Cortical Representation of Sign Language: Comparison of Deaf Signers and Hearing Non-signers

Numerous studies have demonstrated activation of the classical left-hemisphere language areas when native signers process sign language. More recently, specific sign language-related processing has been suggested to occur in homologous areas of the right hemisphere as well. We now show that these cortical areas are also activated in hearing non-signers during passive viewing of signs that for them are linguistically meaningless. Neurlemagnetic activity was stronger in deaf signers than in hearing non-signers in the region of the right superior temporal sulcus and the left dorsal premotor cortex, probably reflecting familiarity and linguistic meaningfulness of the observed movement sequences. In contrast, the right superior parietal lobule, the mesial parieto-occipital region, and the mesial paracentral lobule were more strongly activated in hearing non-signers, apparently reflecting active visuo-motor encoding of complex unfamiliar movement sequences.

Introduction

Although sign languages are expressed through movements of hands, arms and face, they strongly activate the same classical language areas as do spoken languages, i.e. the Wernicke’s and Broca’s regions within the left hemisphere (Corina et al., 1992; Neville et al., 1992; Hickok et al., 1996; McGuire et al., 1997). In addition, sign aphasia typically follows injuries of the left but not of the right hemisphere (Damasio et al., 1986; Hickok et al., 1996, 1998a), suggesting similar left-hemispheric dominance for signed and spoken or written languages. Recent functional magnetic resonance imaging (fMRI) studies suggest that the posterior temporal and inferior frontal regions of the right hemisphere also have a specific role in the linguistic processing of sign language (Neville et al., 1998a,b; Paulesu et al., 1998). The discrepancy between these data and the results from previous lesion studies has elicited a vivid scientific discussion on the right hemisphere’s role in sign language comprehension and production (Corina et al., 1998; Hickok et al., 1998b; Paulesu and Mehler, 1998a,b).

In their fMRI study, Neville et al. compared cortical activation between native signers, deaf and hearing, who were viewing sign language sentences and hearing non-signers reading English sentences (Neville et al. 1998). Similar language-related areas in the left hemisphere responded to both signed and written language, but only sign language activated the homologous areas in the right hemisphere of deaf and hearing signers. Hickok and co-workers argued that the observed right-hemisphere activity might not be related to linguistic processing of signs but instead represent an artifact resulting from comparisons between sign language and written language because, for example, prosody, emotional facial expressions and meaningful non-linguistic gestures are present in signed but absent in written languages (Hickok et al., 1998b). Neville and collaborators also found stronger right-hemisphere activation for sign language than non-sign gestures in native signers whereas hearing non-signers showed no consistent differences in cortical activation between the stimuli (Neville et al., 1998). Based on these findings, Corina et al. claimed that facial information or non-linguistic gestures common to both types of stimuli were unlikely to explain the right-hemisphere activation by sign language in native signers (Corina et al., 1998). Here it is important to note that in the Neville study (Neville et al., 1998), only the non-signs were linguistically meaningless to native signers whereas both signs and non-signs were equally meaningless to non-signers. However, emotional facial expressions and prosody in the context of meaningful and meaningless signs are likely to be processed differently and could thus very well also involve different levels of right-hemisphere activity. For example, a recent lesion study (Adolphs et al., 2000) reported impaired recognition, naming and categorizing of facial emotional expressions following lesions of right inferior parietal, right superior temporal and bilateral inferior frontal regions.

In the present study we examined cortical activation patterns in congenitally deaf signers and in hearing non-signers while they were passively viewing sign language. Because the signs were linguistically meaningful to deaf signers but linguistically meaningless to hearing non-signers, and because signs are known to activate similar language-related areas in deaf and hearing native signers (Bavelier et al., 1998; Neville et al., 1998), we assumed the critical difference between the two groups to be in sign language experience and comprehension. Thus, comparison between the two groups can be considered to reflect differences in cortical activation between sign language observation vs observation of motor actions forming non-sign gestures. The activated areas were evaluated without subdivisions between different tasks or the two subject groups, allowing also examination of areas similarly activated by meaningful and meaningless signs.

Previous positron emission tomography (PET) (Grafton et al., 1996; Rizzolotti et al., 1996b) and magnetoencephalographic (MEG) (Hari et al., 1998; Nishitani and Hari, 2000) studies during observation of hand actions have shown significant activation in the human left inferior frontal lobe (IFL, including Broca’s region), left superior temporal sulcus (STS, including Wernicke’s region) and primary motor cortices. The monkey F5 area, the homologue of the human IFL cortex, contains ‘mirror’ neurons that discharge both when the monkey grasps or manipulates objects, and when he observes another monkey or the experimenter performing similar actions (Gallese et al., 1996; Rizzolotti et al., 1996a). These mirror neurons are assumed to form a system matching execution and observation of motor actions. Rizzolotti and Arbib (Rizzolotti and Arbib, 1998) suggested that the mirror neuron system provides the necessary communication bridge from ‘doing’ to ‘understanding’, also providing the evolutionary gestural basis for human language development.
Based on the previous imaging data on viewing of sign language and hand actions, we assumed that the bilateral superior temporal and inferior frontal regions would be activated by sign observation in both deaf signers and hearing non-signers. However, the strength of activity within these areas could differ between the two groups due to differences in the linguistic meaningfulness of the signs to the observer.

Materials and Methods

Subjects

We recorded MEG signals from seven congenitally, profoundly deaf (six subjects 20–42 years, one subject 74 years, four males, three females) and seven healthy, normally hearing control subjects (ages 23–34; all males). Analysis between four male hearing non-signers and four male deaf signers revealed similar results as the main comparisons, although the significance levels were lower due to the smaller number of subjects compared. There were no significant differences in the pattern of activation between the deaf male and female subjects; neither did the activations of the 74-year-old deaf subject and the younger deaf signers appear different. All subjects were right-handed. The deaf subjects were fluent users of Finnish Sign Language (FSL) which was their first and most prominent language, whereas the hearing control subjects had no previous experience with FSL. When asked specifically after the measurement, the hearing controls were unable to understand, or even guess, the meaning of the observed signs, all of which were non-iconic gestures without involvement of lip movements of the corresponding Finnish words.

Data Acquisition

During the experiment, the subjects passively viewed videotaped individual signs (2–2.5 s in duration) of FSL, presented once every 7 s. During the pause, the first frame of the following sign was displayed continuously to decrease contamination from V1/V2 visual cortex activation due to stimulus appearance. All subjects were instructed to watch carefully the movements of the person appearing on the video. Although most of the signs were bimanual, they involved more strongly the dominant than the non-dominant hand of the native right-handed signer who performed on the video. The stimuli were presented in the center of a screen located in front of the subject (visual angle 10°) and the subject was able to view simultaneously both the hands and the face of the signer without moving her eyes considerably. Magnetic signals were recorded with a helmet-shaped 122-channel Neuromag 122TM magnetometer (Ahonen et al., 1993), while the subject was sitting in a magnetically shielded room with lights turned off. Location of the head with respect to the sensors was determined by measuring the magnetic fields produced by small currents delivered to three coils attached to the scalp. Locations of the coils with respect to the preauricular points and the nasion were measured with a 3D digitizer. The recording passband was 0.03–90 Hz and the sampling rate 600 Hz. The vertical electro-oculogram was recorded simultaneously, and epochs contaminated by eye movements or blinks were rejected. The responses were averaged offline, time-locked to movement onsets in the stimuli. A minimum of 55 responses was averaged from 1.3 s before to 6.2 s after the movement onsets.

Source Modeling

Due to the duration and temporal variability of the videotaped signs, the averaged evoked responses included mainly low frequency components. To increase the signal-to-noise ratio, the averaged signals of each subject were digitally low-pass filtered at 10 Hz. Mean amplitude levels from 1 to 0.5 s before and from 5.7 to 6.2 s after the movement onsets of the stimuli were used to remove the constant level and linear trends. Thereafter the data were analyzed with a Minimum Current Estimate (MCE) program based on minimum L1-norm estimates (Matsuda and Okabe, 1995). MCE presents the current distribution where the total sum of the current is as small as possible, while it still explains most of the measured signals. The method is able to resolve several local or distributed MEG current sources without explicit a priori information about the number of active areas (Uutela et al., 1999), and the results are in good agreement with those obtained by multipole modeling (Nishitani et al., 1999; Uutela et al., 1999). To identify the activated cortical sites, the current distributions were superimposed on individual magnetic resonance images (MRIs).

Statistical Analysis

Activities, studied in regions of interest (ROIs), were calculated as weighted averages; the weighting function was a generalized normal distribution with the peak at the center of the ROI. The full-width half-maximum of the ROI was 35 mm. The mean locations of ROIs for signers and non-signers were within 10 mm from each other, and the ROIs used for group comparisons were centered on these mean locations. The current directions within the ROIs were chosen to explain most of the current directions of both groups. The total activity, averaged across subjects, was compared between signers and non-signers 0–1 s, 1–2 s, 2–3 s and 3–4 s after the movement onsets in the stimuli using the Mann–Whitney test. Significant differences between the groups in the response onset and peak latencies were not detected, possibly due to the considerable jitter (~200 ms) in the movement onsets in the signs.

Results

Passive sign observation elicited sustained magnetic responses over several brain areas in both deaf signers and hearing non-signers (Fig. 1). The mean total activity (averaged across all channels) lasted for ~6 s in both groups of subjects but was ~25% stronger (P < 0.01) in hearing non-signers than in deaf signers.

Evaluation of the individual activation patterns with the MCE revealed large interindividual differences in the number, strength and timing of activated areas in both subject groups. Cortical areas activated consistently across all subjects or across either subject group were selected as ROIs for further analysis. Figure 2 illustrates examples of bilaterally activated cortical sites in those individual deaf signers and hearing non-signers who showed clearest activation within these ROIs. Table 1 summarizes, in Talairach coordinates, the mean source locations of the main areas activated for hearing non-signers. MRIs were available from one deaf signer only, but since the mean locations of ROIs for deaf signers and hearing non-signers were within 10 mm from each other, we assumed them to reflect activity within the same cortical regions in both subject groups. The activation of the IFL agrees with the location of the Brodmann’s area (BA) 44 (McGuire et al., 1997; Iacoboni et al., 1999), and the posterior STS activation with the location of BA 22 (Grafton et al., 1996; Fiez and Petersen, 1998). The temporoparietal occipital activation agrees with the location of the visual motion-specific V5 complex (Decety et al., 1994; Rees et al., 1997), and activation of the superior parietal lobule (SPL) with BA 5 (Iacoboni et al., 1999). Activation close to the primary hand/arm motor area (MI) agrees with the location of BA 4 (Grafton et al., 1993; Kawashima et al., 1994), and the more anterior left dorsal premotor cortex (PMd) activation with BA 6 (Parsons et al., 1995). Activation in the region of the parieto-occipital sulcus (POS) corresponds to the location of the V6 complex (Portin and Hari, 1999), and activation of the mesial cortex of the paracentral lobule (PCL), just anterior to the central sulcus, to mesial BA 4/6.

The classical left-hemisphere language areas within IFL and STS, and the homologous right-hemisphere regions, were activated in all deaf signers in accordance with earlier fMRI results (Neville et al., 1998). Most interestingly, however, signs recruited the same left- and right-hemisphere areas in six out of seven hearing non-signers as well. In one hearing non-signer, the IFL was activated only in the left hemisphere and the STS only in the right hemisphere. Bilateral activation was also observed in the V5 complex in six out of seven deaf signers and in five out of seven hearing non-signers; other subjects showed unilateral
activation. The SPL region was activated bilaterally in five out of seven deaf signers and in all hearing non-signers; in two signers activation was unilateral. In addition, five out of seven deaf signers and six out of seven hearing non-signers showed bilateral M1 activation; other subjects showed unilateral activity.

Figure 3 shows differences in the mean activation patterns between the two groups during sign observation. The left PMd, activated in all deaf signers and in five out of seven hearing non-signers, and the right posterior STS region were activated significantly stronger in deaf signers than hearing non-signers ($P < 0.05$, time interval 0–1 s for PMd and 1–2 s for STS). In contrast, activation of the right SPL region was stronger ($P < 0.05$, 0–1 s) in hearing non-signers than deaf signers. Hearing non-signers also showed stronger activation of the POS region, activated in two out of seven deaf signers and all hearing non-signers ($P < 0.01$, 0–1 s). The PCL was activated in one out of seven deaf signers and six out of seven hearing non-signers ($P < 0.005$, 2–3 s).

Due to large interindividual variability, no statistically significant differences were found between the two groups in the timing of the different activations.

Discussion

Our results show that passive observation of sign language automatically activates certain cortical areas, independently of the meaning of the gestures to the observer. Most interestingly, these automatically activated areas include the classical left-hemisphere language areas of the IFL and STS regions, and the homologous regions of the right hemisphere. Other areas automatically activated by the observed signs were the bilateral V5, SPL, and primary hand/arm motor regions, related to visuospatial and visuomotor encoding of moving stimuli. The cortical activation patterns of our deaf signers and hearing non-signers also differed, probably reflecting the most critical difference between the two groups: the experience and comprehension of sign language.

Automatic activation of the classical left-hemisphere language areas of the IFL and STS regions by the observed signs is in line with previous findings showing a contribution of these areas both to sign language processing (Corina et al., 1992; Neville et al., 1992; Hickok et al., 1996; McGuire et al., 1997; Neville et al., 1998) and to action observation in humans (Grafton et al., 1996; Rizzolatti et al., 1996b; Nishitani and Hari, 2000). It thus seems, as suggested earlier by Rizzolatti and Arbib (Rizzolatti and Arbib, 1998), that language processing and action recognition are indeed closely related. It is of course possible that our hearing
non-signers were trying to guess the meaning of the observed signs and thus covertly activated their language system even if they were not told that the movements consisted of real meaningful signs. However, activation of the left-hemisphere IFL and STS regions has been shown to occur during observation of simple, non-linguistic motor actions as well (Grafton et al., 1996; Rizzolatti et al., 1996b; Nishitani and Hari, 2000). On the other hand, meaningful gestures activate the left IFL and STS regions more than meaningless gestures in both native signers (Neville et al., 1998) and hearing non-signers (Decety et al., 1997), suggesting that linguistic meaningfulness of the observed motor actions is one of the key factors for this left-hemisphere activation. Surprisingly, there were no significant differences in the left-hemisphere IFL and STS activations between our deaf signers and hearing non-signers although the linguistic meaningfulness of the signs certainly differed for the two groups. Unfortunately, we are not able to differentiate whether activations in our hearing non-signers were associated with possible guessing at the meaning of the motor actions or with ‘pure’ action viewing.

Corresponding right-hemisphere IFL and STS activations have previously been reported when native deaf and hearing signers process sign language (Bavelier et al., 1998; Neville et al., 1998). Our results showing clear activation of these right-hemisphere areas also in hearing non-signers suggest a contribution of

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**Figure 2.** Cortical sites activated bilaterally in both deaf signers and hearing non-signers during sign observation. The color codes are related to the mean current strengths across 200 ms time windows. Data are shown for individual subjects, three deaf signers (D1–D3) and three hearing non-signers (H1–H3), with most prominent activation in different ROIs. IFL = inferior frontal lobe; STS = superior temporal sulcus; V5 = visual motion-specific area; SPL = superior parietal lobule; M1 = primary motor cortex.
these areas to action observation as well. On the other hand, the activity within the right posterior STS region was significantly stronger in our deaf signers than in hearing non-signers, in accordance with the previous fMRI findings (Neville et al., 1998) showing greater recruitment of this region during comprehension of meaningful signs than nonsense gestures in both hearing and deaf signers. These results suggest that the recruitment of the posterior STS region in deaf and hearing signers during sign observation occurs beyond the processing demands of action observation. This conclusion is in line with a previous PET study on non-signing subjects who were observing hand actions (Decety et al., 1997). Meaningful actions, consisting of pantomimes, strongly engaged the left IFL and left temporal regions while meaningless actions, signs derived from the American Sign Language, activated predominantly the right occipitoparietal pathway. Thus at least partly distinct systems in the right hemisphere are related to linguistic processing of signs and to visuospatial processing of biologically relevant motion. However, the exact nature of the right-hemisphere STS activation in deaf and hearing signers is still unclear. For example, it is possible that emotional facial expressions and prosody were processed differently by our two groups since the context was meaningful to the deaf signers and meaningless to hearing non-signers; such differences might result in different degrees of right-hemisphere STS activation. This suggestion is in line with a recent lesion study (Adolphs et al., 2000) showing impaired naming of facial emotional expressions following right-hemisphere superior temporal lesions.

Unlike present results, other studies on action viewing have demonstrated a left-hemisphere dominance in the activation of the IFL and STS regions in humans (Grafton et al., 1996; Rizzolatti et al., 1996b; Nishitani and Hari, 2000). The signs used in the present study were mostly bimanual and more complex than reaching, grasping and manipulating an object with one

**Figure 3.** Differences in mean cortical activation between deaf signers and hearing non-signers during sign observation. The current estimates are mean amplitudes across 1 s time windows from the movement onsets to 4 s after. Left: cortical sites showing significantly stronger activation in deaf signers than in hearing non-signers. PMd = dorsal premotor cortex; STS = superior temporal sulcus. Right: cortical sites showing significantly stronger activation in hearing non-signers than in deaf signers. SPL = superior parietal lobule; POS = parieto-occipital sulcus; PCL = paracentral lobule.
hand, movements typically used in action viewing tasks (Grafton et al., 1996; Rizzolatti et al., 1996b; Nishitani and Hari, 2000). It is also to be noted that no objects were used in the present study, and the observed signs could not be recognized or named by the hearing non-signers. These aspects could at least in part explain the symmetry in the activation of the IFL–STS network in our hearing non-signers.

Bilateral activation of the primary hand/arm motor regions during sign observation in both groups of subjects is in line with earlier results on action observation (Hari et al., 1996; Nishitani and Hari, 2000). However, activation within a more anterior PMd region in the left hemisphere was predominant in our deaf signers, possibly reflecting influence of sign language experience and comprehension. The superior area 6 in monkey brain, a homologue to human PMd cortex, is involved in motor preparation, by retrieving from memory the response appropriate to the context, and in execution of the selected movements (Matelli and Luppino, 1997). According to Fadiga and co-workers, visually triggered discharges in the monkey area F4 (or area 6) reflect potential actions directed to particular spatial locations; visual stimuli may automatically evoke one of the potential actions stored in F4 as a sort of motor vocabulary (Fadiga et al., 2000). In humans, lesions in the PMd cortex impair arm movements that require temporal coordination of proximal muscles and associating of hand movements with particular sensory cues (Matelli and Luppino, 1997). Activation of the left-hemisphere PMd area in our deaf signers could reflect automatic retrieval of learned motor sequences from memory. This suggestion is in line with previous PET results suggesting a positive correlation between PMd activation and the degree of improvement in skill during complex motor task training (Kawashima et al., 1998).

Automatic activation of the dorsal visual pathway in both groups of subjects was an expected finding. The V5 complex has been shown to be activated during observation of right-hand reaching movements (Nishitani and Hari, 2000), as well as by movements of a virtual right hand, perceived as if it were the subject’s own hand (Decety et al., 1994).

Although the anterior SPL region was activated bilaterally in both groups, the right-hemisphere activity was stronger in hearing non-signers; this difference may, however, in part reflect the stronger overall activity in hearing non-signers than in deaf signers. The monkey SPL has been suggested to participate in the visuospatial encoding and visuomotor transformation of hand/arm reaching movements, and it has been shown to have direct neural connections to frontal motor and premotor regions (Kalaska et al., 1990; Caminiti et al., 1996; Johnson et al., 1996). In humans, the right anterior SPL region was recently suggested to encode kinesthetic aspects of observed finger movements, and to be activated during imitation of the same movements (Iacoboni et al., 1999).

The medial surface of the POS, the area of the V6 complex, is also involved in visual guiding of reaching movements (Gallezza et al., 1997). The V6 complex receives direct projections from a number of visual areas, including the V5 cortex, and displays a relative emphasis on the visual periphery (Colby et al., 1988; Portin and Hari, 1999). Activation of the mesial paracentral lobule has been observed during attention to somatosensory stimulation (Forss et al., 1996) and during unilateral complex finger movements (Roland et al., 1982), but the functional significance of this activation remains unsettled at present. The involvement of the dorsal visual pathway was in general weaker in our deaf signers, possibly because they immediately understood the observed signs without needing to pay sustained attention to them the way the hearing non-signers had to do. The deaf signers probably processed the signs as symbols, not simply as movements.

Our results demonstrate that cortical representations of sign language and action observation are largely overlapping, in agreement with the hypothesis that language may have developed from oro-facial and brachio-manual gestures (Rizzolatti and Arbib, 1998). However, our findings also indicate that the neural networks recruited by passive observation of sign language in part depend on the familiarity and linguistic meaningfulness of the actions perceived.

Notes
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References


Grafton ST, Woods RP and Mazzotta JC (1993) Within-arm somatotopy in


