 Data acquisition and processing

Imaging was conducted on a Siemens Magnetom TIM Trio whole-body 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 x 192 mm; voxel size 3x3x3 mm³) using an iPAT parallel acquisition sequence (generalized auto-calibrating 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 x 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 1.0.0²⁷ a Nipype^{27,28} based tool. Each T1 weighted volume was corrected for bias field using N4BiasFieldCorrection v2.1.0²⁹ and skullstripped using antsBrainExtraction.sh v2.1.0 (using OASIS template). Cortical surface was estimated using FreeSurfer v6.0.0³⁰. The skullstripped T1w volume was coregistered to skullstripped ICBM 152 Nonlinear Asymmetrical template version 2009c³¹ using nonlinear transformation implemented in ANTs v2.1.0³².

Functional data was slice time corrected using AFNI³³ and motion corrected using MCFLIRT v5.0.9³⁴. This was followed by co-registration to the corresponding T1-weighted volume using boundary based registration 9 degrees of freedom - implemented in FreeSurfer v6.0.0³⁵. 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 v5.0.9³⁶. Voxels from cerebrospinal fluid and white matter were used to create a mask in turn used to extract physiological noise regressors using aCompCor³⁷. Mask was eroded and limited to subcortical regions to limit overlap with gray matter, six principal components were estimated. Frame-wise displacement³⁸ was calculated for each functional run using Nipype implementation. For more details of the pipeline see <https://fmripred.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 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, physiological noise from the preprocessing step, and the response times. This led to one English and one Mandarin output per subject that we used to compute the univariate contrasts. One sample t-tests against zero were then computed for each language (AFNI 3dttest++) and a conjunction analysis (AFNI 3dcalc) was performed to identify areas that significantly activated for both English and Mandarin. The result was a conjunction map thresholded at 2.596 ($p = 0.01$ uncorrected); a fairly liberal threshold was used at this stage in order to include as many areas in the 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. Only correct trials were included in both first-level analyses, with accuracy ranging from 81.25% to 100% correct on the English task and ranging 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. To conduct RSA, a split-half correlation searchlight was

performed within the CoSMoMVPa Matlab toolbox³⁹, using a search sphere radius of 3 voxels. 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 vs. within-language patterns (on-diagonal vs. off-diagonal) was computed using a pairwise *t*-test based on the difference of Fisher-transformed mean correlations⁴⁰. 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 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 within-language than between-languages. 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 age of acquisition

We then conducted 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 L2-L1 proficiency as a continuous regressor and adjusting for AoA, the second with AoA as a continuous regressor and adjusting for the difference in L2-L1 proficiency. 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 $p = 0.01$, using bi-sided thresholding and first-nearest neighbour clustering. Correction for multiple comparisons at $p = 0.01$ was achieved by setting a minimum cluster size of 7 voxels.

3. Results

3.1 Behavioural

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 ($M = 1203.60$ ms, $SD = 202.21$, $M = 1607.88$ ms, $SD = 231.78$, 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

245 cortices.

246

247 **Figure 1.** Areas that significantly activated for both L1 English and L2 Mandarin at $p = .01$
 248 uncorrected. Results are overlaid on a stereotaxic brain in MNI space. L=Left, R= Right.

249

250 3.3 Searchlight with split-half correlation analysis

251 3.3.1 Group-level RSA

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

255 3.3.2 Regression with proficiency and age of acquisition

256 In order to determine whether proficiency or AoA predicted the degree of difference in
 257 representational similarity within- and between-language, subject-wise searchlight maps were

submitted to linear regression. L2-L1 Proficiency 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.

Table 3. Regions where proficiency or AoA significantly predicted z-score

Predictor		Region	MNI			Voxels	<i>t</i>	<i>p</i>
			coordinates					
			<i>x</i>	<i>y</i>	<i>z</i>			
L2-L1 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	4.2	< .001	
	L Precentral gyrus	-33	-9	66	12	4.1	< .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	3.9	.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	3.7	.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 intra-parietal sulcus	-39	-45	48	15	-3.5	.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.

Figure 2. The relationship between difference in L2-L1 proficiency and L2-L1 similarity. Z-score values represent the mean across the entire ROI. Higher z-scores indicate greater differences between correlation values between-language vs. 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.

Figure 3. The relationship between L2 AoA and L2-L1 dissimilarity. Z-score values represent the mean across the entire ROI. Higher z-scores indicate greater differences between correlation values between-language vs. 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.

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 ERP findings that bilinguals have a single, integrated lexicon^{12,41–43}, 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^{6,12}, degree of activation cannot tell us about how each language is being represented.

Consistent with our hypotheses, several regions of the language network showed patterns of representation that differentiated 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^{44–47}. 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 ⁴⁸.

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 ⁴⁹. The separate representation 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, language-dependent differences in this region indicate that this reflects 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 label-feedback hypothesis, which suggests that language modulates ongoing cognitive and perceptual processing ⁵⁰. 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* vs. that of the spoken word 桌子 (the Mandarin word for *table*).

There have been numerous studies showing activation differences between L1 and L2, showing greater activation in language areas for one language versus another ^{7,51,52}, or showing additional areas recruited for L2 processing vs. L1 processing ⁹. These differences have largely been attributed to later acquisition of L2, differences in proficiency, or other external factors affecting how L2 was acquired ^{6,51,53}. In contrast, matched bilinguals tend to show overlapping activity in language regions, with little or no differentiation between languages at the univariate

level^{54–56}. 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.

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 within-language 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, indicating that top-down language knowledge shapes concept representation in the processing stream.

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 non-cognates. Additionally, 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.

360 Acknowledgments: We are grateful to Suzanne Witt for help with the RSA analysis.

361

362 Funding: This work was supported by an NSERC Discovery Grant to M.F.J., a National Key

363 Laboratory of Cognitive Neuroscience and Learning Open-Project Grant to M.F.J. and L.L., and

364 a China NSF Grant ([No. 31970977](#)) to L.L.

365

366 Author Statement: The authors declare no conflict of interest.

367

References

1. Goldrick, M., Putnam, M. & Schwarz, L. Coactivation in bilingual grammars: A computational account of code mixing. *Biling. Lang. Cogn.* **FirstView**, 1–20 (2016).
2. Pyers, E. & Emmorey, K. The Face of Bimodal Bilingualism. *Psychol. Sci.* **19**, 531–536 (2008).
3. Spalek, K., Hoshino, N., Wu, Y. J., Damian, M. & Thierry, G. Speaking two languages at once: Unconscious native word form access in second language production. *Cognition* **133**, 226–231 (2014).
4. Starreveld, P. A., De Groot, A. M. B., Rossmark, B. M. M. & Van Hell, J. G. Parallel language activation during word processing in bilinguals: Evidence from word production in sentence context. *Biling. Lang. Cogn.* **17**, 1–19 (2014).
5. Cao, F., Tao, R., Liu, L., Perfetti, C. A. & Booth, J. R. High Proficiency in a Second Language is Characterized by Greater Involvement of the First Language Network: Evidence from Chinese Learners of English. *J. Cogn. Neurosci.* **25**, 1649–1663 (2013).
6. Indefrey, P. A Meta-analysis of Hemodynamic Studies on First and Second Language Processing: Which Suggested Differences Can We Trust and What Do They Mean? *Lang. Learn.* **56**, 279–304 (2006).
7. Perani, D. *et al.* The role of age of acquisition and language usage in early, high-proficient bilinguals: an fMRI study during verbal fluency. *Hum. Brain Mapp.* **19**, 170–82 (2003).
8. Sun, Y. *et al.* The dynamic nature of assimilation and accommodation procedures in the brains of Chinese-English and English-Chinese bilinguals. *Hum. Brain Mapp.* **36**, 4144–4157 (2015).
9. Wang, Y. *et al.* Neuromagnetic measures of word processing in bilinguals and

- 391 monolinguals. *Clin. Neurophysiol.* **122**, 1706–17 (2011).
- 392 10. Lucas, T. H., McKhann, G. M. & Ojemann, G. Functional separation of languages in the
393 bilingual brain: a comparison of electrical stimulation language mapping in 25 bilingual
394 patients and 117 monolingual control patients. *J. Neurosurg.* **101**, 449–457 (2004).
- 395 11. Nichols, E. S. & Joanisse, M. F. Functional activity and white matter microstructure
396 reveal the independent effects of age of acquisition and proficiency on second-language
397 learning. *Neuroimage* **143**, 15–25 (2016).
- 398 12. van Heuven, W. J. B. & Dijkstra, T. Language comprehension in the bilingual brain: fMRI
399 and ERP support for psycholinguistic models. *Brain Res. Rev.* **64**, 104–122 (2010).
- 400 13. Zeng, T., Branigan, H. P. & Pickering, M. J. Do bilinguals represent between-language
401 relationships beyond the word level in their lexicon? *J. Neurolinguistics* **55**, 100892
402 (2020).
- 403 14. Chee, M. W. L., Tan, E. W. L. & Thiel, T. Mandarin and English Single Word Processing
404 Studied with Functional Magnetic Resonance Imaging. *J. Neurosci.* **19**, 3050–3056
405 (1999).
- 406 15. Nichols, E. S. & Joanisse, M. F. Individual differences predict ERP signatures of second
407 language learning of novel grammatical rules. *Biling. Lang. Cogn.* 1–15 (2017).
408 doi:10.1017/S1366728917000566
- 409 16. Newman, A. J., Tremblay, A., Nichols, E. S., Neville, H. J. H. J. & Ullman, M. T. M. T.
410 The Influence of Language Proficiency on Lexical Semantic Processing in Native and
411 Late Learners of English. *J. Cogn. Neurosci.* **24**, 1205–1223 (2012).
- 412 17. Van Hell, J. G. & Tanner, D. Second Language Proficiency and Cross-Language Lexical
413 Activation. *Lang. Learn.* **62**, 148–171 (2012).

- 414 18. Kriegeskorte, N., Mur, M. & Bandettini, P. Representational similarity analysis -
415 connecting the branches of systems neuroscience. *Front. Syst. Neurosci.* **2**, 4 (2008).
- 416 19. Xu, M., Baldauf, D., Chang, C. Q., Desimone, R. & Tan, L. H. Distinct Distributed
417 patterns of neural activity are associated with two languages in the bilingual brain. *Sci.*
418 *Adv.* **3**, (2017).
- 419 20. Connolly, A. C. *et al.* The representation of biological classes in the human brain. *J.*
420 *Neurosci.* **32**, 2608–18 (2012).
- 421 21. Ejaz, N., Hamada, M. & Diedrichsen, J. Hand use predicts the structure of representations
422 in sensorimotor cortex. *Nat. Neurosci.* **103**, 1–10 (2015).
- 423 22. Fabbri, S., Stubbs, K. M., Cusack, R. & Culham, J. C. Disentangling Representations of
424 Object and Grasp Properties in the Human Brain. *J. Neurosci.* **36**, 7648–62 (2016).
- 425 23. Joanisse, M. F. & DeSouza, D. D. Sensitivity of human auditory cortex to rapid frequency
426 modulation revealed by multivariate representational similarity analysis. *Front. Neurosci.*
427 **8**, 1–10 (2014).
- 428 24. Oldfield, R. C. The assessment and analysis of handedness: The Edinburgh inventory.
429 *Neuropsychologia* **9**, 97–113 (1971).
- 430 25. Baayen, R. H., Piepenbrock, R. & Gulikers, L. CELEX2 LDC96L14. Web Download.
431 *Philadelphia: Linguistic Data Consortium* (1995). doi:10.3758/BF03195456
- 432 26. Cai, Q. & Brysbaert, M. SUBTLEX-CH: Chinese Word and Character Frequencies Based
433 on Film Subtitles. *PLoS One* **5**, e10729 (2010).
- 434 27. Gorgolewski, K. J. *et al.* Nipype. (2018). doi:10.5281/zenodo.596855
- 435 28. Gorgolewski, K. J. *et al.* Nipype: A Flexible, Lightweight and Extensible Neuroimaging
436 Data Processing Framework in Python. *Front. Neuroinform.* **5**, 13 (2011).

- 437 29. Tustison, N. J. *et al.* N4ITK: Improved N3 bias correction. *IEEE Trans. Med. Imaging* **29**,
438 1310–1320 (2010).
- 439 30. Dale, A. M., Fischl, B. & Sereno, M. I. Cortical surface-based analysis. I. Segmentation
440 and surface reconstruction. *Neuroimage* **9**, 179–194 (1999).
- 441 31. Fonov, V. S., Evans, A. C., McKinstry, R. C., Almli, C. R. & Collins, D. L. Unbiased
442 nonlinear average age-appropriate brain templates from birth to adulthood. *Neuroimage*
443 **47**, S102 (2009).
- 444 32. Avants, B. B., Epstein, C. L., Grossman, M. & Gee, J. C. Symmetric diffeomorphic image
445 registration with cross-correlation: Evaluating automated labeling of elderly and
446 neurodegenerative brain. *Med. Image Anal.* **12**, 26–41 (2008).
- 447 33. Cox, R. W. AFNI: Software for Analysis and Visualization of Functional Magnetic
448 Resonance Neuroimages. *Comput. Biomed. Res.* **29**, 162–173 (1996).
- 449 34. Jenkinson, M., Bannister, P., Brady, M. & Smith, S. Improved Optimization for the
450 Robust and Accurate Linear Registration and Motion Correction of Brain Images.
451 *Neuroimage* **17**, 825–841 (2002).
- 452 35. Greve, D. N. & Fischl, B. Accurate and robust brain image alignment using boundary-
453 based registration. *Neuroimage* **48**, 63–72 (2009).
- 454 36. Zhang, Y., Brady, M. & Smith, S. Segmentation of brain MR images through a hidden
455 Markov random field model and the expectation-maximization algorithm. *IEEE Trans.*
456 *Med. Imaging* **20**, 45–57 (2001).
- 457 37. Behzadi, Y., Restom, K., Liao, J. & Liu, T. T. A component based noise correction
458 method (CompCor) for BOLD and perfusion based fMRI. *Neuroimage* **37**, 90–101 (2007).
- 459 38. Power, J. D., Schlaggar, B. L. & Petersen, S. E. Studying Brain Organization via

- 460 Spontaneous fMRI Signal. *Neuron* **84**, 681–696 (2014).
- 461 39. Oosterhof, N. N., Connolly, A. C. & Haxby, J. V. CoSMoMVPA: multi-modal
462 multivariate pattern analysis of neuroimaging data in Matlab / GNU Octave. *Front.*
463 *Neuroinform.* 047118 (2016). doi:10.1101/047118
- 464 40. Haxby, J. V *et al.* Distributed and Overlapping Representations of Faces and Objects in
465 Ventral Temporal Cortex. *Science (80-.).* **293**, 2425–2430 (2001).
- 466 41. Ando, E., Matsuki, K., Sheridan, H. & Jared, D. The locus of Katakana–English masked
467 phonological priming effects. *Biling. Lang. Cogn.* **18**, 101–117 (2015).
- 468 42. Jouravlev, O., Lupker, S. J. & Jared, D. Cross-language phonological activation: Evidence
469 from masked onset priming and ERPs. *Brain Lang.* **134**, 11–22 (2014).
- 470 43. Midgley, K. J., Holcomb, P. J., van Heuven, W. J. B. & Grainger, J. An
471 electrophysiological investigation of cross-language effects of orthographic neighborhood.
472 *Brain Res.* **1246**, 123–135 (2008).
- 473 44. Broca, P. Sur le siège de la faculté du langage articulé. *Bull. la Société d'anthropologie*
474 *Paris* **6**, 377–393 (1865).
- 475 45. Fedorenko, E., Fillmore, P., Smith, K., Bonilha, L. & Fridriksson, J. The superior
476 precentral gyrus of the insula does not appear to be functionally specialized for
477 articulation. *J. Neurophysiol.* **113**, 2376–82 (2015).
- 478 46. Wise, R. J., Greene, J., Buchel, C. & Scott, S. K. Brain regions involved in articulation.
479 *Lancet* **353**, 1057–1061 (1999).
- 480 47. Gao, Z., Guo, X., Liu, C., Mo, Y. & Wang, J. Right inferior frontal gyrus: An integrative
481 hub in tonal bilinguals. *Hum. Brain Mapp.* **41**, 2152–2159 (2020).
- 482 48. Catani, M., Jones, D. K. & Ffytche, D. H. Perisylvian language networks of the human

- 483 brain. *Ann. Neurol.* **57**, 8–16 (2005).
- 484 49. Martin, C. B., Douglas, D., Newsome, R. N., Man, L. L. Y. & Barense, M. D. Integrative
485 and distinctive coding of perceptual and conceptual object features in the ventral visual
486 stream. *Elife* 1–29 (2018). doi:10.1101/186924
- 487 50. Lupyan, G. Linguistically modulated perception and cognition: The label-feedback
488 hypothesis. *Front. Psychol.* **3**, 1–13 (2012).
- 489 51. Chee, M. W. L., Hon, N., Lee, H. L. & Soon, C. S. Relative language proficiency
490 modulates BOLD signal change when bilinguals perform semantic judgments.
491 *Neuroimage* **13**, 1155–1163 (2001).
- 492 52. Ding, G. *et al.* Neural mechanisms underlying semantic and orthographic processing in
493 Chinese-English bilinguals. *Neuroreport* **14**, 1557–1562 (2003).
- 494 53. De Bleser, R. *et al.* The organisation of the bilingual lexicon: A PET study. *J.*
495 *Neurolinguistics* **16**, 439–456 (2003).
- 496 54. Hernandez, A. E., Martinez, A. & Kohnert, K. In Search of the Language Switch: An
497 fMRI Study of Picture Naming in Spanish–English Bilinguals. *Brain Lang.* **73**, 421–431
498 (2000).
- 499 55. Hernandez, A. E., Dapretto, M., Mazziotta, J. & Bookheimer, S. Language switching and
500 language representation in Spanish-English bilinguals: an fMRI study. *Neuroimage* **14**,
501 510–20 (2001).
- 502 56. Rodriguez-Fornells, A. *et al.* Second language interferes with word production in fluent
503 bilinguals: brain potential and functional imaging evidence. *J. Cogn. Neurosci.* **17**, 422–
504 433 (2005).
- 505