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# Dissociating linguistic and nonlinguistic gestural communication in the brain

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**Gestures of the face, arms, and hands are components of signed languages used by Deaf people. Signaling codes, such as the racecourse betting code known as Tic Tac, are also made up of such gestures. Tic Tac lacks the phonological structure of British Sign Language (BSL) but is similar in terms of its visual and articulatory components. Using fMRI, we compared the neural correlates of viewing a gestural language (BSL) and a manual-brachial code (Tic Tac) relative to a low-level baseline task. We compared three groups: Deaf native signers, hearing native signers, and hearing nonsigners. None of the participants had any knowledge of Tic Tac. All three groups activated an extensive frontal-posterior network in response to both types of stimuli. Superior temporal cortex, including the planum temporale, was activated bilaterally in response to both types of gesture in all groups, irrespective of hearing status. The engagement of these traditionally auditory processing regions was greater in Deaf than hearing participants. These data suggest that the planum temporale may be responsive to visual movement in both deaf and hearing people, yet when hearing is absent early in development, the visual processing role of this region is enhanced. Greater activation for BSL than Tic Tac was observed in signers, but not in nonsigners, in the left posterior superior temporal sulcus and gyrus, extending into the supramarginal gyrus. This suggests that the left posterior perisylvian cortex is of fundamental importance to language processing, regardless of the modality in which it is conveyed.**

*Keywords:* Tic Tac; BSL; fMRI

## Introduction

Studies of sign language aphasics provide strong evidence that sign language processing localizes in essentially the same way within the brain of the Deaf[1] native signer as does spoken language in hearing people. Lesions to the classically located language regions, including left inferior frontal and left posterior superior temporal regions, have a profound and specific effect on sign language processing (Corina, 1998a,b; Hickok et al., 1996; Marshall et al., in press; Poizner et al., 1987). However, this classical position requires some modification, at the very least to account for input modality differences between the two languages which must make distinctive demands on cortical regions dedicated to seeing and hearing. For example, MacSweeney et al. (2002a) showed that while audiovisual speech perception (in hearing speakers) and sign language perception (in Deaf signers) activated common classically located language regions, audiovisual speech showed enhanced recruitment of auditory cortices in the superior temporal lobes, while sign language activated occipitotemporal regions involved in visual motion processing to a greater extent than audiovisual speech.

Some neuroimaging studies of sign language processing suggest that it may be necessary to rethink this 'classical language' viewpoint even beyond these input considerations. MacSweeney et al. (2002b) and Emmorey et al. (2002) have suggested that particular aspects of sign language processing that exploit the use of space specifically recruit regions in the parietal lobe. These are not regions that are reliably associated with spoken language processing. Furthermore, studies by Neville et al. (Bavelier et al., 1998; Neville et al., 1998; Newman et al., 2002) have been interpreted to suggest a greater right hemisphere contribution to sign language processing than is typically observed for written language.

The main aim of the study reported here was to explore further the neural systems underlying sign language processing by posing the question as follows: what is the cortical circuitry recruited for the perception of a signed language when compared with a nonlinguistic visual input similar in terms of its perceptual and

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[1] In line with convention 'Deaf' is used here to refer to users of BSL who are members of the Deaf community, whereas 'deaf' refers to the audiological condition of deafness.

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articulatory characteristics? Such a display can be exemplified in the manual-brachial signaling code used by racecourse bookmakers: Tic Tac.

Tic Tac, like signed languages, uses ordered rhythmic sequences to indicate specific information: In this case, betting odds. However, unlike signed languages, Tic Tac does not have an internal contrastive structure based on featural parameters. In a sign language, differences in the features of a single parameter (handshape, hand orientation, place of articulation, or movement) result in a different meaning for the sign as a whole (duality of patterning), as is true of spoken language (Hockett, 1959; Sutton-Spence and Woll, 1999). These similarities in the underlying organization of signs and words have led sign language researchers to use the term 'phonology' for this level of structural description. Fig. 1 shows examples of minimally contrastive sign pairs in British Sign Language (BSL). In Fig. 1a, MY and LIKE differ only in a single handshape feature: MY uses a clenched-fist handshape, while in LIKE, a closed flat handshape is used; in Fig. 1b, the sign pairs differ only in location; in NAME, the articulating hand is located at the forehead, while in AFTERNOON, it is located at the chin.

A Tic Tac sequence makes use of hand configurations and patterns of hand movement in relation to the body. Since these are also components of signed languages, Tic Tac actions could be considered to have some phonetic structure. However, Tic Tac is not viewed as a possible foreign sign language to signers of BSL, since the hand gestures used do not contribute to a phonological system; they are not used contrastively. Nevertheless, Tic Tac sequences have many of the gestural and rhythmic dynamic qualities of natural signed languages. In principle, therefore, the comparison of Tic Tac and BSL has the power to distinguish cortical regions associated with language processing from those associated with its nonlinguistic (or prelinguistic) characteristics. Scott et al. have investigated the cortical correlates of spoken language processing by using a similar approach in which they have constructed auditory material that contains some of its auditory and articulatory properties but which lacks linguistic structure (e.g., Scott and Wise, 2003; Scott et al., 2000). In these studies, natural speech was contrasted with a variety of manipulations of the input source which degraded the intelligibility and phonetic quality of the spoken message while retaining perceived 'speech-likeness' in signal terms. Bilateral activation characterized the processing of both natural and distorted auditory speech input. Classical localization for spoken language, implicating left perisylvian regions, was evident only in close contrasts between real speech and formationally (spectrally, temporally) similar speech-like inputs that lacked speech structure (e.g., Narain et al., 2003).

Fig. 1. (Top row) MY and LIKE—handshape BSL minimal pair: same location, orientation, and movement. (Bottom row) AFTERNOON and NAME—location BSL minimal pair: same handshape, orientation, and movement.

The study reported here reports a close contrast between a natural signed language (BSL) and a similar gestural display (Tic Tac) not known by any of the participants. If the classical theory is correct, then BSL should generate greater activation in left perisylvian regions in native signers than Tic Tac. If the alternative, 'nonclassical,' position is correct, BSL, when compared to Tic Tac, may activate regions beyond those of the classical language areas. In contrast, in hearing people with no sign language knowledge, we predict no differential activation in traditional language regions for BSL compared with Tic Tac.

The second aim of this experiment was to address the extent to which auditory cortex is activated by visual input. Recent studies have demonstrated that grey, but not white, matter volume within regions of cortex that normally support auditory processing is similar in Deaf and hearing people (Emmorey et al., 2003a; Penhune et al., 2003). These regions include Heschl's gyrus, the site of primary auditory cortex (see Penhune et al., 1996), the superior temporal gyrus, and the planum temporale (PT), which lies posterior to Heschl's gyrus on the superior temporal plane (see Shapleske et al., 1999). In hearing people, these regions are involved in processing complex sounds. Several recent reports suggest that they may be also responsive to input from other modalities in people born deaf. Pettito et al. (2000) reported that the perception of discrete signs from two signed languages (ASL and LSQ), as well as invented phonologically well-structured 'nonsense' signs, activated superior temporal cortex bilaterally, including the PT, in Deaf native signers but not in hearing nonsigners. The authors concluded that superior temporal regions are specialized for the analysis of phonologically structured material, whatever its input modality. However, this 'phonological specificity' hypothesis of PT function is not supported by data from Finney et al. (2001) who showed that patterns of simple dot movement can activate auditory processing regions, including Heschl's gyrus and PT, in deaf people.

One way to reconcile these findings is to propose that, in people born deaf, superior temporal cortex, including PT and Heschl's gyrus, may be involved in processing dynamically patterned visual stimuli but may be recruited to a greater extent when these have phonological structure. PT should then be involved to a greater extent in processing BSL than Tic Tac, since Tic Tac itself is not phonologically structured.

Another route by which to address the phonological specificity of PT is to test hearing native signers, that is, hearing people who, having learned sign language as their first language from Deaf parents, are sensitive to its linguistic structure. A strong version of Petitto et al.'s hypothesis would predict equivalent PT activation in deaf and hearing native signers during sign language perception. Contrary to this prediction, in a previous study, we found significantly greater superior temporal activation in Deaf than hearing signers (MacSweeney et al., 2002a). Bavelier et al. (2001) also reported significantly greater activation in posterior superior temporal sulcus (STS) in Deaf than hearing native signers in response to nonlinguistic motion stimuli. These findings suggest that sign language exposure may not be the sole factor that determines activation in superior temporal regions including the PT.

Despite this significant difference in activation between Deaf and hearing signers, we found significant activation in superior temporal regions in hearing native signers when BSL perception was compared with a low-level baseline (MacSweeney et al., 2002a). Some other reports also suggest activation of these regions by visual inputs in hearing people. The stimuli have included silent visual speech (e.g., Calvert et al., 1997; MacSweeney et al., 2000, 2001) and the perception of biological motion (Howard et al., 1996). These findings raise the interesting possibility that the PT may be critical not only for the analysis and segregation of complex auditory signals, considered to be its traditional role (Binder et al., 1996; Griffiths and Warren, 2002; Howard et al., 2000; Scott and Johnsrude, 2003), but may also play a role in the processing of patterned dynamic nonauditory signals. Moreover, this sensitivity may be modulated by hearing status, although not determined by it.

To summarize, the aims of the current study are first, to gain a clearer picture of the regions specific to sign language processing, and second, to explore the role of 'auditory' cortex in response to visual inputs in both Deaf and hearing people. With regard to our first aim, if the classical theory is correct, BSL perception by native signers should lead to greater activation than Tic Tac perception in the classical left hemisphere language regions in posterior superior temporal and inferior prefrontal regions. If sign language processing makes use of additional regions, the BSL V Tic Tac contrast may reveal activation of regions within the right hemisphere and possibly additional parietal activation. Hearing nonsigners are not predicted to show differential activation between these visual inputs in 'traditional' language processing regions.

With regard to our second aim, we predict a replication of our previous finding showing activation in superior temporal cortex, including PT, during BSL perception in both Deaf and hearing signers, which will be greater in Deaf than hearing participants (MacSweeney et al., 2002a). If this activation is not language-specific the same pattern is predicted to occur during Tic Tac perception. Activation in these regions might then also be evident in hearing nonsigners, suggesting that this region may play a role in processing certain temporally patterned visual displays, including gesture, irrespective of language and/or hearing status.

## Methods

### *Participants*

Eighteen right-handed signing participants were tested. All were native signers, having acquired BSL from their Deaf parents. Nine were congenitally profoundly deaf from birth (five males, four females). Their mean age was 30.5 years (range 18–48 years). All Deaf participants performed at or above an age appropriate level on a test of nonverbal IQ (Block Design, WAIS-R). Nine hearing native signers were also tested (three males; six females). Their mean age was 32.8 years (range 20–51 years), and all had good English-language skills as tested on the Group Reading Test (NFER-Nelson, 2002). Six of the hearing native signers were employed as a BSL interpreter or communicator.

There was no significant difference between the Deaf and hearing signing groups on a test of British Sign Language [$t$ = 1.12 (14), $P > 0.1$]. This test was based on a BSL perception test designed for children (Herman et al., 1999), amended for use with an adult population (items were refilmed omitting lipreading cues and used adult BSL register). Eight hearing nonsigners were also tested (four males; four females). Their mean age was 26.3 years (range 18–40 years).

All participants were right-handed and without known neurological or behavioral abnormality. The groups were closely matched on educational achievement. Four Deaf native signers, four hearing native signers, and three hearing nonsigners had completed tertiary education. All participants gave written informed consent to participate in the study which was approved by the relevant Research Ethics Committee. No participants had any knowledge of Tic Tac.

## Stimuli

Participants were shown a continuous silent video of a Deaf native signer who performed both the BSL and the Tic Tac stimuli and who also appeared at rest in the baseline condition.

All BSL sentences were short declarative sentences of approximately 3-s duration. Each sentence comprised four to six distinct signs. English mouth movements were omitted to avoid lipreading by nonsigners. However, other facial articulations, including facial expressions required for BSL, were included (see Sutton-Spence and Woll (1999) for the range of such nonmanual components of BSL). The BSL model brought her hands to resting position on her lap between each sentence. An example of a BSL sentence is shown in Fig. 2 as a key-frame sequence.

The BSL model learned individual Tic Tac gestures, based on brachiomanual signals for individual betting odds (e.g., 10-to-1). The signer then combined these gestures to create 'Tic Tac sentences' of the same length as the BSL sentences, with a return to a rest state between each. To anyone knowing Tic Tac, these 'sentences' would appear as strings of three or four signaled odds. To maximize the perceived articulatory similarity between BSL and Tic Tac, the model added facial gestures (see Fig. 2).

The recorded Tic Tac gestures were analyzed from the standpoint of phonological structure considered internally and also in comparison to BSL. Each of the individual gestures was located within signing space, a region extending from the top of the head to the hips, and the width of the extended elbows, and all used hand configurations which were possible handshapes of BSL, either one- or two-handed. Tic Tac has an intrinsically small lexicon, since it serves only to express betting odds. Only 16 different Tic Tac tokens appeared in the stimulus material, in contrast to 85 BSL tokens.

The videotaped stimuli were projected onto a screen located at the base of the scanner table via a Proxima 8300 LCD projector. The stimuli were then projected to a mirror angled above the subject's head in the scanner.

### *Experimental design*

The experiment used a block design consisting of 21-s epochs. Participants performed five blocks of each of the two experimental conditions (BSL and Tic Tac perception) and 10 blocks of a baseline

Fig. 2. Examples of stimuli. (Top row) Still images from a Tic Tac sentence. (Bottom row) Still images from a BSL sentence—English translation: 'This building is being renovated.'

task. Experimental blocks alternated with the baseline task (e.g., baseline/BSL/baseline/Tic Tac, etc.). The total run lasted 7 min. The presentation of initial experimental condition was counterbalanced across participants such that half of the participants performed the BSL task first and half the Tic Tac task.

### *Experimental condition 1—BSL sentences*

Participants watched five BSL sentences in each block. They were told that one of the five sentences did not make sense (e.g., 'The mug fell off the dream'), and their task was to identify the semantically anomalous sentence using the button box held in their right hand. The relatively sparse occurrence of the meaningless target ensured that, in signers, activation reflected normal linguistic analysis rather than anomaly detection. Hearing nonsigners were told that although they did not know any BSL, they were to try to guess which sentence did not make sense.

### *Experimental condition 2—'Tic Tac sentences'*

As with the BSL stimuli, five 'Tic Tac sentences' were presented in each block. All participants were told—"You will see 'Tic Tac sentences.' Tic Tac is the code used by bookmakers at the races to communicate about the odds on horses. I know you don't know any Tic Tac, but I want you to guess which sentence does not make sense." The requirement to guess the incorrect string was included to equate attentional and decision-making processes across experimental conditions. Since all 'Tic Tac sentences' were unknown to all participants and were equally 'anomalous,' there was no right or wrong response.

### *Baseline condition*

In the baseline condition, the signer was seen at rest. During this period, the participant monitored the display for the occurrence of a visual cue superimposed on the chin of the signer. A small square appeared five times throughout the block for about 1000 ms, that is, at the same rate as gesture sequences were made in the experimental conditions. On four exposures, the square was black, and on one appearance, it was grey. Participants pressed the button box in response to the appearance of the grey square. This control condition, therefore, served to maintain vigilance to the visual display and controlled for the attentional and motor-response parameters of the experimental task, as well as for the perception of a face and body at rest.

All participants practiced these tasks outside the scanner. In both the experimental and baseline blocks, the target sentence or target square was presented randomly in the third, fourth, or fifth position of each series to maintain vigilance throughout the block.

### *Imaging parameters*

Gradient echoplanar MRI data were acquired with a General Electric (Milwaukee, WI, USA) 1.5-T neurooptimized MR system using a standard quadrature head coil. Head movement was minimized by positioning the participant's head between cushioned supports. One hundred and forty T2*-weighted images depicting BOLD contrast were acquired at each of 14 near-axial 7-mm thick planes parallel to the intercommissural (AC-PC) line (0.7-mm interslice gap; TR = 3 s, TE = 40 ms). An inversion recovery EPI dataset was also acquired to facilitate registration of individual fMRI datasets to Talairach space (Talairach and Tournoux, 1988). This comprised 43 near-axial 3-mm slices (0.3-mm gap) which were acquired parallel to the AC-PC line (TE = 80 ms, TI = 180 ms, TR = 16 s).

## Data analysis

Following motion correction, a least-squares fit was carried out between the observed time series at each voxel, and a mixture of two one-parameter gamma variate functions (peak responses 4 and

8 s) convolved with the experimental design (Friston et al., 1998). A statistic describing the standardized power of response was derived by calculating the ratio between the sum of squares due to the model fit and the residual sum of squares (SSQ ratio). Significant values of this statistic were identified by comparison with its null distribution computed by repeating the fitting procedure 10 times at each voxel after wavelet-based permutation of the time series (Bullmore et al., 2001). This procedure preserves the noise structure of the time series during the permutation process and gives good control of type I error rates. The voxelwise SSQ ratios were calculated for each subject from the observed data and following time-series permutation were transformed into standard space of Talairach and Tournoux (1988) as described previously (Brammer et al., 1997). Median activation maps (voxelwise probability of false activation of <0.00004) were computed separately for each group after smoothing the statistic maps with a Gaussian filter (FWHM 7.2 mm).

### *Group analysis*

Further analysis was carried out to identify 3D clusters of voxels showing significant responses to the paradigm (reported in Tables 1–3). This was achieved by first thresholding the median voxel-level SSQ ratio maps at a voxelwise false-positive probability of 0.05. These “activated” voxels were then assembled into 3D-connected clusters and the sum of the SSQ ratios (statistical cluster mass) determined for each cluster. The same procedure was repeated for the median SSQ ratio maps obtained from the wavelet-permuted data to compute the null distribution of statistical cluster masses under the null hypothesis. This distribution could then be used to determine the critical threshold for the cluster mass statistic under the null hypothesis at any required type I error level and applied to the observed cluster mass data to determine significantly activated clusters (for details, see Bullmore et al., 1999).

Table 1
Brain regions activated by Tic Tac and BSL relative to the baseline condition

| Cerebral region | BA | Side | Number of voxels | Coordinates (mm) | | | Side | Number of voxels | Coordinates (mm) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | *X* | *Y* | *Z* | | | *X* | *Y* | *Z* |
| | | | | Tic Tac V baseline | | | | | BSL V baseline | | |
| *Deaf native signers* | | | | | | | | | | | |
| Middle temporal gyrus/ | 21 | L | 401 | −46 | −52 | 2 | L | 361 | −47 | −49 | 4 |
| superior temporal sulcus | | R | 264 | 49 | −41 | 2 | R | 185 | 49 | −41 | 1 |
| Inferior frontal gyrus | 44/45/8 | R | 294 | 42 | 26 | 14 | R | 320 | 41 | 22 | 15 |
| | | L | 125 | −46 | 18 | 19 | L | 182 | −42 | 12 | 29 |
| | 47 | | | | | | L | 20 | −44 | 36 | −1 |
| Anterior cingulate | 32 | L | 15 | −1 | 26 | 35 | R | 68 | 9 | 30 | 29 |
| Putamen | | R | 9 | 16 | 8 | 7 | R | 15 | 16 | 7 | 7 |
| Cerebellum | | | | | | | R | 8 | 41 | −61 | −24 |
| Fusiform gyrus | 18 | R | 6 | 25 | −86 | 4 | | | | | |
| Anterior superior temporal gyrus | 38 | L | 8 | −37 | 20 | −22 | | | | | |
| Inferior/superior parietal lobule | 40/7 | L | 11 | −27 | −51 | 38 | | | | | |
| *Hearing native signers* | | | | | | | | | | | |
| Middle/inferior temporal gyrus | 37 | L | 199 | −45 | −59 | 4 | L | 263 | −47 | −56 | 4 |
| | | R | 216 | 42 | −57 | −5 | R | 185 | 46 | −52 | −2 |
| Fusiform gyrus | 37 | | | | | | R | 6 | 42 | −41 | −18 |
| Inferior frontal gyrus | 9/45 | L | 167 | −42 | 15 | 26 | L | 266 | −42 | 16 | 18 |
| | 45 | R | 122 | 47 | 18 | 22 | R | 199 | 46 | 18 | 16 |
| | 47 | L | 30 | −42 | 24 | −6 | | | | | |
| | | R | 49 | 41 | 23 | −15 | | | | | |
| Middle frontal gyrus | 11 | R | 6 | 38 | 52 | −11 | | | | | |
| Superior/inferior parietal lobule | 7/40 | L | 76 | −30 | −58 | 39 | L | 18 | −37 | −47 | 40 |
| | | | | | | | L | 11 | −22 | −70 | 36 |
| Superior/middle occipital gyrus | 19 | R | 23 | 24 | −75 | 21 | R | 14 | 22 | −78 | 22 |
| *Hearing nonsigners* | | | | | | | | | | | |
| Middle temporal gyrus | 21 | R | 293 | 46 | −50 | −1 | R | 279 | 45 | −52 | −1 |
| | 37 | L | 227 | −45 | −58 | 5 | L | 234 | −39 | −64 | 4 |
| Inferior frontal gyrus | 45/46 | R | 355 | 42 | 31 | 10 | R | 257 | 44 | 22 | 16 |
| | 45 | L | 321 | −43 | 19 | 19 | L | 99 | −43 | 7 | 36 |
| Medial frontal gyrus | 8 | R | 160 | 4 | 38 | 32 | R | 87 | 5 | 33 | 35 |
| Middle frontal gyrus | 10 | L | 13 | −31 | 54 | −10 | R | 71 | 33 | 54 | 0 |
| Superior/inferior parietal lobe | 40/7 | L | 20 | −27 | −51 | 40 | L | 12 | −26 | −48 | 41 |
| | | R | 7 | 32 | −48 | 38 | R | 14 | 35 | −49 | 37 |
| | 7 | R | 7 | 19 | −76 | 31 | | | | | |
| Calcarine sulcus | 17 | L | 27 | −13 | −90 | 3 | | | | | |

Coordinates represent foci of 3D clusters ($P < 0.00125$).

### ANCOVA

Analysis of covariance was used to take account of individual behavioral differences in accuracy of detection of anomalous sentences in BSL in relation to the patterns of activation (see Results below).

Differences in responses ($R$) were inferred at each voxel using the linear model

$$R = a0 + a1H + a2X + e,$$

where $H$ codes a particular condition or group, $X$ is a covariate (when included), and $e$ is the residual error. Maps of the standardized coefficient (size of condition or group difference), ($a1$), were tested for significance against the null distribution of $a1$ (no effect of group membership or condition) generated by repeatedly refitting the above model at each voxel following randomization of group or condition membership ($H$). In some of our analyses, the model was constrained to examine only positive BOLD responses, where the stimulus is followed by an increase in signal intensity peaking between 4 and 8 s. In this case, significant deactivations were excluded from the analyses.

## Results

### Behavioural data

The mean percentage of anomalous BSL sentences correctly identified in the scanner by Deaf signers was 80%; 60% were correctly identified by hearing signers. Performance by both signing groups was well above chance (20%) on this task, although the performance of hearing signers was relatively poor. This is in keeping with our previous findings (MacSweeney et al., 2002a) and is accounted for in the analyses, which covaried for accuracy where appropriate. Hearing nonsigners correctly identified the 35% of the anomalous BSL sentences; this was significantly above chance ($P < 0.01$). The anomalous sentence was always positioned in the third, fourth, or fifth position to maintain attention of the signing participants. Although unaware of this constraint, given the BSL naivety of the nonsigners, it is likely that they refrained from guessing the anomalous sentence until near the end of the block. This may have artificially inflated their hit rate. Since the Tic Tac 'sentences' were invented, there was no right or wrong response.

### MR data

### Tic Tac and BSL perception

To gain a fuller understanding of the complete neural systems underlying gestural processing, the regions activated while watching Tic Tac in contrast to baseline (Fig. 3, top) and BSL in contrast to baseline (Fig. 3, bottom) were explored in each group (see Table 1 for coordinates). All groups activated an extensive frontal-posterior temporal network across both hemispheres for both Tic Tac and BSL. This included the planum temporale for all groups. This was established using the PT probability map from Westbury et al. (1999).

*Deaf signers.* Activation in bilateral posterior cortical regions was extensive in the deaf group for both conditions. It extended from the cerebellum into the posterior inferior temporal gyri, middle temporal gyri, superior temporal sulci (STS), and gyri bilaterally (e.g., Tic Tac: $x = 47, y = -33, z = 9$; $x = -50, y = -52, z = 9$; BSL: $x = 47, y = -37, z = 9$; $x = -53, y = -52, z = 9$). In both conditions, this activation was in the upper bank of the STS in the right hemisphere and slightly more anterior to that observed in the left hemisphere which was situated in the lower bank of the STS.

In addition to recruitment of STS, both conditions also activated more superior regions of the temporal lobe including the planum temporale, posterior to Heschl's gyrus, bilaterally (BSL: $x = -50, y = -46, z = 20$; $x = 61, y = -33, z = 15$; Tic Tac: $x = -57, y = -37, z = 20$; $x = 50, y = -37, z = 20$). This activation incorporated portions of BA42 in the left hemisphere in the Tic Tac condition ($x = -53, y = -30, z = 15$) and in the right hemisphere in response to BSL ($x = 47, y = -33, z = 15$).

For both BSL and Tic Tac, the upper limit of this activation in the right hemisphere was at the planum temporale, but in the left hemisphere, activation extended into the angular gyrus and supramarginal gyrus in the inferior parietal lobule (BA 39 and BA 40).

There was also extensive activation bilaterally in the frontal cortex in both conditions. This extended from the inferior frontal gyrus superiorly through the precentral gyrus and continued slightly more superiorly in the left than the right hemisphere in both conditions. The putamen and the anterior cingulate were also activated significantly in both conditions.

*Hearing native signers.* The pattern observed in the hearing signers was very similar to that in the Deaf group. They showed extensive bilateral activation in both frontal and posterior temporal cortices in both hemispheres for both conditions. There was robust activation in inferior and middle temporal gyri bilaterally, and this extended into the STS and STG in the left hemisphere (e.g., Tic Tac: $x = -47$, $y = -50$, $z = 15$; BSL: $x = -43$, $y = -50$, $z = 9$ and $x = -50$, $y = -46$, $z = 15$). Activation was also observed for both conditions in the left planum temporale (Tic Tac: $x = -50$, $y = -46$, $z = 20$; BSL: $x = -50$, $y = -50$, $z = 20$) and in left lateral tip of Heschl's gyrus (BA42) in the Tic Tac condition ($x = -50$, $y = -7$, $z = 4$). As in the Deaf group, this temporal activation extended into the supramarginal gyrus in the left but not the right hemisphere.

*Hearing nonsigners.* The networks activated in hearing nonsigners were similar to those seen in signing participants. For Tic Tac and BSL, there was extensive bilateral posterior inferior and middle temporal activation which extended through the superior temporal gyrus. Again, this extended into the supramarginal gyrus in the left hemisphere. STS activation was observed in response to Tic Tac ($x = 47, y = -39, z = 9$) and BSL ($x = 47, y = -39, z = 9$ and $x = 43, y = -52, z = 9$). Activation was also observed in the planum temporale bilaterally in both conditions (Tic Tac: $x = -53, y = -50, z = 20$; $x = 61, y = -33, z = 20$; BSL: $x = \pm 53, y = -33, z = 20$). This included activation of BA 42 during observation of both Tic Tac ($x = 57, y = -33, z = 15$) and BSL ($x = 53, y = -33, z = 15$). The extensive frontal activation was left hemisphere-dominant in the Tic Tac condition and more bilateral in the BSL condition.

In summary, there is a very high degree of similarity between the systems supporting BSL and Tic Tac perception regardless of BSL knowledge or hearing status (see Fig. 3). In all groups, activation included the superior temporal sulcus and, more surprisingly, the planum temporale which is usually thought of as an auditory processing region. Of primary interest, however, are those

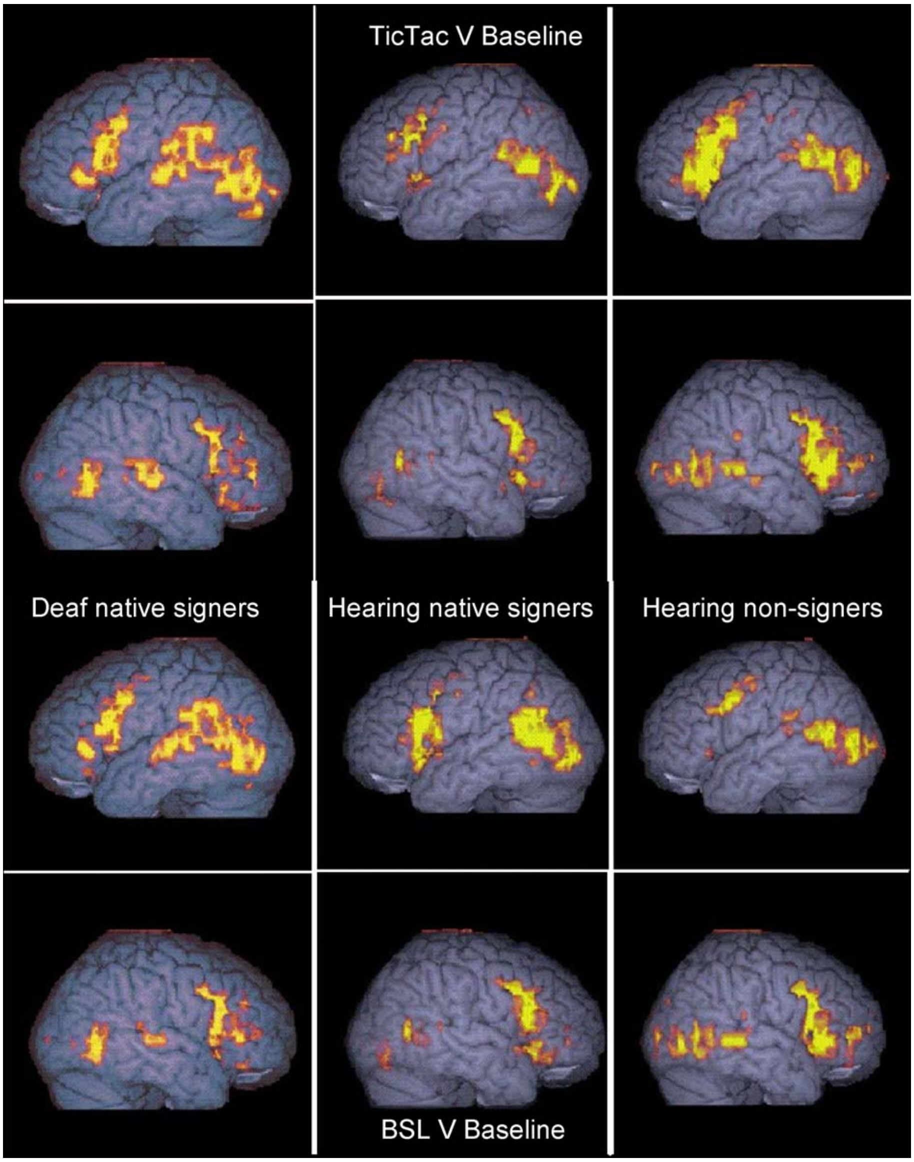

Fig. 3. (Top) Activation by Tic Tac perception in comparison to baseline task in each group. (Bottom) Activation by BSL perception in comparison to baseline task in each group. Activation up to 5 mm from the surface of the cortex is displayed.

regions that are specific to language comprehension. This was explored by comparing BSL and Tic Tac activation directly.

*Comparison of BSL and Tic Tac perception*

Table 2 shows the brain regions activated more by BSL than Tic Tac and vice versa, in relation to baseline for each group. These differential activations are also shown in Fig. 4 for Deaf and hearing signers. The main finding was greater activation in posterior superior temporal regions in the left hemisphere in both signing groups in response to BSL.

*Signing groups.* In both signing groups, activation was more extensive for BSL than Tic Tac. These differential activations were predominantly left-lateralized. In the Deaf group, the main region of difference was focused in the posterior temporal lobe extending into the supramarginal gyrus in the inferior parietal lobule. Activation extended from the fusiform gyrus in the posterior inferior temporal lobe through the middle temporal gyrus, superior temporal sulcus, and superior temporal gyrus into the supramarginal gyrus. The hearing signers showed a very similar pattern. However, this differential activation did not extend superiorly into the supramarginal gyrus as in the Deaf group (see Table 2).

The Deaf group also showed greater activation for BSL than Tic Tac in the frontal lobe. In the left hemisphere, this extended from the precentral gyrus anteriorly to the border with the inferior frontal gyrus. In the right hemisphere, a small cluster of activated voxels was situated in the inferior frontal gyrus.

Both groups showed similar and limited regions of enhanced activation for Tic Tac in comparison to BSL. This was focused in the right hemisphere in posterior inferior temporal/occipital regions.

*Hearing nonsigners.* Hearing nonsigners showed a very different pattern. Regions activated significantly more by BSL than Tic Tac were focused in the middle occipital and posterior middle temporal

Table 2
Brain regions activated more by BSL sentences than Tic Tac and vice versa

| Cerebral region | BA | Side | Number of voxels | Coordinates (mm) | | | Side | Number of voxels | Coordinates (mm) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | *X* | *Y* | *Z* | | | *X* | *Y* | *Z* |
| | | | | BSL > Tic Tac | | | | | Tic Tac > BSL | | |
| *Deaf native signers* | | | | | | | | | | | |
| Precentral gyrus/inferior frontal gyrus | 6/44 | L | 15 | −31 | 0 | 31 | | | | | |
| | | L | 12 | −35 | 0 | 26 | | | | | |
| | 44 | R | 6 | 38 | 7 | 20 | | | | | |
| Fusiform gyrus | 19/37 | L | 6 | −38 | −67 | −2 | R | 7 | 38 | −56 | −2 |
| | | | | | | | R | 13 | 38 | −64 | −7 |
| Middle temporal gyrus/superior temporal sulcus | 21 | L | 8 | −46 | −53 | 9 | | | | | |
| | | L | 6 | −52 | −53 | 4 | | | | | |
| | | L | 6 | −55 | −40 | −2 | | | | | |
| Superior temporal gyrus | 22 | L | 7 | −46 | −47 | 20 | | | | | |
| Supramarginal gyrus | 40 | L | 9 | −48 | −50 | 26 | | | | | |
| *Hearing native signers* | | | | | | | | | | | |
| Inferior temporal gyrus | 37 | L | 15 | −42 | −70 | 4 | | | | | |
| Superior temporal sulcus | 21 | L | 12 | −46 | −53 | 15 | | | | | |
| | 22 | L | 8 | −48 | −56 | 20 | | | | | |
| Lingual gyrus | 18 | | | | | | R | 12 | 24 | −83 | −7 |
| *Hearing nonsigners* | | | | | | | | | | | |
| Middle temporal gyrus | 37 | L | 9 | −38 | −70 | 9 | | | | | |
| | | R | 8 | 46 | −60 | 9 | | | | | |
| Middle occipital gyrus | 19 | L | 17 | −38 | −77 | 4 | | | | | |
| Middle occipital sulcus | 18/19 | L | 6 | −35 | −73 | −2 | | | | | |
| Inferior frontal gyrus/insula | 47 | | | | | | L | 8 | −46 | 17 | −7 |
| | | | | | | | L | 7 | −42 | 17 | −2 |
| Inferior frontal gyrus | 44 | | | | | | R | 12 | 48 | 13 | 9 |
| | | | | | | | R | 7 | 48 | 17 | 15 |
| | | | | | | | L | 6 | −46 | 7 | 26 |
| Precentral gyrus | 4 | | | | | | L | 23 | −35 | −7 | 31 |
| Middle frontal gyrus | 6 | | | | | | L | 9 | −35 | −4 | 37 |
| Anterior cingulate | 32 | | | | | | R | 9 | 7 | 43 | 9 |
| | | | | | | | R | 9 | 7 | 43 | 4 |
| | | | | | | | L | 7 | −4 | 37 | 20 |

Coordinates represent foci of 2D clusters ( $P < 0.00125$).

regions (BAs 37/19/18) and predominantly in the left hemisphere. In contrast to the signing groups, hearing nonsigners showed substantially more activation in relation to Tic Tac than BSL. This was situated in the frontal lobes and involved the inferior frontal gyri bilaterally (BA 44/47), the precentral gyrus/middle frontal gyrus (BA 4/6) in the left hemisphere, and the anterior cingulate.

In summary, these contrasts suggest that when sign language is understood, specific processing demands are made on the left posterior perisylvian cortex.

### *Group comparison of deaf and hearing native signers*

Our previous study (MacSweeney et al., 2002a) reported significantly greater activation in superior temporal regions in Deaf than hearing signers during BSL perception. To explore whether the same effect could be observed with new BSL stimuli and also whether it extended to nonlinguistic manual movements, we compared activation in hearing and Deaf native signers directly. Only voxels with a positive response to the experimental condition in both groups were included in this analysis. Therefore, any significant differences found are due to differences in activation rather than deactivation. Due to performance differences between the two groups, accuracy was used as a covariate in the current analyses (see Methods). However, this did not materially alter the findings.

Table 3 shows the regions differentially activated as a function of hearing status. Hearing signers generated greater activation than Deaf signers in posterior inferior temporal regions at the junction with the occipital lobe, irrespective of gesture-type. During BSL perception specifically, they activated left inferior frontal cortex and the inferior/superior parietal lobule to a greater extent than deaf subjects.

The results also supported our previous finding indicating greater recruitment of superior temporal regions in the Deaf than hearing signers during BSL perception (see MacSweeney et al., 2002a). This enhanced activation was bilateral and extended from the middle temporal gyrus through the superior temporal sulcus and gyrus into parts of the planum temporale. In the left hemisphere, the differential activation also extended into inferior parts of the supramarginal gyrus.

Extending our previous findings, Deaf signers also showed greater bilateral superior temporal activation for Tic Tac than hearing signers. In the left hemisphere, this extended from the inferior temporal gyrus, through middle and superior temporal gyri and into

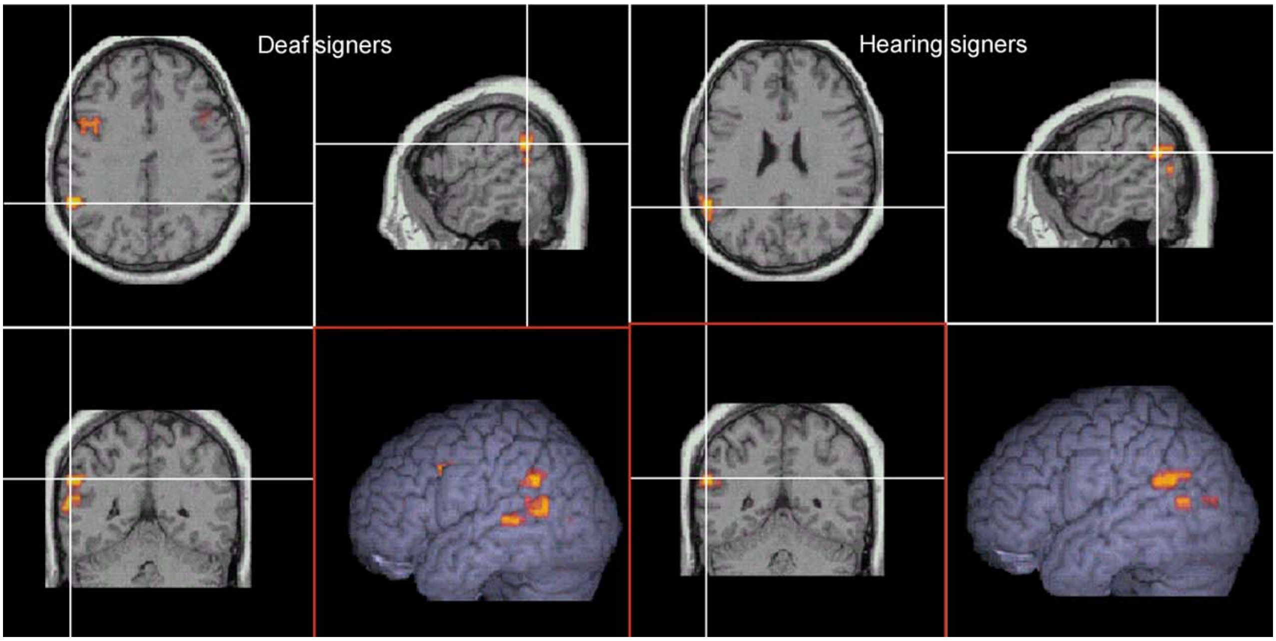

Fig. 4. Regions significantly activated more by BSL than Tic Tac in Deaf and hearing signers. Activation up to 5 mm from the surface of the cortex is displayed. Crosshairs are positioned at: $X = -58$, $Y = -48$, $Z = 31$ for Deaf signers and $X = -58$, $Y = -50$, $Z = 25$ for hearing signers.

the inferior portion of the supramarginal gyrus. The planum temporale was again differentially activated bilaterally. In the right hemisphere, this differential activation included the middle temporal gyrus and the superior temporal sulcus/gyrus, but did not extend into the supramarginal gyrus. Fig. 5 shows the location of the enhanced activation in auditory analogue regions in Deaf compared with hearing signers for both BSL and Tic Tac conditions.

## Discussion

In this study, participants were required to judge linguistic acceptability for short signed sentences. They also attempted this task for sequences that used a visually similar gestural code, Tic Tac. Participants were instructed to look for meaning in both tasks, so it is likely that signing participants applied their BSL knowledge to the Tic Tac stimuli. Nevertheless, BSL-specific activation was evident in native signers. Both Deaf and hearing signers showed greater activation in the left posterior superior temporal cortex when processing BSL relative to Tic Tac. The Deaf group showed further BSL-specific activation in the left supramarginal gyrus and the inferior frontal cortex bilaterally. None of these regions were selectively engaged by BSL processing in nonsigners.

These data demonstrate the fundamental role of the left hemisphere in sign language processing. This is in line with our predictions and the classical language localization literature from lesion studies (Corina, 1998a,b; Hickok et al., 1996, 2002; Marshall et al., in press; Poizner et al., 1987) and previous functional neuroimaging studies of sign language comprehension (MacSweeney et al., 2002a) and production (e.g., Corina et al., 2003; Emmorey et al., 2003b; McGuire et al., 1997; Pettito et al., 2000). Although there was a small focus of BSL-specific activation in the right inferior frontal cortex, overall, there was little evidence to support previous reports of enhanced right hemisphere involvement in sign language processing (e.g., Neville et al., 1998). This may reflect methodological differences between studies. For example, Neville et al.'s signed stimuli may have involved more prosodic features and longer discourse than those used in the present study.

In both Deaf and hearing signers, specificity for BSL was focused in the left posterior perisylvian regions. This involved the posterior left superior temporal sulcus in both groups. In hearing users of spoken English, Wise et al. (2001) conclude that "…the

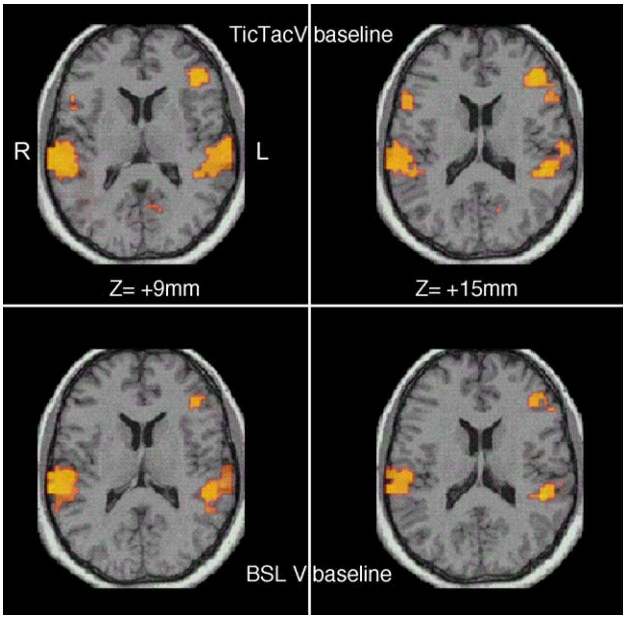

Fig. 5. Deaf native signers only. Slices at $Z = +9$ mm and $Z = +15$ mm illustrate the regions of bilateral superior temporal cortex activated to a greater extent in Deaf than hearing native signers during Tic Tac (top row) and BSL (bottom row) perception, in contrast to baseline (see also Table 3). Only activations were included in this analysis.

Table 3
Regions activated more by Deaf native signers than hearing native signers and vice versa for each condition relative to baseline

| Cerebral region | BA | Side | Number of voxels | Coordinates (mm) | | | Side | Number of voxels | Coordinates (mm) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | *X* | *Y* | *Z* | | | *X* | *Y* | *Z* |
| | | | | BSL V baseline | | | | | Tic Tac V baseline | | |
| *Deaf signers > hearing signers* | | | | | | | | | | | |
| Planum temporale | 22 | L | 96 | −54 | −35 | 14 | L | 83 | −52 | −38 | 20 |
| Superior temporal gyrus | 42/22 | R | 52 | 49 | −30 | 7 | R | 57 | 49 | −29 | 5 |
| Inferior temporal gyrus | 37 | | | | | | L | 89 | −42 | −62 | −9 |
| Inferior/middle frontal gyrus | 45/46 | R | 108 | 41 | 26 | 21 | R | 147 | 42 | 27 | 20 |
| | | | | | | | L | 33 | −49 | 18 | 18 |
| Middle frontal gyrus | 10 | | | | | | R | 6 | 37 | 43 | −18 |
| *Hearing signers > deaf signers* | | | | | | | | | | | |
| Inferior frontal gyrus | 44 | L | 139 | −41 | 7 | 22 | | | | | |
| Inferior temporal gyrus | 37 | L | 78 | −45 | −55 | 7 | L | 31 | −47 | −59 | 7 |
| | | R | 56 | 47 | −56 | −5 | R | 22 | 49 | −55 | 1 |
| Inferior/superior parietal lobule | 7 | L | 20 | −23 | −70 | 32 | | | | | |
| | 40 | L | 16 | −40 | −51 | 41 | | | | | |
| Calcarine sulcus | 17 | | | | | | R | 18 | 26 | −77 | 18 |

Only 'activations' are included, and accuracy is used as a covariate in the BSL analyses. Foci represent centers of 3D clusters of activation ($P < 0.005$).

specific role of the posterior left superior temporal sulcus (is) to transiently represent phonetic sequences. . ." (also see Narain et al., 2003; Scott et al., 2000). Our data suggest that this region may play a similar role in the interpretation of brachiomanual gestural codes. Both Tic Tac and BSL contain sign language phonetic features, and both showed activation in this region. However, only signers showed greater activation in this region for BSL than Tic Tac. This is likely to reflect their greater sensitivity to the larger phonetic repertoire of BSL than Tic Tac.

Another region that was preferentially engaged by BSL, although in Deaf signers only, was the left supramarginal gyrus (SMG). This region has been implicated as a key site for processing sign language phonology. In a cortical stimulation case study of a Deaf signer undergoing surgery (Corina et al., 1999), stimulation here generated sign production errors during repetition, which were mainly phonological in nature. A recent PET study by Emmorey et al. (2003b) supports this interpretation. Participants were asked to produce fingerspelled words, using the American one-handed alphabet or one-handed ASL signs. Activation in SMG was greater for the more phonologically complex production of signs than for fingerspelling. Moreover, we have previously shown that the left SMG is recruited to a greater extent during BSL perception when sentences included sign language classifiers than when they did not (MacSweeney et al., 2002b). There, we argued that enhanced recruitment of the left inferior parietal lobe was due to particularly detailed processing of the location, configuration, and movement of the hands in space (see also Emmorey et al., 2002). Although all signs are defined by these phonological parameters, the interpretation of sign language classifiers is especially sensitive to the detailed articulation and positioning of hands and digits in sign space.

Thus, within the left posterior perisylvian regions, speech and sign may recruit slightly different areas. While posterior parts of the superior temporal gyrus and sulcus are activated by both language inputs, activation of the inferior parietal lobule may be of special significance for sign language. In turn, this may reflect the different articulatory representations of speech, which uses the vocal tract and the face, and sign which uses the fingers, hands, arms, and face in particular spatial configurations.

Greater activation during BSL processing than Tic Tac was also observed in Deaf participants in inferior frontal cortex bilaterally. In the right hemisphere, the focus of this small region of differential activation was in the homologue of Broca area within the inferior frontal gyrus. In the left hemisphere, the differential activation was larger, and the focus was more anterior, in the posterosuperior part of Broca area. Activation within these regions of the inferior frontal cortex is consistent with previous studies of signed sentence comprehension (MacSweeney et al., 2002a; Neville et al., 1998), auditory speech perception (e.g., Papathanassiou et al., 2000; Wise et al., 1991), and silent speechreading (Calvert and Campbell, 2003; Paulesu et al., 2003). Thus, these data reinforce the role of this region in language perception, as well as language production tasks.

### *Hearing nonsigners: gesture-specific activation*

As predicted, there was no differential activation between BSL and Tic Tac in classical language regions in hearing nonsigners. There were, however, differences in the engagement of other regions for the two types of gesture. In nonsigners, BSL was associated with greater activation at the temporo-occipital junction, whereas Tic Tac was associated with more activation in several regions in the prefrontal and anterior cingulate cortex bilaterally. These regions were generally more anterior and inferior to the inferior frontal areas preferentially engaged during BSL processing by the Deaf group. The Tic Tac stimuli used larger gestures, were more symmetrical, contained fewer handshapes and locations, and used less complex digital movement sequences than the BSL stimuli. Thus, one post hoc interpretation of the enhanced prefrontal gyrus activation, in line with predictions regarding 'mirror neurons' (e.g., Buccino et al., 2001; Gallese et al., 1996; Iacoboni et al., 1999), is that this may reflect a greater potential to imitate Tic Tac than BSL sequences in sign-naive participants. The greater engagement of areas involved in visual movement processing for the BSL stimuli suggests that, in the absence of sign language representations, participants analyze these sequences as complex dynamic visuospatial displays.

### *Activation of auditory regions in deaf and hearing participants*

The second aim of the study was to explore the impact of BSL and Tic Tac perception on activation in Heschl's gyrus (HG; primary auditory cortex) and planum temporale (PT). While some activation of the PT has been demonstrated for silent speechreading (Calvert et al., 1997), activation here is not generally observed in studies analyzing visual movement (e.g., Grossman and Blake, 2002; Grossman et al., 2000). Rather, the primary role of the PT is thought to involve the integration of increasingly complex aspects of the auditory signal (see Griffiths and Warren, 2002). Challenging this position, Nishimura et al. (1999) and Pettito et al. (2000) found that sign language activated PT bilaterally in people born deaf. Pettito et al. (2000) extended this finding to phonologically acceptable nonsense signs. Since PT activation was not observed in hearing nonsigners, this led the authors to assert that sign language is unique among visual inputs and makes special claims on this region in signers by virtue of its linguistic status. However, our data suggest that the PT may show sensitivity to nonauditory temporally structured events which are not linguistically structured, even in hearing nonsigners.

Our previous study (MacSweeney et al., 2002a) found activation in PT and STG in both Deaf and hearing signers during BSL perception. In the current study, we replicated this pattern and extended it to a nonlinguistic visual input, Tic Tac, and to hearing nonsigners. All groups, regardless of hearing status or sign language knowledge, activated the PT and STG bilaterally during Tic Tac and BSL perception. Thus, PT, superior temporal gyrus and sulcus all appear to be involved in processing visual gesture sequences. We proposed that this region may nevertheless show linguistic specificity in signers by showing greater activation to BSL than Tic Tac. Only one of the clusters of perisylvian activation that was greater for BSL than Tic Tac in the Deaf group could be considered to fall within the PT, as defined by the probability map of Westbury et al. (1999). Moreover, it comprised only seven voxels, and the probability that this was within the PT was relatively low (5–25%). We were also able to test the phonological specificity hypothesis by comparing hearing signers and nonsigners. During BSL but not Tic Tac processing, hearing signers showed greater activation than nonsigners in left superior temporal cortex. Again, however, the focus of this cluster fell only within the 26–45% confidence region of the Westbury et al. (1999) PT probability map ($x = -43$, $y = -41$, $z = 15$; number of voxels = 11). This may suggest some level of sensitivity to phonological structure in this region. However, an alternative explanation is that it reflects translation of the BSL stimuli into English by hearing signers. This possibility is explored further below.

Thus, while our study suggests some level of sign language specificity within PT, it is not very marked. Any sign phonology specificity in this region is secondary to the much more extensive activation in response to visual gesture.

### *Deaf versus hearing signers*

As in our previous studies and in those of others (e.g., Neville et al., 1998), accuracy in detecting an anomalous sentence was poorer in hearing than Deaf signers. Despite being raised by Deaf signers and being engaged with Deaf culture, a number of factors may account for this difference in performance. First, although they used BSL in the home, the education of hearing signers was not BSL-based. Second, adult hearing signers are less likely to use BSL exclusively.

As predicted, we found greater activation in Deaf than hearing signers during BSL perception in regions traditionally considered to be responsible for auditory processing. Since accuracy was a covariate in the group analyses, we can be confident that this difference reflects hearing status rather than BSL proficiency. Moreover, Tic Tac also activated auditory cortex more in Deaf than hearing signers. These group differences support the notion that there is extensive functional plasticity within auditory processing regions in the absence of auditory input (see Bavelier and Neville, 2002 for review), which does not appear to be specific to linguistic input.

Whether primary auditory cortex, within Heschl's gyrus (HG), can be activated by nonauditory inputs in deaf people is less clear. Finney et al. (2001, 2003) reported activation in right HG in deaf people watching dot movement patterns. Although the Talairach coordinates in the present study suggest enhanced activation in Deaf than hearing signers in the region of HG ($X = 43$, $Y = -33$, $Z = 9–15$), this foci of activation do not fall within the Rademacher et al. (2001) probabilistic map of primary auditory cortex. We explored this issue further by locating HG in each Deaf participant, using their high-resolution structural image and determining whether this region showed significant activation. In most participants, the main focus was posterior to HG in PT. In one of the nine deaf individuals, a medial posterior portion of HG, the analogue of primary auditory cortex in hearing people, was activated. In the majority of the nine, however, activation included the tip of HG at its junction with superior temporal gyrus, an area equivalent to secondary auditory cortex in hearing people. The data in the current study were not collected with the primary objective of locating activation in this region. Obtaining structural and functional data specifically collected to optimize visualization of Heschl's gyrus will be a useful development in understanding the function of this area in deaf people.

Regardless of this, there is now substantial evidence for cross-modal plasticity in secondary and association auditory cortices in people born profoundly deaf. It seems plausible that the delineation of those cortical regions traditionally considered to be modality-specific and their association areas reflects the integrity of all sensory systems early in development.

Greater activation in hearing than Deaf native signers was identified for both BSL and Tic Tac in the inferior temporal gyri bilaterally. Where sign language and heard speech compete from an early age for superior temporal activation, heard language appears to dominate, and activation for signed language is then observed in more inferior regions of the temporal lobe. The present experiment required participants to 'look for meaning' in both BSL and Tic Tac. Therefore, this design does not allow further speculation concerning the source of this shift: It may reflect linguistic processing and/or simple visual movement processing differences as a function of hearing status.

When processing BSL, hearing signers also generated greater activation than the deaf group in left inferior frontal gyrus and left inferior parietal lobule extending into the superior parietal lobule. This activation was specific to the BSL contrast. Two thirds of the hearing signers who participated in this study were BSL interpreters or communicators. It is likely that professional aptitude may be associated with the enhancement and refinement of a number of cognitive skills such as short-term memory and rehearsal via 'inner sign' or 'inner speech.' Exactly how these skills may impact on the neural systems supporting sign language comprehension in a noninterpreting environment is not clear. One possibility is that the additional left inferior frontal and parietal activation in this group reflects the memory component (e.g., Coull et al., 1996) involved in the translation of the BSL stimuli. This may be a processing style readily engaged by BSL interpreters and communicators. This argument may be applicable to all hearing children of Deaf parents, who often act as informal 'interpreters.' Individual variability in sign language skill must be considered in future studies to clarify the impact of the bilingual/bimodal language experience and sign language proficiency on the neural systems supporting language processing. The behavioral and neuroimaging data to date suggest that it may be unwise to base accounts of sign language processing on hearing native signers alone or on comparisons between deaf and hearing native signers that do not take proficiency differences into account.

### *Implications for the role of the planum temporale*

Our data show activation in response to visual gesture within the PT, a region generally considered to be dedicated to acoustic processing. All groups showed activation in this region in response to BSL and Tic Tac. PT activation has been reported in hearing subjects during silent speech perception (see Calvert and Campbell, 2003; Campbell et al., 2001; MacSweeney et al., 2001). However, the stimuli in the present study used few English lip patterns; therefore, this is unlikely to account for PT activation in hearing nonsigners. The PT also appears to play a role in verbal self-monitoring (e.g., McGuire et al., 1996). Since participants were asked to guess which of the perceived BSL and Tic Tac sentences did not make sense, activation in the hearing nonsigners and perhaps hearing signers may reflect attempts to interpret the gestural input into English. Such an explanation may account for the lack of PT activation in the hearing nonsigners studied by Pettito et al. (2000), which required passive viewing of single signs.

However, it may be more parsimonious to consider the basic function of the PT to be similar across all groups, although modulated by sign language knowledge and hearing status. In macaque, area Tpt has been shown to respond not only to auditory inputs, but also to nonauditory stimuli (Baylis et al., 1987; Hasselmo et al., 1989). Since this is a potential homologue of area PT in human, it is possible that it is the dynamic movement quality of the stimuli to which this area is responding in all groups. Support for this possibility comes from reports of activation of neighboring regions by moving visual stimuli. An early fMRI study by Howard et al. (1996) reported activation in Heschl's gyrus in hearing people perceiving biological motion. While the posterior STS is usually considered to be the key region for motion processing (e.g., Allison et al., 2000; Grossman and Blake, 2002), the possibility that more superior temporal regions are sensitive to visual movement in both deaf (Finney et al., 2001, 2003) and hearing people may be worthy of further investigation.

In summary, the left posterior superior temporal gyrus and sulcus extending into the supramarginal gyrus appear to be the primary regions implicated in sign language comprehension. Regions normally considered to process complex auditory signals, specifically the planum temporale, were activated bilaterally by visual gesture analysis in all groups—irrespective of language knowledge and hearing status. Activation here was greater in Deaf than hearing participants, suggesting that its recruitment to visual analysis is most evident in the absence of auditory input. The extent to which this neuroplasticity is affected by age of onset of deafness applies to nonmoving visual inputs, or inputs from other modalities remains to be explored.

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