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FUNCTIONAL magnetic resonance imaging was used to assess inter-subject variability in the cortical representation of language comprehension processes. Moderately fluent French–English bilinguals were scanned while they listened to stories in their first language (L1 = French) or in a second language (L2 = English) acquired at school after the age of seven. In all subjects, listening to L1 always activated a similar set of areas in the left temporal lobe, clustered along the left superior temporal sulcus. Listening to L2, however, activated a highly variable network of left and right temporal and frontal areas, sometimes restricted only to right-hemispheric regions. These results support the hypothesis that first language acquisition relies on a dedicated left-hemispheric cerebral network, while late second language acquisition is not necessarily associated with a reproducible biological substrate. The postulated contribution of the right hemisphere to L2 comprehension¹ is found to hold only on average, individual subjects varying from complete right lateralization to standard left lateralization for L2.

Key words: Bilingualism; Language; Lateralization; Speech; Temporal lobe

Anatomical variability in the cortical representation of first and second language

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Introduction

Do similar cerebral networks support first and second language acquisition? When a polyglot suffers a brain lesion, aphasia is occasionally observed in only one of the languages originally mastered.^{1,2} This dissociation, together with evidence from electrical cortical stimulation,³ suggests that different brain areas are recruited for learning and processing the first language (L1) and the second language (L2). Brain imaging studies in groups of bilingual subjects have also revealed differences between L1 and L2 representation.^{4–7} Neuropsychological and imaging studies have failed to pinpoint a consistent neuronal substrate for second language acquisition, however, perhaps because they were obtained in various languages, using variable tasks, and with subjects of varying levels of proficiency. Inter-subject variability may have prevented the emergence of consistent results, particularly in PET studies based on group averaging.

Functional magnetic resonance imaging (fMRI) is a method ideally suited for single-subject analyses, because it permits the assessment of significantly activated areas in individual subjects without requiring group averaging. The present study aimed at assessing inter-subject variability in the cortical representation of language comprehension processes in L1 and L2. We used whole-brain 3-Tesla echo-planar fMRI to explore the cerebral networks underlying comprehension of stories in L1 and L2, in line with our previous work on story listening using PET.^{5,8} Eight subjects were imaged while they listened to different stories in their native language (L1 = French) or in a second language that they had learned at school after the age of seven, and for which they had a moderate proficiency level (L2 = English). In both languages, short stories were recorded by a native speaker, digitally edited and cut into three blocks of 36 seconds. These blocks were then presented in alternation with a control condition

consisting of three blocks of 36 seconds of backward speech (the tape of a story in Japanese, played backwards). This design subtracted out brain activity related to early auditory processing and isolated the regions specifically involved in the processing of real speech, either in L1 or L2.

Method

Subjects. Eight right-handed male French students, native French speakers, aged between 21 and 25, gave informed consent to participate in this study. All were born from French parents and had not been exposed to English before the age of seven. They had learned English as a second language at school and none had lived in an English-speaking country for more than one year. Good understanding of spoken English was verified, prior to the experiment, using word translation and sentence comprehension tests, and during the experiment, by asking difficult factual questions about the stories immediately after each scan (one-tailed paired *t*-test for a greater number of errors in English than in French: $t(7) = 1.00$, $p = 0.18$, not significant).

Stimuli. Stories were recorded on digital audiotape by two native French (F) or English (E) speakers and were digitally cut at sentence boundaries to obtain fragments of 36 seconds each. Three such fragments were alternated with three fragments of a control condition consisting of Japanese speech played backwards (B). Two experimental conditions were run in counterbalanced order: F-B-F-B-F-B and E-B-E-B-E-B. English and French versions of the same stories were counterbalanced across subjects such that if one subject heard story A in French and story B in English, another subject heard story A in English and story B in French. Five subjects also listened to a replication of these conditions using three independent short stories instead of a single story cut into three fragments. Stimuli were presented over standard headphones customized for fMRI experiments and inserted in a noise-protecting helmet that provided isolation from scanner noise.

Image acquisition. Experiments were performed on a 3T whole-body system (Bruker, Germany). The study was approved by a National Ethics Committee for Biomedical Research. The subject's head was fixed by foam cushions and bands to limit motion artifacts. Shimming on the selected slices was carried out before each acquisition. Eighteen axial contiguous slices of 5 mm thickness and 22 cm field of view were scanned every 6 seconds for 216 s (36 volumes) using a gradient-echo echo-planar imaging (EPI)

sequence (repetition time/echo time/flip angle = 6000 ms/40 ms/90°, 64 × 64 pixel matrix) sensitive to BOLD contrast (local increases in blood flow and oxygenation). To improve the anatomical identification of the activated regions, high-resolution 2-D T1-weighted slices matching the EPI slices were also acquired using an inversion-recovery sequence (inversion time/repetition time/echo time/flip angle = 800 ms/3000 ms/8 ms/90°, 256 × 256 pixel matrix).

Data analysis. Images were initially processed using custom software written under IDL (Interactive Data Language, Research System Inc., Boulder, CO). Images were first checked for absence of head motion, and evidence of motion exceeding one pixel implied no further analysis. Activation maps were calculated on a pixel-by-pixel basis based on the correlation coefficient⁹ between the MR signal time course for each pixel and a waveform derived from the processing paradigm, taking into account the hemodynamic nature of the response. The first three images of each series were discarded from analysis, because the magnetization was not steady at the beginning of the experiment. A cluster of pixels was considered active when it consisted of at least 3 contiguous pixels, each with a correlation coefficient above 0.45. Assuming independent observations, the threshold of 0.45 corresponds to a Student's *t* of 3.14 and to a pixel-based one-tailed probability of 0.00185 (with 31 degrees of freedom). We estimate that requiring at least 3 contiguous such pixels brings the probability of finding a cluster at any given location down to $p < 3.6 \times 10^{-5}$ (uncorrected for multiple comparisons across the brain volume). Correction for temporal correlation between successive images¹⁰ was not done given the long repetition time between images.

Because the correlation procedure allows only for within-condition comparisons (i.e. F *vs* B or E *vs* B), but not for between-conditions comparisons (e.g. F *vs* E), the data were also reanalyzed using SPM96. Images were corrected for subject motion, normalized to Talairach coordinates using a linear transform calculated on the T1 images, and smoothed (FWHM = 5 mm). The intensity level of each pixel was then modeled using a linear regression with 8 variables, namely two temporal activation functions for each of the four block types: French story (F), backward speech control for the French condition (BF), English story (E) and backward speech control for the English condition (BE). Active areas in L1 and L2 were determined using the main effect terms F-BE and E-BE, using a voxelwise significance level of 0.001 corrected for multiple comparison across the brain volume to $p < 0.05$. Differences between L1 and L2 were tested using the interaction term (F-BF)–

(E-BE), with an uncorrected significance level of 0.001. Correlation- and SPM-based analyses gave highly consistent results, thus testifying to the reliability of the statistical measures used and indicating that the intersubject variability observed for L2 was not due only to the intrinsically noisy nature of fMRI data.

Results

When listening to L1, there was a remarkable consistency in the observed activated areas in the left hemisphere (Fig. 1). All subjects showed activity in the left temporal lobe all along the superior temporal sulcus (STS) as well as in neighboring portions of the superior and middle temporal gyri (STG, MTG), often extending forward into the temporal pole (TP; 4 subjects) and backward into the left angular gyrus (AG; 4 subjects). Although similar activity was occasionally found in the right temporal lobe, including

the right STS (6 subjects) and TP (2 subjects), it was always weaker, highly variable from subject to subject, and never extended backward into the right AG. In six out of eight subjects, a significantly larger number of active pixels were found in the left than in the right temporal lobe (χ^2 tests, all p s < 0.005). Outside the temporal lobe, the only consistent focus of activation was found near the intersection of the inferior frontal sulcus (IFS) and the precentral sulcus (PrS), bordering Brodman's areas 8, 9, 44 and 6 (superior to Broca's area proper; see Fig. 1). This region was active in the left hemisphere of 6 subjects, and in the right hemisphere of 3 subjects.

Listening to L2 uncovered much greater inter-subject variability. No single anatomical area was found active in more than six subjects (Fig. 1). Six subjects showed activation foci in the left temporal lobe (STS, STG, MTG), but the active pixels showed considerable dispersion contrasting with their tight localisation to the banks of the STS when listening to L1 (Fig. 1). Furthermore, no activity was found

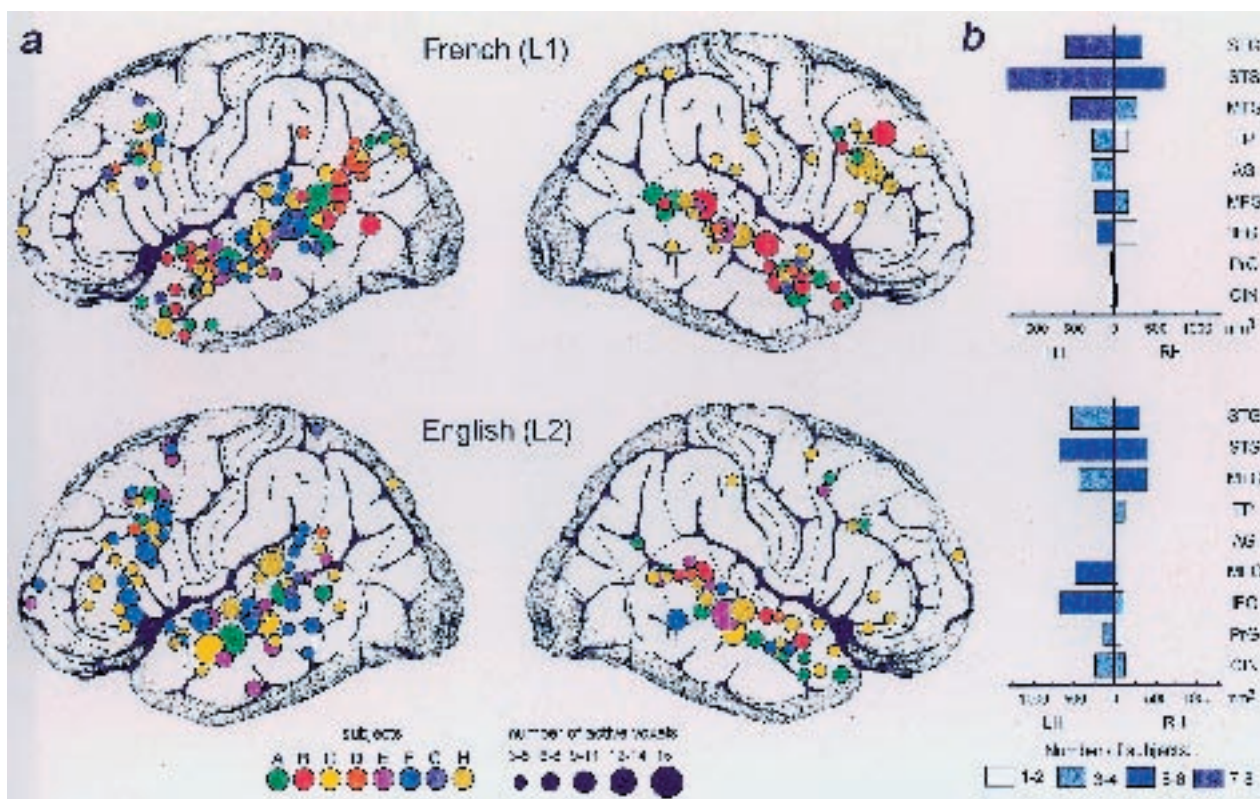
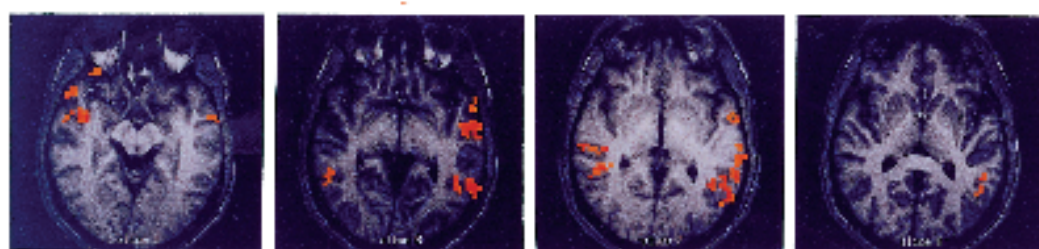
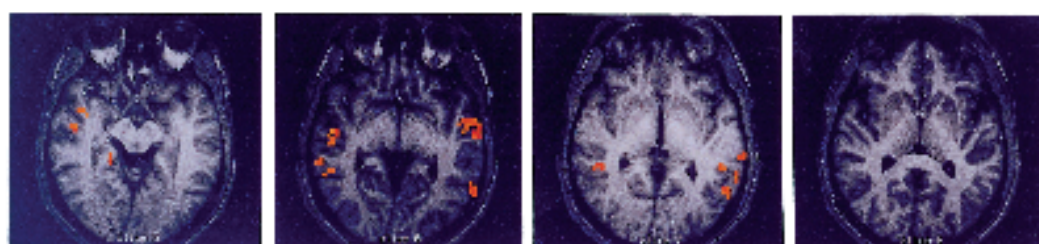


FIG. 1. Intersubject variability in the cortical representation of language is greater in L2 than in L1. (a) Activity observed in single subjects when listening to L1 or L2 plotted on a standardized atlas of cerebral neuroanatomy²⁷ for purposes of inter-subject comparison. Each subject was assigned a distinct color. Each disk indexes one active cluster of voxels, with size proportional to the volume of activation. Note the tight overlap of activation from all 8 subjects in the left temporal lobe (including the temporal pole and posterior language area) when listening to L1, which is not observed in the right hemisphere in L1 or in either hemisphere in L2. While listening to L2, no activation was observed in the temporal poles or the angular gyrus, but some subjects showed additional activation in the left inferior frontal gyrus, and in the anterior cingulate (not shown). In both L1 and L2, left and right temporal activation spares the region surrounding the primary auditory area, which was presumably active in both the stories and the backward speech control. (b) Average active volume (mm³) in anatomical regions of interest individually defined on anatomical MR images. Only anatomical regions that were found active in at least three subjects are reported. Abbreviations: STG: superior temporal gyrus; STS: superior temporal sulcus; MTG: middle temporal gyrus; TP: temporal pole; AG: angular gyrus; SFG: superior frontal gyrus; MFG: middle frontal gyrus; PrG: precentral gyrus; Cin: anterior cingulate gyrus.

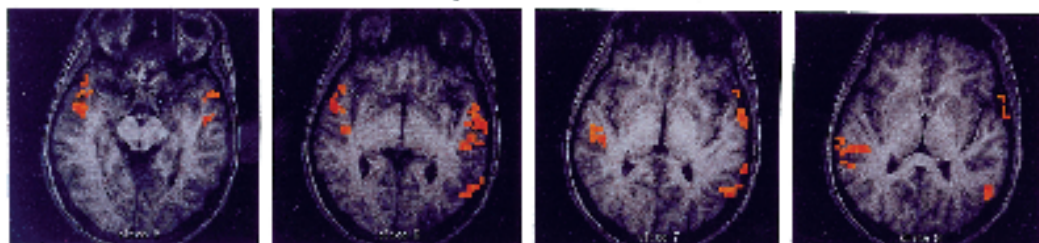
Subject A, French



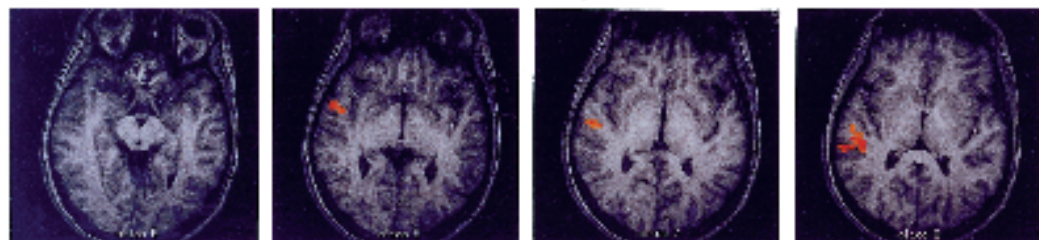
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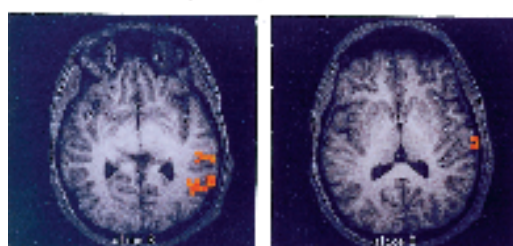
Subject B, French



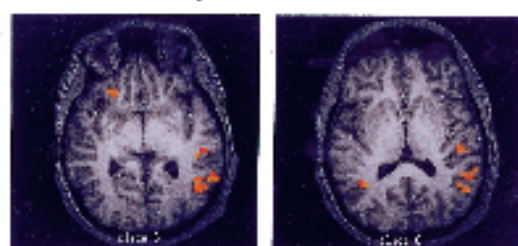
Subject B, English



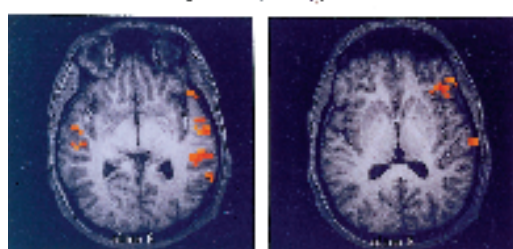
Subject F, French 1



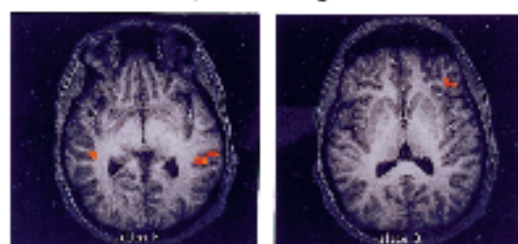
Subject F, French 2



Subject F, English 1



Subject F, English 2



in the left TP and AG. The remaining two subjects showed a striking absence of activations in the left temporal region while listening to L2. Only their *right* temporal lobe was active. Hence those subjects showed left-hemispheric dominance for comprehension in L1, but right-hemispheric dominance for comprehension in L2. One such subject is depicted in Fig. 2 (subject B). When listening to L1, this subject showed intense activity in the left STS and the left anterior temporal region, together with some activation in the right anterior and middle temporal lobe. When listening to L2, there was a complete disappearance of activity in the left temporal lobe at the chosen level of significance; the only significantly active areas were found in the *right* STG, MTG and TP, in a region anterior to, though partially overlapping with, that found when this subject listened to L1.

Even when subjects showed left temporal activity in L2, its volume was often smaller than in L1, and listening to L2 activated additional small subregions in the right temporal lobe (mostly the right STG and STS; see e.g. Fig. 2, subject A, slice 6). To assess whether this trend towards a reduced left-lateralization for L2 than for L1 was significant despite the considerable inter-subject variability, an analysis of variance was performed on the volume of active tissue in the left and right STS. A significant interaction between hemisphere and language was found ($F(1,6) = 15.6$, $p = 0.0075$). While listening to L1, the average active volumes were 1378 mm³ in the left STS and 456 mm³ in the right STS, a highly significant asymmetry ($F(1,6) = 20.6$, $p = 0.004$). While listening to L2, the asymmetry decreased to a much smaller, though still significant value (left STS: 666 mm³; right STS: 327 mm³; $F(1,6) = 7.18$, $p = 0.037$).

Variable activation while listening to L2 was also observed in cerebral regions outside the temporal lobe. Three subjects showed a highly specific activation of the left inferior frontal gyrus (Broca's area) and of the inferior precentral sulcus in L2 which was not found in L1 (see Fig. 1; Fig. 2, subject F). Four subjects also showed activity in the left and right anterior cingulate when listening to L2, but not when listening to L1. Finally, six subjects showed a frontal

activation at the intersection of the IFS and the PrG in L2, in a region very similar to that found in L1.

The qualitative differences between L1 and L2 seen with correlation analysis were confirmed statistically using an individual analysis with SPM. For instance, the greater activation of the left STS during L1 than during L2 in subject B (see Fig. 2) was confirmed (two foci with $Z = 4.50$ and $Z = 4.27$), as was the L2-specific activation of the left IFG in subject F (see Fig. 2; $Z = 4.66$). Seven subjects showed discrete foci of activation in the left or right temporal lobe for which listening to L1 yielded significantly greater activation ($p < 0.001$) than listening to L2, relative to backward speech. Four subjects showed foci with the converse difference ($L2 > L1$, $p < 0.01$). In many cases, these language-specific foci were very near one another. For instance, subject D showed one left posterior STS focus where $L1 > L2$ (Talairach coordinates -54 , -57 , 15 ; $Z = 5.16$), and another focus, only 15 mm more anterior, where $L2 > L1$ (Talairach coordinates -63 , -42 , 12 ; $Z = 4.02$). The exact anatomical location of these foci, however, varied from subject to subject.

Discussion

The pattern of activation in L1 replicated and extended the results of previous PET studies of brain activity while listening to single words¹¹⁻¹⁵ and to continuous speech in the first language.^{5,8,16} In the latter studies, activity averaged across subjects was reported in the left STG and MTG, the left posterior temporal lobe, and the bilateral TP. The increased anatomical accuracy afforded by the present method shows that temporal lobe activity while processing continuous speech in L1 is mostly concentrated in the banks and depth of the STS, once activity in primary and secondary auditory areas related to acoustic processing is subtracted. The bilateral temporal poles, which showed intense activity in PET, were only modestly activated here probably because of a loss of signal due to magnetic field inhomogeneities in the inferior anterior temporal region. Previous PET studies of listening to contin-

FIG. 2. Transaxial slices through the temporal and inferior frontal cortices of three subjects listening to French or English sentences alternating with backward speech. The right side of images corresponds to the subject's left. While listening to their native language, French, subjects A (top panel) and B (middle panel) showed highly similar intense left-lateralized activations along the left superior temporal sulcus (STS) extending anteriorly into the left temporal pole (TP) and posteriorly into the left angular gyrus (AG) (slices not shown). The right STS and TP were also active. In subject F (bottom panel), activity was more strictly left-lateralized in the vicinity of the STS, with little or no posterior and anterior extensions. When subjects listened to their second language, English, highly variable activation patterns were found. In subject A, activation decreased considerably relative to the French condition in the left STS and failed to reach significance in the left AG and left and right TP. An additional focus of activation was however found in the right STS (slice 6). In subject B, active pixels were only found in the right temporal lobe, in sectors close to but not necessarily identical with those previously found active in French; no significant pixels were found in the left hemisphere. In subject F, activity was found in the left STS (in sectors partially non-overlapping with those found in French), but also in the right STS and in the *pars triangularis* sector of the inferior frontal gyrus (IFG). In this subject, two replications of each condition, each time with different stories in French and in English, demonstrated the reliability of the IFG activation despite some variability in the number and exact localization of active pixels.

uous speech in L1 also reported weak activation of the left inferior frontal gyrus (Brodmann's area 45)^{5,8,16} and of the left Brodmann area 8⁸ while listening to L1. While these exact regions were not observed in the present study with higher spatial resolution, perhaps due to differences in subjects, languages and/or task demands, a frontal activation was found at the intersection of IFS and PrS, bordering the regions activated in previous studies.

The highly reproducible left temporal activations when listening to L1 confirm that a dedicated network of left hemispheric cerebral areas, mostly localized to the left STS, underlies native speech comprehension.¹⁷ Our data indicate that, in late and moderately proficient learners of L2, this network fails to be consistently recruited for second-language comprehension. Indeed, some subjects showed only right-hemispheric activations in L2 in temporal areas homologous to those observed in their left hemisphere while listening to L1. Other subjects showed activity in the left superior temporal sulcus in L2, but with greater dispersion than in L1 and with occasional differences in exact topography. A similar distinction between subregions for L1 and L2 within the same general anatomical areas has been observed in a recent fMRI study of language production.¹⁸ Our work shows that a similar dissociation is found between speech comprehension in L1 and L2 in left and right temporal areas.

In our work, several subjects showed significant activations of the left inferior frontal gyrus and of the anterior cingulate only when listening to L2, but not when listening to L1. The anterior cingulate region has been implicated in attentive, controlled or 'central executive' processing tasks^{19,20} suggesting that some subjects had to engage greater attentional resources for processing L2 than for the more automatized processing of their maternal language. The inferior frontal activation may have reflected a strategy of internally rehearsing the English words using an articulatory loop²¹ to maintain L2 sentences in working memory while processing them.

Our results may contribute to clarify the complex issue of aphasia in bilinguals. Based on a review of neuropsychological cases, Albert and Obler¹ originally suggested a decreased degree of leftward lateralization for the second language. This conclusion remains controversial, however, because counterexamples are frequent.^{22,23} Our data provide some grounds for reconciliation by showing both how, on average, lateralization of activity to the left temporal lobe is significantly reduced in L2 compared to L1, and how individual subjects show considerable variation in their lateralization pattern for L2, anywhere from complete right lateralization to standard left lateralization.

In a previous PET study of a group of bilingual subjects comparable to the present population, we had failed to observe activation while listening to L2 above and beyond that observed for an unknown language.⁵ The present results suggest that brain activity related to lexical, syntactic and semantic processing in L2 failed to emerge in that group study because it was inconsistently localized from subject to subject. Thus our observations emphasize an important methodological difficulty for brain imaging studies based on group averaging. Such studies may fail to identify active areas that are relevant to cognitive function, but whose localization varies considerably across subjects.

What factors might be responsible for inter-subject variability in the anatomical representation of L2? All our subjects were right-handed male bilinguals who had acquired L2 after the age of seven and who had achieved only a moderate level of proficiency in L2. The dissimilarity between languages, which may be an important factor in bilingualism,² was also kept constant (French *vs* English). Nevertheless, the residual variability among subjects might be due to the exact conditions under which they acquired L2. Different methods of teaching L2 might favor different strategies for language processing, and hence distinct cerebral circuits. Acquisition of L1, on the other hand, proceeds under very similar conditions for all subjects.

Another potential factor of variability is a putative intrinsic difference in brain organization. Interestingly, even in L1, the extent of right hemispheric activation varied considerably across subjects, and a significant correlation was found between the volumes of right temporal activation in L1 and in L2 ($r_2 = 47.3\%$, $p < .02$). Hence, different subjects vary in their use of the right hemisphere for language, be it for L1 or L2. This intrinsic variability in language lateralization, whose origins remain to be discovered, appears to contribute to variability in L2 representation.

A third important factor, finally, may be the exact age at which L2 was acquired. Indeed, previous behavioral²⁴ and brain-imaging^{6,18} evidence suggests that maturational changes affect the ability to acquire a second language. Further work is clearly needed to clarify the respective influences of initial biological architecture, timing of exposure to various languages, acquisition method, and eventual proficiency in each language, on the cortical organization of bilinguals. In particular, studies of individuals who achieve a high level of proficiency in a late-acquired second language should help test whether there is a permanent loss of plasticity in left temporal language areas with age and maturation, or whether these areas can be eventually recruited in fluent individuals following

intense learning. Brain-imaging studies of motor learning^{25,26} have revealed increased distributed activity in prefrontal and parietal cortices in the initial stages of acquisition of a motor skill, followed by a concentration of activation to sensori-motor and supplementary motor areas once skillful performance is achieved. If second-language acquisition follows a similar time course, one might expect a progressive concentration of activations while listening to L2 to the classical left perisylvian language network as subjects move from a moderate to a high level of proficiency in L2.

Conclusion

This study illustrates the feasibility of using fMRI to study the cerebral networks involved in first and second language processing in the human brain. Reliable left temporal activations were found while listening to L1, reproducing previous PET results.^{5,8,16} While listening to L2, activations were strikingly more variable, with decreased left-lateralization or even complete right lateralization. The present study was not designed to determine whether the observed differences between L1 and L2 were imputable to phonological, prosodic, syntactic or semantic levels of speech processing. Nevertheless, the results support the hypothesis that first language acquisition relies on a dedicated left-hemispheric cerebral network, while late second language acquisition is not necessarily associated with a reproducible biological substrate.

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