

Neural substrates for verbal working memory in deaf signers: fMRI study and lesion case report

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Abstract

The nature of the representations maintained in verbal working memory is a topic of debate. Some authors argue for a modality-dependent code, tied to particular sensory or motor systems. Others argue for a modality-neutral code. Sign language affords a unique perspective because it factors out the effects of modality. In an fMRI experiment, deaf participants viewed and covertly rehearsed strings of non-sense signs; analyses focused on regions responsive in both sensory and rehearsal phases. Compared with previous findings in hearing subjects, deaf subjects showed a significantly increased involvement of parietal regions. A lesion case study indicates that this network is left-dominant. The findings support the hypothesis that linguistic working memory is supported by modality-specific neural systems, but some modality-neutral systems may also be involved.

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1. Introduction

Natural sign languages of the Deaf provide a unique opportunity to study the influence of sensory and motor experience on the neural organization of higher cognitive systems, particularly those involved with language. Accordingly, the neural systems supporting sign language production and comprehension have been studied intensively over the last two decades with a variety of experimental methodologies (Hickok & Bellugi, 2001). Here we explore the neural basis of another language-related ability, verbal working memory. In the behavioral literature, there is debate over the format of the representations maintained in verbal working memory. Some argue for a sensory and/or motor articulatory code (Wilson, 2001);

others promote a modality-neutral representational format (Jones & Tremblay, 2000). Sign language provides some leverage on this debate because it allows sensorimotor factors to be dissociated from higher-level linguistic representations (e.g., phonological structure).

Behavioral studies on working memory for sign language have demonstrated that some of the major behavioral hallmarks of verbal working memory are also evident in working memory studies of sign language (Wilson & Emmorey, 1997, 1998). For example, two central effects accounted for in Baddeley's "phonological loop" model (Baddeley, 1992)—the effects of phonological similarity and articulatory suppression—appear to hold for sign language as well (Wilson & Emmorey, 1997, 1998), suggesting some similarities in the kinds of processes that are involved in the systems. However, substantial differences have also been observed which indicate modality-specific effects in working memory.

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Whereas the presence of task-irrelevant auditory information can degrade immediate serial recall for spoken language stimuli in hearing subjects (Jones & Macken, 1996; Salamé & Baddeley, 1982), task-irrelevant *visual* information can interfere with immediate recall of sign-language stimuli in deaf signers (Wilson, 2001). Thus, behavioral evidence suggests some modality-independent features of verbal working memory (similar kinds of effects hold across modalities) but also indicates a fair degree of modality specificity (visual interference affects sign retention whereas auditory interference affects speech retention).

The neural substrate supporting verbal working memory processes has been extensively investigated in hearing/speaking individuals (Smith & Jonides, 1997). The majority of these studies have implicated a frontoparietal network including Broca's area, a dorsolateral premotor region, and inferior parietal cortex, among others. The posterior site has been argued to be the locus of the "storage" component of verbal working memory, whereas the frontal regions are thought to support articulatory rehearsal (Smith & Jonides, 1997). Two recent studies have further clarified the role and location of the posterior activation in verbal working memory tasks (Buchsbaum, Hickok, & Humphries, 2001; Hickok, Buchsbaum, Humphries, & Muftuler, 2003). Capitalizing on the behavioral observation that auditory information has obligatory access to the storage component of verbal working memory (i.e., irrelevant sounds interfere with serial recall), these studies sought to identify regions that responded both during auditory presentation of speech and during maintenance (i.e., rehearsal) of that information. The paradigm involved presenting subjects auditorily with speech stimuli and then asking them to rehearse silently those items for an extended period of time, thus allowing for the deconvolution of the auditory and rehearsal phases of the trial. A robust auditory + rehearsal activation was found in every subject in both experiments in a parietal–temporal region at the posterior most aspect of the Sylvian fissure (referred to as area Spt). In addition, it was found that this region responded similarly when melodic stimuli were heard and then rehearsed (hummed) silently (Hickok et al., 2003). The response profile of this region is consistent with behavioral evidence about obligatory access to the storage component of verbal working memory, including its non-specificity for speech. Additional regions also showed auditory–motor responses (posterior superior temporal sulcus, Broca's area, and dorsolateral premotor cortex) suggesting that area Spt is part of a larger cortical network, consistent with previous data showing a fronto-posterior network supporting verbal working memory.

The specific question addressed in the present fMRI study was whether the neural network supporting working memory for sign language in native Deaf signers

would align with the regions known to be involved in working memory for spoken language. In other words, is there a modality effect in verbal working memory? To factor out the obvious differences expected to be found between signed and spoken language in peripheral sensory–motor processes, we used the same paradigm adopted in the above-described studies. Namely, trials consisted of both sensory (video presentation of nonsense signs) and rehearsal (covert signing) phases, and co-activation in both phases was taken to indicate a region's involvement in working memory. By focusing on regions that respond both during the sensory encoding phase and during the motor rehearsal phase, we hoped to explore systems involved in core aspects of working memory and not purely sensory or higher-order (e.g., attentional) processing components. If we find a high degree of correspondence between activations on this task with deaf subjects (present study) compared to activations in hearing subjects using the same paradigm (previous studies), this would be consistent with a modality-independent view of linguistic working memory.

2. Experiment 1: fMRI

2.1. Materials and methods

2.1.1. Subjects

This study was approved, and carried out, in full compliance with the guidelines set forth by the Human Subjects Institutional Review Boards of the University of California, Irvine, and the Salk Institute for Biological Studies. Participants included ten native deaf (born deaf to deaf parents), right-handed subjects (7 males, 3 females; mean age = 38.3 years) whose preferred sign language is American Sign Language (ASL).

2.1.2. Task

Sign language stimuli consisted of pseudosigns, that is, manual gestures that did not carry meaning but conformed to the phonotactic rules of ASL. Pseudosigns with a high degrees of similarity to real signs were avoided to minimize semantic coding. Pseudosigns were used (1) for consistency with the previously published study using spoken pseudowords, and (2) to minimize semantic-related processing. Previous work has indicated that pseudosigns, like pseudowords, are processed phonologically as opposed to being processed as non-structured manual gestures (Emmorey, 1995). Sign stimuli were generated and digitally recorded by a team of native ASL signers. A single trial started with the video presentation of three pseudosigns lasting approximately 3 s. The offset of the last sign was the cue to begin rehearsing covertly the set of three signs. A fixation crosshair was present on the screen during this rehearsal

phase, which lasted 15 s. The same set of three pseudo-signs was then re-presented, cueing the subject to stop rehearsing. A 15-s rest period followed immediately, again with a fixation crosshair, and then a new set of three pseudosigns initiated the next trial. (Summary trial structure: *view signs* (3 s) → *covertly rehearse signs* (15 s) → *view signs* (3 s) → *rest* (15 s).) The fMRI recording was carried out over four runs (each lasting 4 min and 22 s), each containing seven trials for a total of 28 trials over all runs.

All subjects participated in a practice session before imaging. During the practice session, subjects were presented with the same trial structure using items similar to those in the MRI recordings. During practice, subjects *overtly* rehearsed each set of pseudo-signs, which allowed us to ensure that they understood and were capable of carrying out the task. The concept of covert rehearsal was explained and practiced during pre-testing. *fMRI*: scanning was conducted at 1.5 T on a Siemens Vision scanner using a gradient-echo EPI sequence with the following parameters: TE = 40, TR = 2 s, FOV 256 mm, matrix = 64 × 64, voxel dimensions = 6 × 4 × 4 (mm). Sixteen (6-mm-thick) contiguous axial slices were acquired so as to cover brain regions relevant to the study. In addition, all subjects received a high-resolution (180 sagittal slices, voxel dimensions = 1 mm, 1 mm, 1 mm) MPRAGE scan for use as an anatomically detailed background for statistical activation maps.

2.1.3. fMRI analysis

Image preprocessing and statistical analyses were carried out using FEAT (fMRI Expert Analysis Tool) Version 5.00, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). The images of every scanning run were concatenated to form, for each subject, a set of four 4-dimensional (ANALYZE 7.5) data files. After correction for sampling offsets in EPI slice acquisition, all runs were motion-corrected with the middle volume (the 66th image) serving as the registration reference. Spatial (5 mm FWHM) and high pass temporal (100-s cut-off) filtering were then applied to each of the 4-dimensional data files. Each subject's high resolution MRI was aligned with FLIRT (FMRIB's Linear Image Registration Tool) to the standard MNI (Montreal Neurological Institute) template; a 12-point affine transformation was derived and saved. All functional runs were then aligned with a 6-point rigid body to the high-resolution MRI, and again these transformations were saved to disk.

2.1.4. Statistical analysis

Statistical analysis was carried out in three stages (within run, across runs/within subject, and across subjects) using FLAME (FMRIB's Local Analysis of Mixed Effects). This strategy allows for the modeling of random effects at both the "run" (sometimes referred to

as "session") and subject levels. Further, variances occurring at lower levels of the analysis are carried up to higher levels so that inferences made at the "group" level take into account the intra-run and intra-subject variances occurring in the nested strata. To avoid confusion, we note the statistical model employed here is best described as a hierarchical *mixed effects* model, though this type of model is often referred to as "random effects" in the brain imaging literature.

Time series were modeled using multiple regression in which each task event type (VIEW SIGNS, REHEARSE SIGNS, VIEW SIGNS AGAIN) was represented by a separate regressor that was formed by convolving a gamma function ($\alpha = 6$, $\beta = 3$) with the binary sequence (0 = off, 1 = on) representing for each second of scanning the presence or absence of the event. Each of these regressors was contrasted with rest, and statistical images were generated and thresholded using clusters determined by $Z > 2.3$ and a (corrected) cluster significance threshold of $p = .01$ (Friston, Jezzard, & Turner, 1994; Worsley, Evans, Marrett, & Neelin, 1992). The voxel-wise intersection of the thresholded Z -maps for the VIEW SIGNS and REHEARSE SIGNS contrasts was then computed to determine what brain regions were active during *both* perception and covert rehearsal of signs. The resultant intersection map, then, represents those voxels for which both contrasts (VIEW SIGNS, REHEARSE SIGNS) have a Z value > 2.33 and belong to a cluster of appropriate size for a cluster-corrected p value of .01. However, the intersection map itself was not subjected to a cluster level significance criterion, because each of its logical inputs had already been thresholded. All statistical images were created at both the single subject and group levels.

2.2. Results

Figs. 1 and 2 show regions that exhibited a significant response to both sensory and rehearsal phases of the task. Note that frontal regions, including the posterior inferior frontal gyrus and more dorsal premotor cortex, shown previously to be active in verbal working memory tasks in hearing subjects, are active in the present study. These frontal activations are more extensive in the left hemisphere. Several posterior sites are also active, including posterior STS bilaterally, posterior parietal cortex bilaterally, and the posterior temporal-parietal boundary location (Spt) noted in recent studies (left only). A closer examination of the posterior activation sites revealed that although area Spt was active in most (7 of 10) Deaf subjects, it is clearly not the most dominant response in posterior cortices as it is in hearing/speaking subjects (Hickok et al., 2003). Instead, the more dorsal posterior parietal site was the most consistently activated region in the Deaf sample. This site does not show sensory + rehearsal properties in working

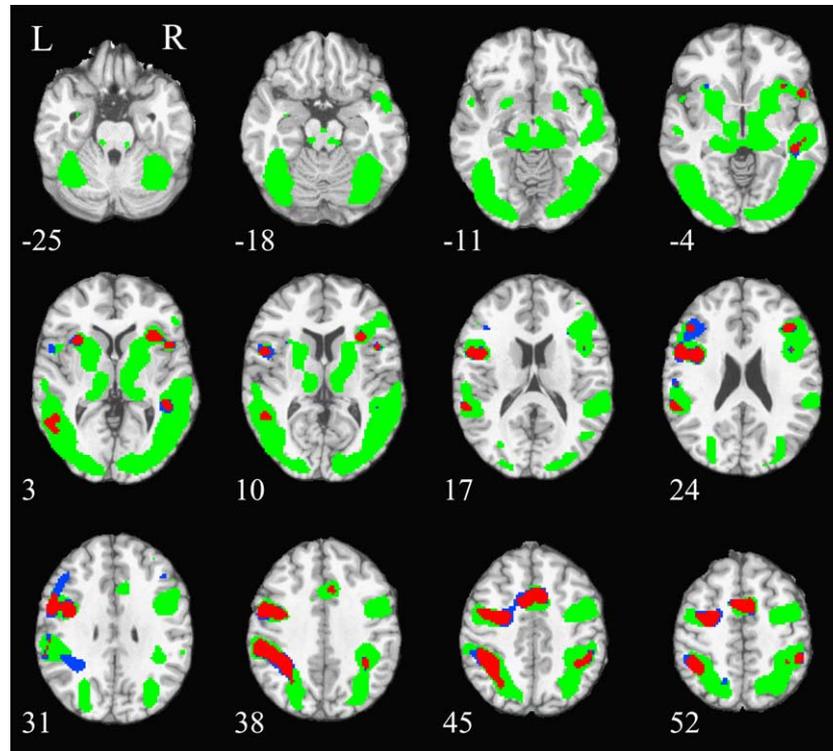


Fig. 1. Axial slices showing activation during the perception of signs (green), the covert rehearsal of signs (blue), and the conjunction of perception and rehearsal (red).

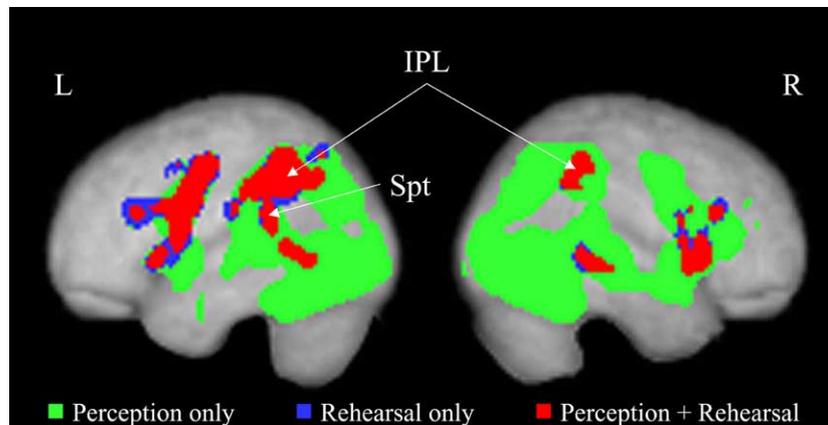


Fig. 2. Lateral activation sites projected onto volume rendered MNI152 anatomical images. See text for discussion of labeled regions. IPL, inferior parietal lobe; Spt, superior parietal-temporal.

memory tasks in hearing subjects. Table 1 presents a full list of areas with group-wise sensory + rehearsal activations.

2.3. Experiment 1 discussion

The fMRI study described above indicates a fronto-parietal circuit supporting short-term memory for sign. This network differs partially from that thought to support short-term memory for spoken language particularly with respect to the posterior regions involved: sign language appears to recruit a more dorsal parietal net-

work than does spoken language which relies more on ventral parietal/temporal locations. This finding suggests some significant modality-specific effects in linguistic working memory. However, similarities were also observed, including involvement of frontal structures and a left dominance in activation distribution (see Figs. 1 and 2). These similarities may reflect modality-independent components of linguistic working memory, or as discussed more thoroughly below, some form of cortical plasticity in which a region that would normally be associated with one sensory-motor channel (i.e., those supporting speech-related processes) is recruited in deaf

Table 1
Regions activated both during the perception and covert rehearsal of sign stimuli

<i>x</i>	<i>y</i>	<i>z</i>	Region	BA	<i>Z</i> score	Cluster volume (mm ³)
2	0	50	Medial frontal gyrus	6	5.011	3456
−40	−2	38	L precentral gyrus	6	5.38	5216
−48	4	12	L inferior frontal gyrus	44/6	4.947	4688
−60	−38	20	L superior temporal gyrus	22	4.705	1520
−44	−44	44	L inferior parietal lobule	40	5.33	6656
46	−46	42	R inferior parietal lobule	40	5.848	2808
−58	−52	2	L middle temporal gyrus	21	5.059	2072
40	28	24	R middle frontal gyrus	46	3.288	1856
34	18	6	R inferior frontal gyrus	45/47	6.09	1344
46	12	6	R inferior frontal gyrus	44/45	4.319	1144
54	−26	−8	R middle temporal gyrus	21	4.158	2056
−36	14	2	L inferior frontal gyrus	47	4.754	240

Z scores correspond to maximum value within each cluster that was achieved by *both* the perception and rehearsal predictors.

individuals for use in a different sensory–motor channel (i.e., those supporting sign language-related processes).

3. Experiment 2: Lesion case study

LHD-150 is a right-handed woman, who was born deaf (cause unknown), attended a residential school for the Deaf, and used ASL as her primary language throughout her life beginning approximately at age 5 years. She came to medical attention following the sudden onset of right-sided weakness and headache. A T2-weighted MRI acquired 3 days post-stroke revealed a middle cerebral artery distribution infarct involving left frontal and parietal lobes (Fig. 3). The left temporal lobe was largely spared except for some involvement in the posterior dorsal superior temporal gyrus, probably including area Spt. Thus, regions that are implicated in auditory comprehension deficits in hearing patients— involvement of the posterior middle temporal gyrus appears to be the necessary and sufficient condition (Dronkers, Redfern, & Knight, 2000)—were not involved. Our behavioral testing was carried out 2 weeks post-stroke.¹ LHD-150's age at testing was 77 years.

Sign language evaluation indicated the following: (i) LHD-150's *sign language production* was fluent, defined by her ability to generate complete and fluent sentences at least occasionally (“non-fluency” in language production is defined as a failure to generate even occasional connected utterances (Goodglass & Kaplan, 1983)). Her production did, however, contain frequent pauses and hesitations, during which she appeared to struggle with sign-finding difficulties. Paraphasic errors were also noted in her production; errors were predominantly semantic substitutions. (ii) LHD-150's *sign comprehension* was good for both individual signs (12 out of 12 correct in matching individual object and action signs to

pictures) and sentence-level stimuli (18 out of 18 correct on a sentence-to-picture matching test; 13 out of 13 correct on a test requiring yes/no responses to questions such as “Are you now living in Arizona?”; 6 out of 6 correct in following one-step commands such as “point to the red square”). LHD-150's good sign comprehension, coupled with the nearly complete sparing of the temporal lobe, is consistent with the previous claim that significant sign comprehension deficits are associated with substantial damage to the left temporal lobe (Hickok, Love-Geffen, & Klima, 2002). (iii) Tests of *sign-finding* abilities indicated a moderate deficit (48 correct out of 63 on a picture-naming task; 11 deaf elderly controls: mean = 57.6, *SD* = 4.76). Thus, LHD-150 presented with a relatively mild aphasia characterized primarily by moderate word-finding difficulties that were evident both on formal naming tasks and in conversational sign production.

Family members indicated, however, that since LHD-150's stroke, she had a particularly short memory span for signs presented to her. To test for a possible deficit in short-term memory for signs, we presented LHD-150 with an immediate recall test using common signs as stimuli. Sets of ASL signs were presented to LHD-150 by a native Deaf signer, and LHD-150 was instructed to reproduce the list immediately. This proved to be an extremely difficult task for LHD-150, even for a list length of two signs: although she could correctly repeat single signs (5/5 correct), she correctly repeated back only 2 of 9 two-item sets, and the correct responses appeared effortful (neither set was recalled in the correct order, and in one set there was a substantial pause before recall of the remaining item). On every item LHD-150 failed, at least one of the two signs in the stimulus set was correctly recalled. Two trials with three-sign sets were administered (0/2 correct), before testing was stopped. In addition, she had difficulty making a same–different discrimination between two sets of two signs. In this task, one investigator signed a two-sign list, and a second investigator produced another two-sign list that

¹ Unfortunately, we were only able to test LHD-150 on this one occasion.

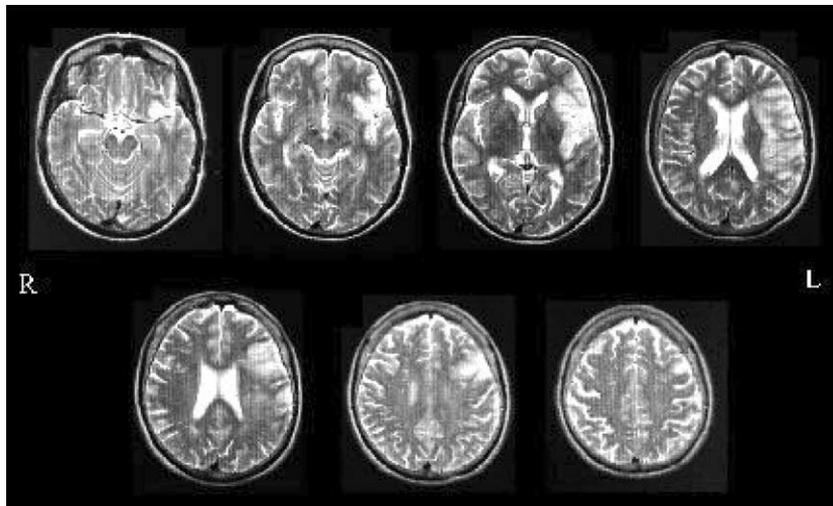


Fig. 3. T-2 MRI showing left fronto-parietal stroke in case LHD-150.

was either identical to the first or differed by one item. LHD-150 was asked simply to respond same or different. Nine trials were administered before testing was halted: 4 out of 9 correct (hit rate = 0.42, false alarm rate = 0.5). This testing indicated a fairly severe short-term memory deficit for sign language stimuli.

3.1. Experiment 2 discussion

LHD-150 presented with a mild fluent aphasia characterized by paraphasic output (predominately semantic in nature) and moderate word (sign) finding abilities both on formal testing and in conversational production. Her comprehension was normal on all tests administered. LHD-150's most prominent symptom was a deficit in immediate recall of sign stimuli. This clinical profile is similar, although not identical, to the classical presentation of conduction aphasia, which is characterized by good comprehension, word finding difficulties, and a deficit in verbatim repetition (Goodglass, 1992). The classic hearing patient with conduction aphasia, like LHD-150, also produces paraphasic errors in speech production, although unlike our present case, these errors tend to be phonemic in nature.

4. Discussion

The present study indicates both some similarities and some major differences in the neural organization of verbal short-term memory for speech and sign language. On a broad scale, both systems rely on a widely distributed network, including frontal, parietal, and temporal cortices. Within this broad network, there are regions that appear to be common to the two language formats. These common areas can be found in posterior frontal regions (premotor cortex and opercular regions, pre-

dominantly on the left), left temporal–parietal junction, and posterior superior temporal sulcus (bilaterally). Importantly, there are also regions that are more stimulus-specific, including a greater reliance on a left temporal–frontal circuit for speech, and a greater reliance on a parieto-frontal circuit for sign. These differences suggest that at least some aspects of linguistic working memory are modality specific.² The case study presented here indicates that a left frontoparietal lesion can produce substantial deficits in short-term memory for sign language, suggestive of a left-dominant working memory system for deaf signers similar to the left dominant verbal STM organization for hearing individuals.

Several previous studies of the neural basis of working memory, including human and animal work, have documented stimulus-specific effects both in frontal and posterior cortices (i.e., the network that is activated depends on the information that is to be maintained in working memory, such as spatial vs. object vs. verbal information) (Fuster, 1995; Goldman-Rakic, O'Scalaidhe, & Chafee, 2000; Smith & Jonides, 1997). The present fMRI study adds to this literature, and extends it by suggesting that there are modality-specific effects in working memory even within formally similar representational systems such as signed and spoken language. The modality-specific effects might be interpreted as neural systems supporting sensory–motor integration. It has been hypothesized that one function of parietal lobe systems in primates (including humans) is to interface visual input with various motor effector systems

² Another possible interpretation of these differences is that deaf signers and hearing speakers use different cognitive strategies for performing linguistic working memory tasks. Behavioral data showing that deaf signers show functionally similar effects in working memory tasks (articulatory suppression, phonological similarity, etc.) argue against this interpretation, however.

(the dorsal stream) (Colby & Goldberg, 1999; Milner & Goodale, 1995; Rizzolatti, Fogassi, & Gallese, 1997), and some authors have argued for memory-related functions of these parietal networks (Murata, Gallese, Kaseda, & Sakata, 1996). Building on this work in the visual domain, Hickok, Poeppel, and colleagues (Hickok et al., 2003; Hickok & Poeppel, 2000, 2004) argued that verbal working memory can be explained in terms of a functional network that supports auditory–motor integration. On this view, a region in the posterior Sylvian fissure at the parietal–temporal boundary (Spt) is the auditory–motor functional equivalent of previously described dorsal parietal visuo–motor integration regions. This auditory–motor network, it is argued (Hickok et al., 2003; Hickok & Poeppel, 2000, 2004), is necessary for non-working memory speech functions (e.g., acoustic guidance/tuning of speech articulatory gestures in development (Doupe & Kuhl, 1999)). Once established, however, the network can be co-opted to support verbal working memory. If a sensory–motor foundation for working memory is on the right track—and recent behavioral arguments suggest it is (Wilson, 2001)—it makes sense that sign language processing, which presumably requires a greater reliance on visuo–motor integration, involves dorsal parietal regions more extensively in working memory tasks, whereas spoken language, which relies more on auditory–motor integration, implicates a network more tightly connected to the auditory system (Hickok et al., 2003). These posterior sensory–motor sites are presumably part of a larger circuit involving frontal cortical fields.³ Previous observations that the perception and imitation of gesture (in hearing subjects) activate similar parietal regions (Decety et al., 1997; Hermsdorfer et al., 2001) is consistent with this view.

It remains to be explained, under this sensory–motor hypothesis, why some regions, Spt in particular, show modality–neutral effects. Spt is thought to be a hub in an auditory–motor integration network, and as such, supports verbal working memory for speech (Hickok et al., 2003; Hickok & Poeppel, 2004). We have suggested here that a more dorsal region in the parietal lobe supports visual–motor integration, and therefore verbal working memory for sign language. The fact that deaf subjects show sensory + rehearsal responses in the parietal lobe using our paradigm, whereas hearing subjects do not (for speech), is supportive of this position. But then why does Spt, which is purported to be an auditory–motor interface, show sensory + rehearsal responses in deaf

subjects performing a visual–motor task? There are several possibilities. One is that activation in Spt represents some form of compensatory plasticity, whereby canonical auditory/speech-related systems are recruited for sign-related functions in cases of auditory deprivation. Another possibility is that Spt is involved in some higher-order supramodal process, such as some form of phonological computation, which is common to both language systems. Although this is a possible explanation for the verbal working memory data for speech and sign, it does not explain why the perception and covert rehearsal of tonal stimuli activate Spt at least as well as phonological stimuli (in hearing subjects) (Hickok et al., 2003). A final possibility, is that Spt is not critically linked to the auditory system, but rather is critically linked to the orofacial effector system. That is, Spt may be multimodal on the sensory side, but unimodal on the motor side. This would explain its involvement in the perception and rehearsal of speech and tonal stimuli because both involve orofacial effectors. Sign language also has a significant orofacial component. Perhaps the activation of both, parietal regions (manual effectors) and Spt (orofacial effectors) reflect the involvement of the two effector systems in sign language. This hypothesis can be tested straightforwardly in future studies by systematic varying the sensory input and motor output.

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³ Several imaging studies of verbal working memory in hearing patients have reported parietal lobe activations. However, these locations do not appear to show sensory responses, and have been argued to reflect some higher-order, perhaps attentional, process (for discussion, see Becker, MacAndrew, & Fiez, 1999; Hickok et al., 2003). The networks we are referring to here, are those which show both sensory and rehearsal period responses.

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