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Language Lateralization Shifts with Learning by Adults

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Abstract

For the majority of the population, language is a left hemisphere lateralized function. During childhood, a pattern of increasing left lateralization for language has been described in brain imaging studies, suggesting this trait develops. This development could reflect change due to brain maturation or change due to skill acquisition, given that children acquire and refine language skills as they mature. We test the possibility that skill acquisition, independent of age-associated maturation can result in shifts in language lateralization in classic language cortex. We imaged adults exposed to unfamiliar language during three successive fMRI scans. Participants were then asked to identify specific words embedded in Norwegian sentences. Exposure to these sentences, relative to complex tones, resulted in consistent activation in the left and right superior temporal gyrus. Activation in this region became increasingly left lateralized with repeated exposure to the unfamiliar language. These results demonstrate that shifts in lateralization can be produced in the short-term within a learning context, independent of maturation.

Keywords

Brain; fMRI; language; learning; laterality

Introduction

That language is a left hemisphere dominant function is well accepted. What drives this pattern of lateralization remains a matter of debate. The discovery of early-appearing structural asymmetries within perisylvian cortex (Chi, Dooling, & Gilles, 1977; Wada, Clarke, & Hamm, 1975) appeared to support the idea that lateralization is an inborn phenomenon, a result of hemispheric differences in neuroanatomy that bias the brain towards left hemisphere language dominance. However, subsequent work has documented a surprising lack of correspondence between cortical asymmetries and language lateralization (Greve, Van der Haegen, Cai, Stufflebeam, Sabuncu, Fischl, & Brysbaert, 2013; Keller, Roberts, Garcia-Finana, et al., 2011). This has led to reconceptualization of the origins of functional laterality (Bishop, 2013; Hervé, Zago, Petit, Mazoyer, & Tzourio-Mazoyer, 2013; Minagawa-Kawai, Cristia, & Dupoux, 2011).

We know that infants and toddlers show left-lateralized activation related to the processing of speech (Bortfeld, Fava, & Boas, 2009; Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2006), suggesting a genetically-mediated component that contributes to a broader language lateralization (Bishop, 2013). However, there is also reason to believe that laterality is not a fixed phenomenon. Both cross-sectional and longitudinal imaging studies of children suggest that brain activation shows age-related changes for language tasks. Although typically left lateralized early in childhood, children show age-related increases in lateralization for language-specific pitch characteristics (Sato, Sogabe, & Mazuka, 2010), and tasks involving semantic and syntactic processing (Holland, Vannest, Mecoli, Iacola, Tillema, Karunanayaka, Yuan, Plante, & Byars, 2007; Szaflarski, Altaye, Rajagopal, Eaton, Meng, Plante, & Holland, 2012), as well as expressive language tasks (Kadis, Pang, Mills, Taylor, McAndrews, & Smith, 2011). There are task-related differences in the degree of lateralization reported, but the pattern of increasingly left-ward lateralization with age is prevalent in the child imaging literature. This has led some to state that “functional lateralization is the result of maturational processes” (p. 71, Hervé et al., 2013)

The difficulty with this conclusion is that studies of children involve an inherent confound between maturation and skill acquisition. Groups of children imaged at different ages or longitudinally are typically in the process of developing the language skills under examination. Other important changes co-occur with skill acquisition that can confound interpretation of fMRI data. For example, McNealy Mazziotta, & Dapretto (2011) used an artificial language task that required children to identify tri-syllabic units within ongoing syllable streams. Their subjects (ages 5 to adult) demonstrated a significant age-related shift in lateralization during this task, favoring stronger left hemisphere involvement. They also obtained pubertal development scores in 10-13 year olds as a measure of physical maturation. Pubertal development scores correlated with activation positively in the left supramarginal gyrus and negatively in the right superior temporal gyrus, seen during an artificial language learning task. These asymmetrical hemispheric effects suggest physical maturation, independent of task performance, could contribute to changes in laterality.

This idea has further support from a recent study of language processing that has found age-related shifts in fMRI signal (which comes largely from venous blood flow) but not for

signal from simultaneously collected arterial spin labeling images (which depends on arterial blood flow) (Schmithorst et al., in press). This study required children to listen to a series of stories while undergoing simultaneous BOLD and ASL imaging. The authors report differences in the signal generated by these two imaging methods, strongly suggesting age-related changes in neuronalvascular coupling. This physiological correlate of maturation could affect laterality estimates obtained with BOLD fMRI obtained during childhood.

Age-related changes in lateralization are not confined to the childhood years. Szaflarski, Holland, Schmithorst, and Byars (2006) reported increasingly strong left lateralization during childhood and decreasing left lateralization for language during adulthood. This might suggest a curvilinear relation between age and lateralization. However, this study used a verb-generation task, which requires both semantic knowledge and cognitive control. Vocabulary growth increases over the lifespan (Ramscar, Hendrix, Shaoul, Milin, & Baayen, 2014), whereas cognitive control increases during childhood and decreases with aging. This decrease in function could lead to reduced activation in the left inferior frontal and superior temporal regions (Persson, Sylvester, Nelson, Welsh, Jonides, & Reuter-Lorenz, 2004). Therefore, the sources of the reported lateralization changes are difficult to isolate.

One approach to address these types of confounds is to examine the potential for lateralization change in young adults as they are in the process of acquiring language skills. The idea that adult learners, like children, might show a learning-related shift in brain lateralization is consistent with the 'Learning Biases Hypothesis' (Minagawa-Kawai et al., 2011). This account posits that left lateralization for language is a consequence of the process of learning a language rather than an inborn property of brain organization. Specifically, within this theoretical framework, language solidifies as a left lateralized process because of the recruitment of predominantly left hemisphere neural resources during language acquisition. Rather than using a pre-existing, genetically determined, language-dedicated network to acquire language, the learner begins the process of language acquisition by utilizing more basic but still left lateralized processing resources. A language network emerges as these more basic resources are increasingly used in concert as language is acquired. This theory would suggest that this laterality is at least in part experience-dependent rather than simply a genetically controlled maturational process.

Minagawa-Kawai et al (2011) contrast this hypothesis with two alternate theoretical accounts common in the literature. The 'Signal-Driven Hypothesis' postulates that hemispheric biases for processing low-level perceptual features are mirrored in language processing. Unlike the Learning Biases Hypothesis, the Signal Driven Hypothesis might predict age-related change if underlying changes in brain structure and function affected the accuracy or efficiency of these lower-level perceptual processes. However, once these lower-level processes are fully developed, no further age- or experience-related change should occur. Therefore, the Signal Driven Hypothesis would not predict a learning related shift in lateralization for adults, who have already fully developed their low level perceptual processes.

The ‘Domain-Driven Hypothesis’ adopts the idea of a modular network specifically designed for language, and this language-specific network happens to be left lateralized in most individuals. This hypothesis is consistent with nativist views of language as an inborn ability that may be triggered by experience, but not learned in any traditional sense of the word. Importantly, the language network, under this view, is often considered to be largely or entirely pre-specified by the human genetic code and fully capable of processing any language input it receives. Therefore, this theoretical view is least consistent with the notion of experience-driven change in lateralization.

Minagawa-Kawai et al (2011) point to indirect evidence in support of the Learning Biases hypothesis. Imaging studies of adults exposed to unfamiliar languages tend to show reduced left lateralization of auditory cortex activation relative to that seen for familiar languages (Mazoyer, Tzourio, Frak Syrota, & Muruyama, 1993; Perani, Dehaene, Grassi et al., 1996; Wilson & Iacoboni, 2006). Also relevant to this position is a finding that structural changes in the anterior and posterior language areas can accompany second language acquisition (Mårtensson, Eriksson, Bodammer, et al., 2012; Stein, Federspiel, Koenig et al., 2012). However, a strong test of the Learning Biases Hypothesis would be to demonstrate that lateralization of the functional activation within classic language cortex shifts during a period of time in which adults are engaged in learning.

To dissociate brain changes associated with language learning from other biological effects requires a task in which adults can reliably demonstrate learning within a single experimental session, rather than across longer periods of time. Statistical learning studies provide models for how rapid learning can be achieved. Prior behavioral studies demonstrate that both infants and adults can reliably segment individual words within minutes of exposure to natural language stimuli (Kittleson, Aguilar, Tokerud, Plante, & Asbjørnsen, 2010; Pelucchi, Hay, & Saffran, 2009). This learning relies on the learner’s perception of statistical regularities that occur within the continuous speech stream (Saffran, Aslin, & Newport, 1996; Saffran, Newport, & Aslin, 1996). Learners realize that syllables that have a high degree of co-occurrence are likely to be word units. Rapid learning is facilitated by highly predictable statistical information that reliably highlights individual words in running speech. Statistical learning, therefore, offers an ideal context to test the idea that lateralization might be linked to learning, rather than to maturation.

In the present study, we directly test the hypothesis that learning affects lateralization of cortical areas classically associated with language functioning. To address this question, it was important to view learning as it happens. Therefore, we used a task that could be learned while participants underwent fMRI scanning, rather than training them over an extended period of time and assessing the outcome of learning that had occurred earlier, outside the scanner.

The Learning Biases Hypothesis would predict that adults exposed to an unfamiliar language should show a lateralization shift as they learn to identify individual words within connected speech. Specifically, this task in particular should co-opt more basic processes that are themselves left lateralized. We suggest that these task-critical processes include functions like the recognition of sounds as speech (left superior temporal lobe, Osnes,

Hugdahl, Hjelmervik, & Specht, 2011; Specht, Osnes, & Hugdahl, 2009) and the ability to use statistical information in order to recognize word units within running speech (left superior temporal lobe, Hickok, 2012 or inferior frontal gyrus, Karuza, Newport, Aslin, Starling, Tivarus, & Bavelier, 2013). In contrast, the absence of a shift in language lateralization would be consistent with the idea that maturational factors were primarily responsible for producing laterality shifts previously seen in studies of children.

Method

Participants

Sixteen adults (7m, 9f; mean age 24 years, SD=8 years) participated in the study. Five were left handed and eleven right handed. None reported a history of neurological disorders, learning disability, language disorder, or speech-language therapy as a child. We included both right- and left-handed participants. Left-handers are often excluded from imaging studies of language because of concerns that these individuals may show anomalous dominance patterns. However, most left-handed individuals, even those in the process of acquiring language (Szaflarski et al., 2012), demonstrate left hemisphere language dominance and some right-handers can show right hemisphere language dominance. This makes handedness an imprecise and even misleading indicator of dominance (Bishop, 2013). The inclusion of both left and right handed participants provides a more representative sample of the population and allows for an opportunity to examine any potential variation with handedness on an individual level.

All participants were interviewed concerning their knowledge and exposure to other languages. None reported speaking or understanding Norwegian or any closely-related language (e.g., Swedish, Dutch). None reported medical conditions, developmental or acquired disorders likely to alter brain function, and none reported contra-indicators for MRI scanning. All provided written informed consent as approved by the University of Arizona Institutional Review Board.

Materials

Norwegian Stimuli—The stimuli were those used previously in a behavioral study that demonstrated novice adult listeners could segment Norwegian words embedded into spoken sentences. Conversely, adults who were not exposed to the words in sentences could not differentiate the stimulus words from Norwegian-like non-words (Kittleson et al., 2010).

The stimuli consisted of 54 Norwegian sentences digitally recorded by a male native speaker in the Bergen dialect following the Bokmål orthography. Each sentence included one of nine bi-syllabic Norwegian words that were the learning targets for this experiment. For example, the target word ‘lever’ was heard in the sentence “Den som lever får se.” and “Vi lever godt på en inntekt.” as well as in 4 additional sentences. With the exception of grammatical morphemes (e.g., articles, gender markings), the remaining nontarget words in each sentence were unique to that sentence and did not repeat across sentences. This produced a high degree of statistical predictability between the two syllables of the target words, but a low statistical predictability between any other pair of two adjacent syllables in the entire set of

sentences. The statistical characteristics of the sentence stimuli were published previously in Kittleson et al, (2010).

Control Stimuli—During each scan, signal obtained during blocked exposure to the Norwegian stimuli was contrasted with that resulting from blocked exposure to complex tone stimuli. Complex tones were constructed by first creating pure tones between 200 and 2500 Hz. These tones varied in duration from 1800ms to 3200ms, making them similar to the length of the Norwegian sentences. The pure tones were then modulated in frequency and amplitude to create a complex acoustic envelope that was unique for each tone. Finally, two tones of the same duration (one at or below 625 Hz and one at or above 1800 Hz) were combined into the final complex tone. The resulting complex tone shared many characteristics of speech (e.g., a time-varying fundamental frequency, multiple frequencies represented in the signal, amplitude modulation), but clearly did not sound like speech.

Test Stimuli—After each scan, participants were tested concerning what they had learned. The test items were clipped directly from the audio file of the High Predictability input so that they were exact matches to the syllables heard during the scan. Each correct test item was one of the nine target word tokens heard during the scan. Each incorrect nonword test items consisted of one of the two syllables from each target word plus an immediately adjacent syllable that occurred in one of the Norwegian sentences heard during the scan. Therefore, for incorrect test items, the participants had heard one of the syllables as frequently as they heard the correct items, controlling, as much as possible for a general familiarity effect. Like the correct test items, participants also had heard each of the two syllables of the incorrect test items together during the scan (controlling for a general co-occurrence effect). Importantly, a prior behavioral study demonstrated that the true Norwegian words used as test items here could not be distinguished from the nonword test items by English-speaking individuals who had not previously been exposed to the words in their sentence contexts (Kittleson et al., 2010).

Procedures

Sentence and tone stimuli were arranged in nine alternating blocks of six sentences and six complex tones. Sentences containing the same target word were aggregated into the same scan block. Each sentence and tone block was preceded by a cue (“Listen to these sentences.”, “Just relax.”), to indicate what was expected of the participant during the immediately following block. Participants were instructed to listen to the Norwegian stimuli during each scan and they were told they would be tested on what they had learned about the Norwegian input after each scan. No responses were required by the participants during the actual scans.

After each scan, and while still in the scanner, participants completed a two alternative forced-choice test of their learning of the target words. No imaging data was collected at this time. Participants were presented audio files of each of the nine target words and nine nonwords. Test items were presented in a computer-generated random order. Participants indicated their decision concerning whether each test item was a real Norwegian word using

a button press. No feedback was provided concerning participants' responses. This test was self paced, but typically lasted approximately 2 minutes.

The fMRI scans were obtained using a spiral in/out sequence (Glover & Law, 2001) on a GE 3T system with an 8-channel array (TR 2600, TE 30, Flip angle 90, FOV 240, Matrix 64×64, voxel dimension 3.75×3.75×5, 173 time points). Full-brain coverage was obtained with 26 contiguous slices. Nine prestimulus volumes were obtained to assure that equilibrium was reached prior to the onset of stimuli and two post-stimuli TRs were obtained to allow the hemodynamic response to decrease prior to the end of the scan. The remaining TRs were divided into 18 blocks of 9 TRs each. Each block corresponded to a 2 TR cue period in which participants were alerted to the task for that block ("Listen to these sentences." "Just relax."), followed by 7 TRs during which the relevant stimuli were played. Stimuli were presented as alternating blocks of spoken Norwegian sentences or complex sounds, with a total of 9 blocks of each. The total scan time was 7 minutes, 29.8 seconds. The total time for the three scans and three test periods was approximately 25 to 30 minutes.

High-resolution (1×1×1.4mm voxel, Number of excitations=1, field of view=256mm, 256×256 matrix) SPGR scans were also obtained in the sagittal plane (TR=5.145ms, TE=1.988ms, inversion time=500ms, Flip angle 15). These were aligned with the functional scans during post processing and were used to locate the anatomical regions that represented classic language cortex.

Analysis was conducted using AFNI (AFNI_2011_05_26_1457). Volumes were registered to a base image, linear drift was removed and slice-time offsets were corrected during preprocessing. Each scan was de-spiked and normalized to an average spiral image template for the subject set. Data were smoothed using a 7mm FWHM Gaussian kernel. Data were then analyzed using a general linear model to estimate BOLD response. Group averaged activation that was positively associated with sentence blocks was thresholded at $p < .05$ corrected for multiple comparisons at a brain-wide level.

Although we originally planned to examine laterality in both of the classically-defined language regions (superior temporal gyrus and inferior frontal gyrus), only the superior temporal gyrus showed consistent bilateral activation in all three scans. Therefore, we focused on this region of interest (ROI) specifically. Our approach to characterizing lateralization in this ROI is consistent with previous work that has demonstrated that restricting laterality calculations to only those regions that show task-related activation reduces the spurious influence of more diffuse activation areas (Abbott, Waites, Lillywhite, & Jackson, 2010; Wilke & Lidzba, 2007). This, in turn, improves both sensitivity and stability of the laterality index (Abbott et al., 2010; Holland et al., 2001; Wilke & Lidzba, 2007). We used average t-values within the right and left superior temporal gyrus ROI as the measure of hemispheric activation. These were obtained for each subject, and a laterality index for each subject was calculated using the formula $(L-R)/[(L+R)/2]$.

The superior temporal gyrus ROI was created from a group average t-statistic activation map. We created left and right hemisphere masks from the group-averaged data, and thresholded at $p < .05$ with FWE correction for multiple comparisons. Masks were developed

by first masking significant activation in each hemisphere for this region. We then flipped each mask across the hemisphere midline along the x-axis. Consequently, all of the activation originally located in the right hemisphere was projected onto the left hemisphere and vice versa. The original and flipped masks were then merged to create bilaterally symmetrical masks that reflected the regions activated in both the right and left hemispheres combined. These symmetrical masks allowed for calculation of laterality estimates generated from the same number of voxels in each hemisphere. These procedures were repeated for each of the three scans so that each scan had a unique group-averaged mask that reflected the combined right and left hemisphere activation for that scan.

To assure that the trends in lateralization over the period of learning were unrelated to thresholding decisions, we calculated the laterality index for the region of interest using three different levels of correction. In the first analysis, individual subjects' activation data were not thresholded or corrected at all. Instead, all activation, whether statistically significant or not, that appeared within the masked areas was averaged within the left and right hemisphere mask. In the second condition, a threshold of $p < 0.05$ (uncorrected for multiple comparisons) was applied to each subject's activation map, and only voxels that exceeded this threshold were used to calculate the average activation for the right and left hemisphere masks. This procedure served to eliminate voxels-wise activation that was probably unrelated to the task demands. The third condition applied a more conservative thresholding criterion of $p < .05$, with FWE correction for multiple comparisons brain-wide. Again, the average activation for suprathreshold voxels within the symmetrical left and right hemisphere masks was calculated.

As mentioned above, the inferior frontal gyrus (Broca's area on the left) was not consistently activated for all three scans. As Figure 2 indicates, a region of pars opercularis was active in the left hemisphere during scan 2 and 3. Activation in this area did not exceed threshold in the right hemisphere during any scan. Therefore, when this area was active, it was entirely left lateralized.

Results

Behavioral results

Figure 1 displays the behavioral data obtained immediately after each scan. The degree of learning is expressed as d' , which reflects participants' discrimination of true Norwegian words from Norwegian pseudowords. Recall that participants received just under 4 minutes of exposure to Norwegian input during each scan. Therefore, we were primarily interested in whether the d' data indicated that measurable learning had occurred. This was operationalized as d' values that differed significantly from chance.

The d' values were significantly greater than chance during all three scans (Scan 1: d' mean[SD] = 0.41[0.71], $t = 2.31$, $p = .017$; Scan 2: 0.80[1.08] $t = 2.97$, $p = .005$; Scan 3: 0.70[0.50], $t = 5.56$, $p = .00027$). The significantly above-chance performance indicates adults did learn from the input during the scans. The degree of learning was modest overall, as might be expected for the very brief period of exposure provided during each scan and the modest increase over time was not statistically significant ($F(2,30) = 0.996$, $p = .38$;

$\eta^2=0.207$). Therefore, the overall pattern of behavioral results is consistent with learning that is beyond chance levels after scan 1, but with small and statistically nonsignificant change over the course of the subsequent scans.

Activation results

Lateral views of task-related activation are provided in Figure 2. As Figure 2 indicates, only the superior temporal gyrus (STG) was active bilaterally ($p<.05$ corrected) for all three scans. The region activated was centered in the STG and extended to the superior temporal sulcus. The peak activation in this region was quite spatially consistent (see Table 1). Note that the more posterior regions of the STG, proposed to provide a bridge between phonological and semantic processing were not active (Hickok, 2012). This is consistent with the lack of access to semantic information in the task.

The change in the laterality indices for the STG is provided in Figure 3. This figure indicates that the absolute lateralization index is sensitive to thresholding criteria. Critical for the present study, lateralization increased from scan 1 to 3, regardless of the thresholding criterion applied. A repeated measures ANOVA of the laterality index for the activation t values indicated a significant main effect for time ($F(2,30)=8.44$, $p=.001$, $\eta^2=0.36$). Least squares comparisons indicated that the leftward laterality was greater for scan 3 than scan 1 ($p=.001$) and that laterality indices for scans 1 vs. 2 and scans 2 vs. 3 did not differ significantly ($p=.05$ in each case).

We also considered the results for right- vs. left-handed subjects. These results should be considered preliminary, given the small number of left-handed individuals in the participant group. As shown in Figure 4, however, both right- and left-handed participants showed an overall pattern of increasing leftward lateralization over the period of learning. Moreover, the range of laterality values for the left handed individuals fell within that of the right handed individuals during each scan.

Discussion

Consistent with the Learning Biases Hypothesis, the brains of adult learners showed a leftward shift in activation of superior temporal gyrus during a period in which they demonstrated unguided learning of words from an unfamiliar language. Unlike the changes in laterality previously described for children at different ages, this laterality shift occurred within the timeframe of a single experimental session. This suggests that laterality is more dynamic than has been previously thought. Lateralization shifts have previously been documented to occur with increasing age in childhood (Kadis et al., 2011; Holland et al., 2007; Sato et al, 2010; Szaflarski et al., 2006; Szaflarski et al., 2012), or with second language learning over extended periods of time (e.g., Mårtensson et al., 2012; Stein et al., 2013). To our knowledge, this is the first demonstration of a significant laterality shift that occurred on the order of minutes.

Like the changes seen during childhood, the laterality shift seen in the present study with adults was the product of increasing activation, particularly within the left hemisphere language regions. This result as seen in adults does not rule out maturational contributions to

the changes in laterality seen in childhood (e.g., McNealy et al., 2011). However, it does establish that maturation alone is not the sole explanation for lateralization shifts (cf. Hervé et al., 2013). Our results make clear that learning, in the absence of developmental maturation, can affect lateralization.

Our adult subjects showed a pattern of increasing left hemisphere lateralization when asked to segment individual words in an unfamiliar language. Norwegian, like English, is a Germanic language. The phoneme set for the two languages overlap (but are not identical) and the two languages share a dominant trochaic stress pattern (although the pattern is stronger in Norwegian than in English). Both phonological and stress features are known to assist learners in segmenting words from running speech (Jusczyk, 1999) and the degree to which the two languages are similar likely assisted the learners in this task. However, it noteworthy that the learners showed a laterality shift despite the fact that learners could have relied on their knowledge of English to some degree to assist in segmenting Norwegian speech.

The increase in left hemisphere lateralization in the present study is distinctly different from the pattern of activation change seen with habituation paradigms for an already acquired language (Inspector, Manor, Amir, Kushnir, & Karni, 2013; Thiel, Shanks, Henson, & Dolan, 2003; Zevin & McCandliss, 2005) or in repetition priming studies (e.g., Beckmann, Jenkinson, Woolrich, Behrens, Flitney, Devlin, & Smith, 2006; McDonald, Thesen, Carlson, et al., 2010). In these experiments, repeated exposure to language stimuli resulted in reduced activation. In particular, Beckmann et al (2006) reported bilateral signal reductions within the superior temporal gyrus with repeated presentation of sentence stimuli. The distribution of this activity was very similar to the temporal lobe activation in the present study. Therefore, the laterality shifts observed in the present study are unlikely to be a side effect of repeated exposure to the language stimuli, given that this is typically associated with reduced activation for studies in which the language is already familiar to the participants.

The Learning Biases hypothesis of language lateralization directly links changes in language lateralization to the process of learning. This differentiates it from both Signal-Driven and Domain-Driven hypotheses (Minegawa-Kawai et al., 2011). In the present study adults heard identical stimuli in each scan. Therefore, the acoustic signal was unchanged from scan 1 to 3. The fact that laterality changed during this period is incompatible with the idea that the nature of the basic acoustic properties of language is the sole driver of left hemisphere lateralization or that a left hemisphere resident, modular processing mechanism automatically processes any language input. However, the Learning Biases hypothesis specifies that language becomes left hemisphere lateralized because the process of learning a language marshals primarily left-hemisphere dominant resources. It is therefore possible that the initial left-hemisphere lateralization seen during scan 1 reflects early recruitment of left hemisphere dominant skills that are directly relevant to this particular language learning task.

In our study, adults were exposed to an unfamiliar language spoken in an accent foreign to the listeners. These phonological patterns were often dissimilar to the listeners' own lexical representations, based on their native language. Repetition of the stimuli in subsequent scans

would serve to make the phonology more familiar, and perhaps even more speech-like, to the listener with time. In prior studies, regions within the superior temporal gyrus had a graded response to sounds that reflected a continuum from non-speech sound to a speech sound (Vouloumanos, Kiehl, Werker, & Liddle, 2001; Osnes et al., 2011; Specht et al., 2009). As sounds became more speech-like in that study, activation in regions within the superior temporal gyrus was more extensive in the left hemisphere compared to the right. One region, just posterior to Heschl's gyrus, showed a graded response as morphed vowel and musical tones became increasingly vowel-like (Osnes et al., 2011). A second region extending into the superior temporal sulcus became more left lateralized as a morphed white noise and consonant-vowel syllable combination became more syllable-like (Specht et al., 2009). In the present study, exposure to an unfamiliar foreign language may offer a parallel context. Individual phonemes can be difficult to perceive initially in an unfamiliar language, but tend to become more recognizable with continued experience. Therefore, the recruitment of brain regions that respond as sound is perceived as speech is likely to be critical when faced with an unfamiliar language.

The learning task required learners not only to become familiar with accented speech, but also to discover individual words within the continuous acoustic speech signal. Hickok (2012) proposed that the ventral auditory processing stream within a dual processing stream model (Hickok & Poeppel, 2004), which includes the superior temporal gyrus, may be the source of forward prediction during listening. In our study, once the input is recognizable as specific phoneme strings, word segmentation can be described in terms of forward prediction (the syllable 'kik' is reliably followed by 'kert' to form the word 'kikkert'). As listeners move from a state in which it is difficult to distinguish the individual sounds of speech to a state in which they can make forward predictions concerning sound sequences, the superior temporal gyrus should be increasingly engaged. Our results are consistent with this proposal.

We further note that the dorsal stream of the dual stream model includes areas active in our data. Although not strictly within the scope of the present study, Figure 1 clearly shows strong activation in the left motor cortex during scans 2 and 3. The dual stream model of Hickok & Poeppel (2004) also accounts for such activation as representing covert articulatory coding of speech information. As the Norwegian stimuli were perceived as increasingly speech-like with each subsequent scan, this should lead to a stronger likelihood of covert articulatory coding. Covert articulatory coding, as predicted by the dual stream model, is consistent with the pattern of increasing activation within the left motor cortex seen in Figure 2.

The frontal activation was represented only in the left hemisphere from the second scan on. Some have claimed that IFG activates in listening only when individuals are asked to make explicit judgments about sublexical information (Hickok & Poeppel, 2004). Likewise, Karuza et al., 2013 reported that this area correlated with judgments of syllable strings as word or nonword units heard previously during exposure to an artificial language, and remembered during a post-scan test phase. In the present study, the learning task inherently required recognition of words embedded in running speech, but did not require explicit judgments about the stimuli during the period of scanning. Therefore, activation in the IFG in the

present study may relate to memory processes. However, it is also possible that activation in this region relates to another aspect of the task. Osnes and colleagues (Osnes, Hugdahl, Hjelmervik, & Specht, 2012) reported that the pars opercularis region of the inferior frontal gyrus activated when listeners were told to expect to hear a vowel as part of a tone-vowel blend, but not when there was no expectation of speech content. Our participants were told explicitly that they were listening to Norwegian. This may have promoted engagement of this specific sub-region of the inferior frontal gyrus. Moreover, repeated exposure to the Norwegian stimuli may have increased the ability of the participants to ‘hear speech’ over the course of the experiment.

Learning-related changes are not unique to the domain of language. Others have reported activation-related changes for visuo-spatial learning (e.g., Hötting, Holzschneider, Stenzel, Wolbers, & Röder, 2013; Küper, Wünnemann, Thürling, et al., 2014; Nemmi, Boccia, Piccardi, Galati, & Guariglia, 2013), motor movements (e.g., Landau & D’Esposito, 2006; Meister, Krings, Foltys, Boroojerdi, Müller, Töpper, & Thron, 2005; Vogt, S., Buccino, G., Wohlschläger et al., 2007), and musical experience (Chen, Rae, & Watkins, 2012; Ellis, Bruijn, Norton, Winner, & Schlaug, 2013; Ellis Norton, Overy, Winner, Alsop, & Schlaug, 2012; Fujioka, Ross, Kakigi, Pantev, & Trainor, 2006; Koelsch, Fritz, Schulze, Alsop, & Schlaug, 2005). Although either learning or just greater experience in visuo-spatial and motor domains is often associated with a reduction in brain activation or skill acquisition (Hötting et al., 2013; Nemmi et al., 2013; Vogt et al., 2007), laterality shifts have been reported for aspects of music learning. Listening to trained vs. untrained melodies resulted in a reduction of activation in right but not left superior temporal gyrus (Chen et al., 2012). A left hemisphere increase in activation has been associated with hours of musical training for the left superior temporal gyrus (Ellis et al., 2012) and left supramarginal gyrus (Ellis et al., 2013). Similarly, children with violin training showed larger electrophysiologic response over left hemisphere electrode sites to violin tones, compared with their untrained peers (Fujioka et al., 2006). Note, however, that others (Koelsch et al., 2005) have reported bilateral activation increases in inferior frontal and superior temporal regions both for musicians vs. non-musicians and for adults vs. children. Their task required judgment of tone sequences and showed an overall pattern of right lateralization.

These findings for auditory but nonverbal stimuli (music) indicate that the laterality shift reported here is not limited to the task employed in the present study. However, it is interesting that the stimuli employed in studies of these two domains share important similarities, both in terms of their nature and related brain physiology (Koelsch, 2005). Not only are music and spoken words represented in the auditory modality, the distributional properties of both lend themselves to statistical learning (Creel, Newport, & Aslin, 2004; Kuhn & Dienes, 2008; Loui, Wessel, Hudson Kam, 2010; Tillmann & McAdams, 2004). This latter feature has lead some to claim that sensitivity to statistical regularities is a common process underlying both language and music learning (François & Schön, 2014; Pearce, Ruiz, Kapasi, Wiggins, & Bhattacharya, 2010; Schön & François, 2011). Indeed, some studies have suggested that musical training can positively affect the ability to perform speech segmentation tasks (Shook, Marian, Bartolotti, & Schroeder, 2013; François, Chobert, Besson, & Schön, 2013) supporting the hypothesis that these two skills rely on common left hemisphere lateralized processes. Others (Koelsch, 2005; Koelsch & Siebel,

2005) have claimed that the structural organization of music forms a musical syntax and semantics that leads to processing by brain regions that also support processing of spoken language.

Conclusion

Although a global left-hemisphere dominance appears to characterize language processing from very young ages (Bortfeld et al., 2009; Dehaene-Lambertz et al., 2006), this human trait is not a fixed phenomenon. Here we demonstrate that such shifts can also be induced in the short-term as the brain becomes familiar with the sound patterns that represent words embedded in a novel language. The pattern of increasing left hemisphere lateralization parallels increases in lateralization seen during childhood, rather than resembling the decreasing pattern described for the adult years (Szflarski et al., 2006). Taken together, the evidence suggests that lateralization is a highly dynamic construct rather than reflecting either an inborn processing mechanism or developmental maturation alone. Left hemisphere lateralization may be driven by the initial recruitment of left lateralized neural resources best suited for the processing of speech input, with the increasing leftward lateralization reflecting a consequence of the learning that those resources support.

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Figure 1. Behavioral performance during post-scan testing. The d prime values indicate responses were better than chance for all three scans. Standard Error bars are provided around the mean d' values.

Figure 2.
Lateral views of activation. The left hemisphere is displayed on the left side of the figure.
Maps display the t statistic values at a brain-wide corrected threshold of $p < .05$.

Figure 3.

Laterality indices for the superior temporal gyrus (STG) region. Laterality is calculated as $(L-R)/(L+R/2)$ with more positive numbers corresponding to greater leftward lateralization. Leftward lateralization shifts over the period of learning are seen when data within the temporal love ROI is unthresholded, or thresholded at $p < .05$ uncorrected and $p < .05$ corrected for multiple comparisons. Standard Error bars are provided around the mean laterality values.

Figure 4.

Laterality indices for left and right handed participants. Data is for unthresholded activation within the superior temporal gyrus. Boxes indicate 1SD and whiskers correspond to minimum and maximum values for the participants. The center line divides left hemisphere lateralization (top half) from right hemisphere lateralization (bottom half).

Table 1

MNI coordinates for peak superior temporal gyrus activation.

	Left Hemisphere X, Y, Z	Right Hemisphere X, Y, Z
Scan 1	62, -24, 4	-62, -18, 0
Scan 2	62, -24, 6	-64, -18, -2
Scan 3	62, -24, 6	-62, -18, -2