

The cortical organization of audio-visual sentence comprehension: an fMRI study at 4 Tesla

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Abstract

Neuroimaging studies of written and spoken sentence processing report greater left hemisphere than right hemisphere activation. However, a large majority of our experience with language is face-to-face interaction, which is much richer in information. The current study examines the neural organization of audio-visual (AV) sentence processing using functional magnetic resonance imaging (fMRI) at 4 Tesla. Participants viewed the face and upper body of a speaker via a video screen while listening to her produce, in alternating blocks, English sentences and sentences composed of pronounceable non-words. Audio-visual sentence processing was associated with activation in the left hemisphere in Broca's area, dorsolateral prefrontal cortex, the superior precentral sulcus, anterior and middle portions of the lateral sulcus, middle superior portions of the temporal sulcus, supramarginal gyrus and angular gyrus. Further, AV sentence processing elicited activation in the right anterior and middle lateral sulcus. Between-hemisphere analyses revealed a left hemisphere dominant pattern of activation. The findings support the hypothesis that the left hemisphere may be biased to process language independently of the modality through which it is perceived. These results are discussed in the context of previous neuroimaging results using American Sign Language (ASL).

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1. Introduction

Discovering how language is instantiated in the human brain is a central issue in human neuropsychology. Early clinical studies of language showed that damage to the left hemisphere (LH) impairs production [7] and comprehension [72]. The advent of neuroimaging techniques, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), has permitted a more detailed characterization of the neural representation of cognitive function, including language. The bulk of this research has focused on processing single words (e.g., Refs.

[16,25,50,52,54,63,69,73,74]). These imaging studies reveal a robust LH greater than right hemisphere (RH) asymmetry for word processing, including activations in the inferior frontal region (including Broca's area), the posterior perisylvian region (including Wernicke's area, or the posterior lateral superior temporal gyrus, and the supramarginal gyrus (SMG)) and the angular gyrus (AG).

Although studying single word processing can provide valuable insight into the functional organization of acoustic, phonological, orthographic, morphological and lexical processing, it cannot address aspects of sentence processing such as sentential semantics, syntax and prosody. Indeed, a great deal of our language experience involves face-to-face discourse in which words are combined into an infinite number of utterances. The present study examines sentence

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processing using audio-visual (AV) presentation to examine the cerebral organization of sentence processing as it occurs in a richer, more ecologically valid environment than reading or listening.

To date, neuroimaging research on sentence processing has investigated both written and spoken forms. Studies of sentence reading show more LH than RH activation [2,22,23,65,70]. Studies of sentence reading that have manipulated syntax also show a LH greater than RH asymmetry as a function of syntactic complexity, including activation in the pars opercularis (BA44) [11,22,24,34,45,57,66] and pars triangularis (BA45) [13,22,23,34,45,57] of Broca's area and in the LH posterior superior temporal cortex [15,22,24,34,45,57]. Even in studies in which syntactic processing elicited activation in RH brain regions, the overall activation was still greater in the left than the right hemisphere [11,13,14,22,24,34,45]. Consistent with neuroimaging studies of word processing, studies of reading sentences show more LH than RH activation including activation in classical language areas of the LH.

Although many studies of auditory sentence processing report significant activation in the right temporal lobe [20,25,26,28,29,38,40,44,45,48,58,62,74], there is a reliable preponderance of the left over the right temporal cortex activation across auditory sentence processing imaging studies [20,27–29,40,58,62]. For example, using fMRI, Schlosser et al. [62] found that, in native speakers of English, processing well-formed spoken English sentences (compared to sentences in an unfamiliar language) elicited robust activation in the left superior temporal sulcus (STS) and less robust activation in the left inferior frontal gyrus and the right STS. A language by hemisphere interaction displayed a strongly LH greater than RH activation pattern for the English sentence condition. Using PET, Mazoyer et al. [40] found a similar pattern of activation in monolingual French speaking adults listening to French stories. Importantly, these data showed a LH asymmetry for each significant brain region. Even in the absence of significant lateralization, auditory sentence processing studies typically report stronger activation for the LH than the RH (e.g., Ref. [45]).

Although the findings from neuroimaging research using written and spoken sentences provide converging evidence that sentence processing is LH dominant, there is a paucity of research describing the neural representation of AV sentence processing. This is somewhat curious, as language is very often perceived through the combined audio and visual modalities. Indeed, even very young infants match facial movements with their corresponding sounds [37], and 18 month olds reliably use the direction of a speaker's eye gaze to establish links between words and novel objects [1]. From the very beginning and throughout one's life, a great deal of language is experienced through the simultaneous presentation of auditory and visual information. Multiple behavioral studies with adults have shown that the perception of speech sounds is influenced by accompanying visual cues; speech percep-

tion is facilitated when auditory and visual information are congruent [8,9,21,32] and impeded when language inputs are incongruent [40,41].

Despite our prevalent use of AV language and the many behavioral studies of AV presentation of speech sounds and words, there is a paucity of neuroimaging studies of sentence processing using AV stimuli (with an exception of MacSweeney et al. [39]). In order to understand how language is actually processed in real contexts, it is imperative to study sentence processing using ecologically valid stimuli. It is quite possible that the neural organization of AV sentence processing may not be greater in the LH than the RH. Behavioral and neuropsychological research has shown that processing facial expression and affective prosody depend upon the functional integrity of the RH. Individuals with damage to the RH show reduced facial expressivity in natural conversation compared to those with damage to the LH and healthy controls [6]. Lesions to the RH have been shown to impair prosodic production [49,59], the ability to repeat prosodically [60] and comprehension of affective prosody [33,67]. The RH has also been shown to be important for processing linguistic prosody, or word stress [5,6,49,71]. In addition, the role of the RH in affective prosodic processing has also been demonstrated in neurologically healthy individuals [31].

In addition to examining aural sentence processing in a modality that is rich in information, the results of the AV sentence processing condition may help illuminate the nature of the RH activation found in previous studies of sign language comprehension. Previous neuroimaging studies of sign language demonstrate that, unlike written and spoken language, signed language comprehension elicits bilateral activation [46,47,51,64]. AV and signed languages contain features that are not characteristic of written language such as prosody and cues to lexical information from the face. In addition, while the development of reading requires explicit instruction, AV and signed languages come naturally and spontaneously to most children. These modalities also differ in their age of acquisition; children are exposed to AV and/or sign language from birth or before whereas learning to read begins at 5 to 7 years of age, depending on local educational practices.

Since native signers processing American Sign Language (ASL) sentences demonstrate bilateral activation [46], if ASL and AV activations are similar, this would suggest that the RH is activated when sentence processing stimuli are presented in a primary form, includes the viewing of the producer, and/or prosody. However, to the extent that they differ, it would suggest that RH regions are specialized for the types of visual processing that are unique to sign language, for example, spatial syntax.

The goal of the present study was to identify the pattern of activation produced as participants processed AV English sentences. To the extent that language processing is reliant on modality-independent LH regions, we predicted that AV language, as with written and spoken language,

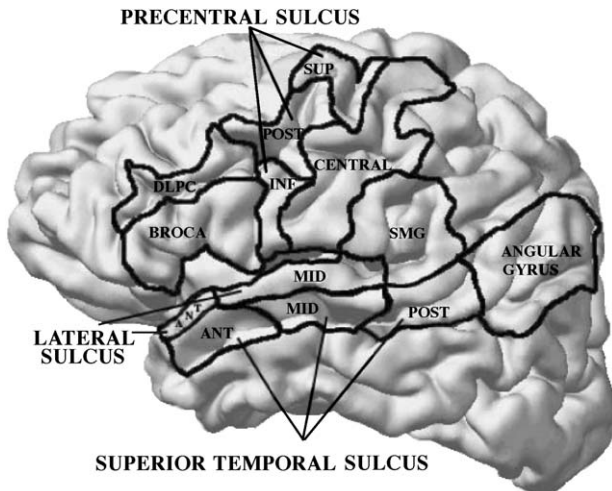


Fig. 1. Anatomical regions of interest.

elicits a similar LH greater than RH pattern of activation. However, it may be that the richness of information present in natural, AV sentences recruits the participation of additional LH and RH regions not typically shown to be involved in written or spoken language processing. This would suggest that, within the domain of language, the type and manner in which the information is transmitted affects the network of regions involved in its processing. This would present a challenge for current models of language processing based on unimodal stimulus presentations that do not reflect the conditions under which language is most commonly learned and used. Given the findings from previous studies of auditory sentence processing, we predicted activation in the superior temporal cortex of both hemispheres for AV sentence processing.

2. Methods

2.1. Participants

The seven adult participants (five females, two males) in this experiment were healthy, right-handed, monolingual English speakers. Participants ranged from 23 to 34 years of age (mean = 29.3 years) with a mean education level of 3.4 years of college (range = high school graduate to 7 years of college (4 years of college plus 3 years of professional studies)). All participants provided informed consent (according to NIH guidelines) and were paid an honorarium; they were free to withdraw their participation at any time without prejudice.

2.2. Stimuli, experimental design and task

To permit a direct comparison between the findings from the present study and those reported elsewhere, the methods used here are nearly identical to those used in our previous studies of written [2] and signed [46,47] sentence processing.

All stimuli were videotaped and projected onto a video screen positioned at the foot end of the scanner and viewed with a mirror located above the participants' eyes. In the AV sentence condition, participants viewed videotape consisting of the face and upper body of a female speaker (visual angle approximately 6.8° wide, 5° high) while listening to the sentences presented binaurally, through custom-built, MR-compatible headphones, at a comfortable auditory level that was still discernable above scanner noise. The AV sentence condition consisted of four alternating blocks of simple declarative sentences (e.g., "He put the worm on the hook.") and sentences composed of pronounceable non-words (e.g., "Clase vontrell sne plef melrond."), presented at the rate of natural speech. In addition, a written English sentence condition was included to extend the findings reported in a previous parallel study of sentence reading [2] that used consonant strings as a control. The written sentence condition also consisted of four alternating blocks of simple declarative sentences; presented one word at a time. Each word (or pronounceable non-word) was shown for 400 ms with a 200-ms inter-word interval; a 1-s ISI separated the sentences.

Each participant attended two experimental sessions. Data from only one cerebral hemisphere were collected in a given session (see below). For each session, stimuli were presented over four runs: two of AV English and two of written English. Runs of AV English and written English were alternated. The order of hemisphere, stimulus set and runs (i.e., beginning with AV presentation or

Table 1
Level of activation for audio-visual English for regions of interest

Region (Brodmann's area)	LH	RH
<i>Frontal</i>		
Broca's area (44/45)	0.032*	ns
Dorsolateral prefrontal cortex (9/46)	0.031*	ns
Precentral sulcus		
Inferior (6/44)	ns	ns
Posterior (6)	ns	ns
Superior (6)	0.022*	ns
Central sulcus (3/4)	ns	ns
<i>Temporal</i>		
Lateral sulcus		
Anterior (22)	0.010*	0.011*
Middle (22/41)	0.002**	0.012*
Superior temporal sulcus		
Anterior (22)	ns	ns
Middle (22/41/42)	0.032*	ns
Posterior (22/42)	ns	ns
<i>Parietal</i>		
Angular gyrus (39)	0.035*	ns
Supramarginal ^a gyrus (40)	0.007*	ns

P-values for each hemisphere, combined percent pixels and percent change blood oxygenation; ** $p < 0.005$, * $p < 0.05$, ns = nonsignificant ($p \geq 0.05$).

^a Supramarginal gyrus = SMG proper and the posterior superior lateral sulcus.

written presentation and beginning with English or non-word sentences) was randomized across participants. Each run consisted of four 64-s cycles of language (AV or written English sentences) and baseline (AV or written sentences composed of pronounceable non-words). None of the stimuli were repeated within or across sessions. Participants were given two short practice runs—one run of AV English and one run of written English—to become familiar with the stimulus materials, scanner noise and experimental task.

Following each run, participants were asked a series of yes/no, word/pronounceable non-word recognition questions in order to ensure their attention to the stimuli.

2.3. fMRI scans

A 4-Tesla whole body MR unit, fitted with a z-axis removable head gradient coil [68] was used to acquire gradient-echo echo planar images. A 20-cm diameter transmit/radio-frequency surface coil was positioned on one side of the participants' head, permitting adequate signal of one cerebral hemisphere. Each experimental run yielded 64 functional images per slice and lasted 256 s.

Eight sagittal slices were collected, beginning at the lateral surface and extending 40 mm in depth (TR=4000 ms, TE=28 ms, resolution $2.5 \times 2.5 \times 5$ mm). At the end of each run, high-resolution gradient-echo GRASS scans were obtained. These structural images corresponded to the EPI slices (TR=200 ms, TE=10 ms, flip angle=15°) and permitted identification of activated brain regions.

2.4. fMRI analysis

The fMRI parameters and data analyses were the same as those reported in Newman et al. [47]. Individual sets were first checked for motion artifacts using the SPM96 software package (Wellcome Department of Cognitive Neurology, London, UK). Since no motion correction algorithm could be applied to the data, a strict inclusion threshold was used. Runs with motion less than 0.3 mm were retained for further analysis; this resulted in the retention of 20 sets of the AV condition (9 English first, 11 non-words first) and 17 sets for the written condition (8 English first, 9 written non-words first). The MR structural images were delineated based on sulcal anatomy into regions according to Rademacher et al.'s [56] division of

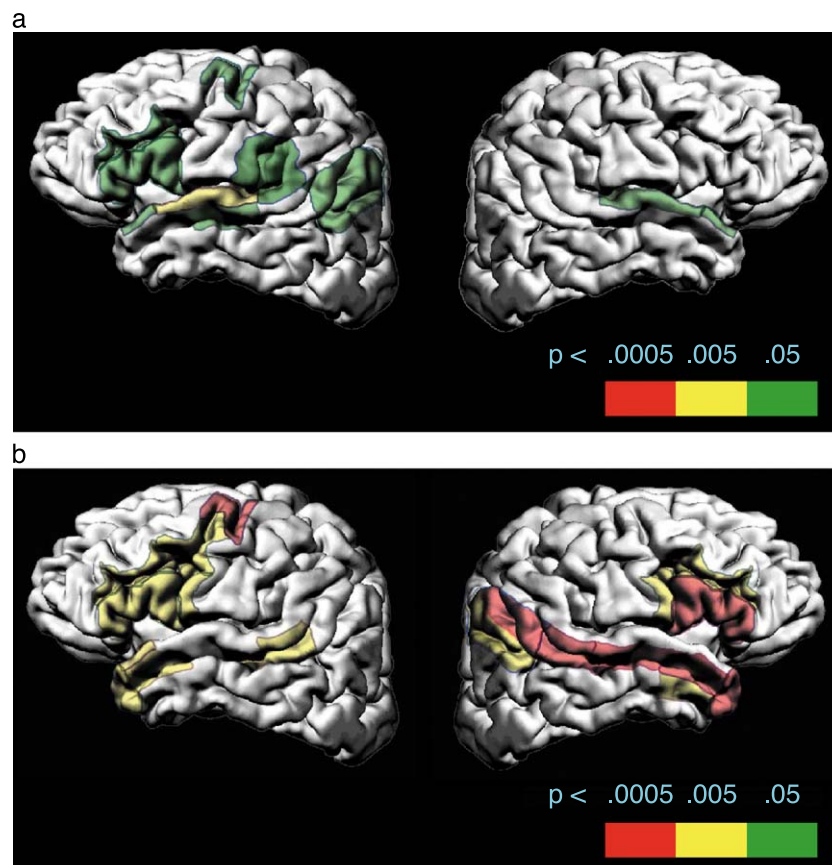


Fig. 2. (a) Cortical areas displaying activation for audio-visual English sentences. (b) Summary of cortical areas displaying activation for American Sign Language. Note. The data in (b) are from “Cerebral organization for language in deaf and hearing subjects: Biological constraints and effects of experience,” by H.J. Neville et al., 1998, Proceedings of the National Academy of Science, 95, p. 925. Reprinted with permission granted from the National Academy of Sciences.

the cortical lateral surface. This method preserves the highly variable morphological pattern found between individual subjects and even between hemispheres [35,75]. The ROIs included in the analysis were defined a priori based on regions activated in our previous studies of sentence processing [2,46,47] (see Fig. 1).

Since the experimental design consisted of alternating blocks of English and pronounceable non-word sentences, a cross-correlation analysis was first performed on the data to identify active voxels. Voxels that exceeded the correlation threshold ($r \geq 0.5$, effective degrees of freedom = 35, $p = 0.001$ for each voxel [30]) were retained for further analysis. Secondly, between-subjects analyses were performed for each brain region with runs entered as the independent variable and the log transformations of (i) the spatial extent of activation and (ii) the percent change of blood oxygenation entered as the dependent variables. The spatial extent of activation was expressed as a ratio of the number of active voxels to the total number of voxels for each region. The percent change of blood oxygenation was computed for active voxels. The multivariate analysis relied on Hotelling's T^2 statistic, a variant of the Student's t and was performed using BMDP statistical software. Activation within each region was assessed against the null hypothesis that the level of activation of each ROI was zero ($p < 0.05$). A comparison for hemisphere was performed by entering this variable as a factor.

3. Results

3.1. Behavioral test

A 2×2 ANOVA with modality (AV English vs. written English) and sentence type (well-formed vs. pronounceable non-word) revealed that participants recognized words in well-formed English sentences (86.6% for AV English and 80.9% for written English) better than words in sentences composed of pronounceable non-words (54.5% for AV English and 72.8% for written English) ($F(1,13) = 64.578$, $p < 0.0001$). Performance did not vary across modality ($F(1,13) = 2.143$, $p = 0.167$). A significant modality by sentence type interaction ($F(1,13) = 11.696$, $p = 0.005$) was due to an especially large effect of sentence type for AV English. Performance on the recognition task was poor for AV pronounceable non-word sentences.

3.2. Imaging

When processing AV English sentences, widespread significant activations were evident in the LH. These included Broca's area ($F(2,7) = 5.90$, $p = 0.032$), DLPC ($F(2,7) = 5.95$, $p = 0.031$), superior precentral sulcus ($F(2,7) = 6.89$, $p = 0.022$), anterior and middle portions of the lateral sulcus ($F(2,7) = 9.56$, $p = 0.010$, $F(2,7) = 17.56$, $p = 0.002$, respectively), middle STS ($F(2,7) = 5.89$,

$p = 0.032$), SMG ($F(2,7) = 11.13$, $p = 0.007$) and the AG ($F(2,7) = 5.61$, $p = 0.035$). AV English sentences also recruited the RH anterior and middle portions of the lateral sulcus ($F(2,9) = 7.68$, $p = 0.011$ and $F(2,9) = 7.44$, $p = 0.012$, respectively) (Table 1 and Fig. 2a).

MANOVAs for each region comparing activation across hemispheres for AV English sentences showed a significant LH greater than RH asymmetry for five regions (Table 2): inferior precentral sulcus ($F(2,17) = 3.73$, $p = 0.046$), superior precentral sulcus ($F(2,17) = 5.90$, $p = 0.011$), posterior precentral sulcus ($F(2,17) = 5.27$, $p = 0.017$), middle STS ($F(2,17) = 4.00$, $p = 0.038$), and the AG ($F(2,17) = 5.44$, $p = 0.015$). Importantly, no brain regions displayed significantly more activation in the RH than the left for AV English sentences. Moreover, in the ROIs that displayed activation in both the left and right hemispheres for AV English (part of the superior temporal cortex), the magnitude and spatial extent of activation were consistently stronger in the LH.

Processing written English sentences elicited only marginally significant activation in the LH, including DLPC ($F(2,6) = 4.92$, $p = 0.054$) and the middle portion of the

Table 2
Hemispheric asymmetry of activations for audio-visual English

Region (Brodmann's area)	Laterality index	p -value (LH>RH)
<i>Frontal</i>		
Broca's area (44/45)		
Dorsolateral prefrontal cortex (9/46)		
Precentral sulcus		
Inferior (6/44)	200	0.046*
Posterior (6)	200	0.017*
Superior (6)	200	0.011*
Central sulcus (3/4)		
<i>Temporal</i>		
Lateral sulcus		
Anterior (22)		
Middle (22/41)		
Superior temporal sulcus		
Anterior (22)		
Middle (22/41/42)	83.9	0.038*
Posterior (22/42)		
<i>Parietal</i>		
Angular gyrus (39)	140.9	0.015*
Supramarginal ^a gyrus (40)		

Laterality index was calculated for each region that displayed a hemisphere effect. Positive values reflect greater LH activity, negative values reflect greater activity in the RH. Probability values are from MANOVAs comparing English sentences with sentences composed of pronounceable non-words in the left and right hemispheres within each ROI ($*p < 0.05$). Laterality index = T^2 LH region - T^2 RH region, divided by the mean T^2 of the LH and RH regions, multiplied by 100 (i.e., $(T^2 \text{ LH region} - T^2 \text{ RH region}) / ((T^2 \text{ LH region} + T^2 \text{ RH region}) / 2) \times 100$).

^a Supramarginal gyrus = SMG proper and the posterior superior lateral sulcus.

lateral sulcus ($F(2,6)=4.73$, $p=0.058$). No brain regions were significantly active within the RH (all p -values <0.10), supporting the large body of research showing more LH than RH activation for written language processing.

4. Discussion

Audio-visual English sentence processing elicited activation in both the left and right superior temporal cortices, consistent with the finding that this region is involved in processing complex auditory stimuli such as speech (see Binder [3] for a review). However, consistent with previous studies of sentence reading, AV sentence processing activated the LH more strongly than the right. In this section, we will discuss these findings in greater detail, in terms of their implications both for models of language processing in general and within the context of previous neuroimaging studies of ASL sentence processing.

As expected, participants were better at recognizing words from English sentences than items from sentences composed of pronounceable non-words. These data support a large literature suggesting that encoding information for meaning leads to better recognition than encoding non-meaningful stimuli [17]. They also confirm that participants were paying attention to and processing the AV and written English sentences in this study.

Audio-visual sentences elicited activation within a network of regions in both hemispheres. In the LH, activation was found in Broca's area, DLPC, the superior precentral sulcus, the anterior and middle portions of the lateral sulcus, the middle STS, SMG, and the AG. Additionally, RH activation occurred in the anterior and middle portions of the lateral sulcus.

The pattern of activation for AV sentence processing is consistent with the findings of a recent fMRI study examining the neural organization of AV sentences. Using fMRI, MacSweeney et al. [39] found that AV sentence processing elicited extensive activation including the inferior frontal cortex (including Broca's area) and the superior temporal cortex. In contrast to the present study, MacSweeney et al. [39] found bilateral activation within this fronto-temporal network. Their employment of a non-linguistic baseline (detecting infrequent tones while viewing a still speaker) may have revealed a number of additional processes for the experimental condition, including those related to socially relevant biological motion, which has recently been shown to rely on the inferior frontal and superior temporal cortices of both hemispheres [61]. Consistent with this hypothesis, Campbell et al. [10] found that silent speech reading and non-linguistic facial gurning (compared to viewing a still face) elicited activation in the right STS/STG, whereas only facial movements related to speech reading elicited bilateral activation in the STS/STG as well as in the inferior frontal cortex (BA 44/45). In the present study, AV sentences,

compared to a baseline of sentences composed of pronounceable non-words, may isolate only those aspects of communication that are specific to language.

For the written English condition, no regions attained statistical significance. Relaxing the significance threshold revealed moderately significant activation in the left DLPC and middle lateral sulcus (p -values $0.05 > 0.10$). No brain regions were active within the RH (all p -values <0.10). This pattern of activation reported in the present study is in agreement with the findings from previous neuroimaging studies of written sentence processing [2,11,13–15,22–24,34,45,57,65,66]. For example, Bavelier et al. [2] reported that covertly reading sentences (compared to viewing consonant strings) produced increased activation in the left DLPC and in the middle lateral sulcus. In addition, sentence reading was associated with activation in the left inferior frontal cortex including Broca's area and the inferior and superior portions of the precentral sulcus, the superior temporal cortex including STS and Wernicke's area, the SMG and the AG and the right middle STS. However, the activation in the present study was less statistically robust than levels reported in previous studies using the same fMRI parameters and statistical analysis [2,46,47]. This may be due to the greater similarity between the control and experimental conditions in the present study. Specifically, the difference between written English sentences and consonant strings [2,46,47] is greater than the difference between written English sentences and sentences composed of pronounceable non-words, as pronounceable non-word sentences contain more phonological and syntactic information than consonant strings. Since the present study contains fewer differences between the conditions compared, we would expect less brain activation [53]. Moreover, previous studies of word and non-word reading have found that both rely on common brain regions [36,42,43,55]. In fact, some studies of reading report greater activation for pseudowords than for real words [43,55], suggesting that pseudoword reading may elicit a full lexical search (but see Binder et al. [4]).

Adopting a lexical search strategy for processing non-words may not extend to the AV comparison possibly because of procedural differences across modalities. While, within each modality, the effects of sensory information were controlled for, the two modalities differed in the amount and rate of language-relevant information presented. The AV sentences were presented at the rate of natural speech, whereas studies of sentence reading typically present stimuli one word at a time. Since parsing an unfamiliar language is difficult [18,19], participants may not have segmented the AV control; nor might they have had sufficient time to perform a full lexico-semantic search. The failure to segment the AV non-word speech stream is supported by their behavioural performance indicating that participants were particularly poor at recognizing pronounceable non-word AV sentences; in fact, they were no better than chance.

Another non-exclusive possibility is that the different amount of activation for the AV and written modalities, might be due to the presence of features that are not characteristic of written language. These include prosody, facial expression cues, and cues to lexical identity from lip movements conveyed through a primary form of language. All of these characteristics may have contributed to the different levels of activation between the two modalities.

Most importantly, the between-hemisphere comparison confirmed that, like written language, AV English sentence processing relies on the LH to a greater extent than the right. In agreement with previous studies using spoken sentences [12,27,29,40,62], this finding supports the hypothesis that the LH is biased to process written, spoken and AV language processing. This LH greater than RH asymmetry, that is independent of presentation modality for an aural/oral language does not, however, appear to hold in the case of a language learned solely through the visual modality.

4.1. Aural–oral vs. visual–manual (sign) language

Functional neuroimaging investigations of sign language report that native signers processing sentences in ASL also show activation within the LH, including the classic LH language areas. However, processing ASL sentences (compared to strings of meaningless gestures formally similar to ASL) also recruits the RH STS and AG in both deaf and hearing native signers [46]. Deaf native signers additionally display RH activation in the homologue of Broca's area, the inferior precentral sulcus, DLPC, anterior middle temporal sulcus and temporal pole. In contrast to the findings for AV English presented here, for ASL, the overall pattern of activation is bilateral with the activated RH regions attaining equal or greater significance values than their LH counterparts. ASL, like AV language, contains features that are not characteristic of written English—early acquisition, facial expression and prosody. While both conditions that include this information (AV English and ASL) activate RH superior temporal regions, there are considerable differences in the overall pattern of RH activity between aural–oral and visual–manual languages. ASL (but not AV English) activates inferior frontal and inferior parietal regions. Further, distinct patterns of asymmetry are evident for English (LH greater, regardless of modality) and ASL (bilateral). Hence, the data from the present study do not support the hypothesis that prosody, facial expression and early acquisition of language are the only factors underlying the RH activation observed for ASL sentence processing. These shared features may be the cause of the shared superior temporal activations found for both languages. However, the greater and more extensive RH activation elicited by ASL may be associated with processing requirements of some unique feature of that language, such as visuo-spatial lexical or syntactic information. Studies are currently underway to investigate this possibility.

In this study, we utilized the fMRI technique to investigate AV sentence processing using experimental and control conditions that parallel our previous study of ASL sentence processing. Our results support the hypothesis that the LH may be biased to process language independently of the modality through which it is perceived.

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