Functional Roles of Broca's Area and SMG:
Evidence from Cortical Stimulation Mapping in a Deaf Signer

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The importance of the left hemisphere in language function has been firmly established and current work strives to understand regional specializations within the perisylvian language areas. This paper reports a case study of a deaf user of American Sign Language undergoing an awake cortical stimulation mapping procedure. Patterns of sign errors accompanying electrical stimulation of Broca's area and the supramarginal gyrus (SMG) are reported. Our findings show Broca's area to be involved in the motor execution of sign language. These data demonstrate that the linguistic specificity of Broca's area is not limited to speech behavior. In addition, unusual semantic–phonological errors were observed with stimulation to the SMG; these data may implicate the SMG in the binding of linguistic features in the service of language production. Taken together, these findings provide important insight into the linguistic specificity of Broca's area and the functional role of the supramarginal gyrus in language processing.   © 1999 Academic Press

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INTRODUCTION

The role of the left hemisphere perisylvian areas in language function has been firmly established by decades of clinical research involving subjects who have incurred acute brain damage. Within the past 10 years it has become clear that this left hemisphere specialization for language is observed not only for users of spoken languages, but for deaf users of signed languages as well (Poizner *et al.,* 1987; Hickok, *et al.,*

1996a; Corina, 1998). More recent work strives to elucidate regional specialization within the left hemisphere perisylvian regions in relation to the multiple functional systems involved in human language processing (e.g., phonological encoding, lexical access, grammatical parsing, motor implementation). In this regard, lesion studies have significant limitations; lesions are often large and not circumscribed to specific regions of interest and often impact several processing systems, further obscuring functional–anatomical relationships. Thus, there is a growing emphasis on using alternative techniques to ascertain specific cortical regional specialization within the left hemisphere. Some of these techniques include functional neuroimaging of blood flow (Petersen *et al.,* 1988; Binder *et al.,* 1997), the measurement of electrical and magnetic fields generated by the brain (Osterhout, 1994; Lounasmaa *et al.,* 1996), and electrical stimulation of the cortex, which produces short-lasting reversible functional lesions (Flitman *et al.,* 1998; Ojemann, 1995). These techniques are beginning to provide novel insight into the complex functional–anatomical relationships within the left hemisphere systems subserving language.

The present paper reports data from a very rare clinical case of a deaf user of American Sign Language (ASL) undergoing an awake cortical stimulation mapping (CSM) procedure during left temporal lobe resection for treatment of a seizure disorder. Following standard techniques, temporal lobe resection is guided by electrophysiological and cortical stimulation mapping findings obtained during a part of the operation in which the patient is awake but under local anesthesia. The CSM procedure identifies sites of language and motor function through application of a localized electrical current at specific cortical sites. Sites of stimulation within the left-temporal, inferior-frontal, and parietal exposure are pseudo-randomly selected for the purpose of identifying cortical regions responsible for motor and language function. During the mapping of motor areas, a subject is observed for movements of the face, jaw, hand, etc., and is asked to report any sensation he/she

experiences under conditions of stimulation. During the language-mapping portion of the procedure, a subject may be required to name pictures or read written words. Disruption of the ability to perform the task during stimulation is taken as evidence of cortical regions integral to the language task (Whitaker, 1998).

In the present case a standard motor mapping procedure was used. However, the language mapping procedure was adapted for sign language assessment, as ASL was this subject's primary and preferred mode of communication. The subject (patient S.T.) was required to perform two tasks: name (in sign) line drawings of common objects and repeat signs presented on videotape. Stimulation to several sites in the perisylvian region evoked object naming disruption, and two sites in particular resulted in repeated disruption with consistent characteristics. These sites, an anterior frontal site located within Broca's area, and a posterior parietal opercular site within the supramarginal gyrus, serve as the main focus of this paper. The data provide valuable insight into the functional specificity of Broca's area and the functional role of the supramarginal gyrus (SMG).

Functional Roles of Broca's Area

Broca's area lies in the frontal opercular region and is typically defined as the posterior third of the left inferior frontal gyrus, encompassing Brodmann's areas (BA) 44 and 45. Traditional accounts of aphasics with damage to Broca's area describe patients with effortful speech production but with intact language comprehension. However, the precise role of Broca's area in language behaviors remains controversial (Mohr *et al.,* 1978; Goodglass, 1993; Zatorre *et al.,* 1996). For example, the anatomical proximity of Broca's area to motor and sensory cortex of the Rolandic fissure has fueled speculation that speech difficulties evidenced in Broca's aphasics may simply reflect sensorimotor disruption of the speech articulators rather than a linguistic deficit per se. Moreover, patients described as Broca's aphasics are known to have not only speech fluency difficulties, but subtle language comprehension deficits as well (Goodglass, 1993). Consistent with these findings, recent imaging studies have demonstrated regional subspecialization of Broca's area. Price and colleagues have shown that while posterior frontal regions BA 44 and BA 6 (premotor mouth and face regions) are active in tasks requiring repetition and reading aloud, the anterior extent (BA 45) is active in cases of single word perception (Price *et al.,* 1996).

The current study provides valuable insight into the contribution of the posterior portion of Broca's area to language function. To date, no studies have evaluated the role of Broca's area in users of manual-gestural languages with the precision afforded by the CSM technique. Examining whether functional disruptions of sign language are observed during electrical stimulation to Broca's area provides an opportunity to assess the functional specificity of this region. The data obtained in the present study are pertinent to the question of whether this region's function relates specifically to speech behavior or more generally to language behavior, both spoken and signed.

Functional Roles of Supramarginal Gyrus

The parietal lobe is a polymodal association area that has been implicated in a large range of motor, sensory, spatial, and attention functions. However, the functional specializations within this large cortical area have been difficult to discern. The supramarginal gyrus lies within the parietal opercular area and is identified as the convolution that caps the posterior ascending ramus of the sylvian fissure (BA 40) (Steinmetz *et al.,* 1990). Early studies have suggested the importance of this association area in spatial behaviors, particularly those involving praxis and attention (Benton, 1969). More recent studies have implicated the supramarginal gyrus in a variety of language-related behaviors, especially those involving the phonological component of language structure (D'emonet *et al.,* 1994). For example, speech errors have been observed with stimulation of the SMG in studies of oral naming (Ojemann *et al.,* 1989), and aphasics with involvement of the SMG often show deficits in acoustic–phonetic processing (Caplan *et al.,* 1995). In addition, there is compelling evidence that the SMG plays an important role in the selection and/or activation of phonemic sequences in the service of language-related tasks (Kertesz, 1993; Bell *et al.,* 1990). Interestingly, some studies have suggested that the SMG may play a broader role in tasks requiring the confluence of hand movements and phonemic selection. For example, the SMG has been implicated in some forms of acquired writing impairments, specifically phonological agraphia (Penniello *et al.,* 1995; Roeltgen and Heilman, 1984; Alexander *et al.,* 1992). The contributions of the SMG to sign language behavior are not well understood. However, the inventory of functions associated with the SMG would, *a priori,* flag this anatomical convergence zone as serving an important function in the programming of manual-linguistic behaviors.

The disparate functions currently attributed to the SMG are brought together in the present study in an unusual and informative manner. Because the domain of interest, sign language, is a primary language system that requires complex sequences of hand movements, this study provides an opportunity to examine the interaction between linguistic, praxic, and attentional mechanisms involved in language. Furthermore, the anatomical specificity afforded by our image coregistration techniques (Modayur *et al.,* 1997) provides

great refinement in the localization of function associated with this parietal opercular region.

METHODS

Subject Characteristics

Subject S.T. is a 50-year-old, right-handed male with a profound hearing loss (left ear, right ear > 90 dB) as a result of spinal meningitis at 18 months of age. He attended day programs and residential schools for the deaf, has an 8th grade education, and has been employed as a maintenance worker. WAIS-R performance scale testing estimates an I.Q. of 81. S.T. is a fluent signer of American Sign Language. ASL is his preferred and only mode of effective communication; S.T.'s speech is functionally unintelligible, and he makes no effort to communicate vocally.

Complex partial seizures with some secondary generalization began at approximately 38 years of age. Preoperative evaluation identified left temporal onset of S.T.'s medically refractory seizures. MRI scan and postoperative histological analysis of tissues revealed medial temporal hippocampal sclerosis and cystic lesion in the hilus of the hippocampus.

Wada Testing

Wada testing procedures adapted for ASL were used to established memory and language lateralization (Dodrill and Ojemann, 1997). On memory measures, sodium amobarbital injections to the left and right hemispheres resulted in borderline and impaired performance, respectively, indicating bilateral memory functions. In contrast, during language testing only the left hemisphere injection resulted in sign-blockage and object naming errors; there were no language errors observed with injections to the right hemisphere. These results are consistent with a left-hemisphere dominance for ASL in this subject.

Cortical Stimulation Mapping

The cortex was mapped with 4-s trains of 60-Hz, 2.5-ms biphasic square waves from a constant current stimulator delivered through electrodes 5 mm apart at 6 mA, the largest current that did not evoke after-discharges from the sampled cortex. Language test items were presented at 4-s intervals by either slide projector or videotape. Stimulation occurred on every second or third item, with no site repeated successively. In the language mapping portion of the procedure, a total of 24 sites were examined. The total number of trials (stimulated and nonstimulated) was 106 for object naming and 53 for sign repetition. The mean number of stimulated trials per site was 4.6 (range 1–12) for naming and 2.8 (range 1–6) for repetition. Signed responses during the procedure were video-

taped and scored with respect to their preoperative baseline measures. Authors D.C. and S.M. (both fluent users of ASL) and a native deaf research assistant evaluated signed responses with respect to well-established principles of ASL linguistic structure.

Language Testing Procedures

Stimuli used for the object naming portion of language mapping were line drawings of 49 items that S.T. consistently named with one-handed signs. For the repetition task, a deaf signer was videotaped producing 20 signs and 20 nonsigns. Nonsigns were constructed by recombining existing ASL hand shapes, movements, and locations into novel, sign-like constructions. The nonsign forms did not violate phonotactic constraints of ASL and may be considered the equivalent of pronounceable nonwords (e.g., "nust"). Thus, the articulatory demands that these nonsign forms place on the signer are identical to those present with actual signs. However, the nonsigns are without lexical–semantic content.

S.T. underwent extensive preoperative practice and testing with all stimuli. During preoperative sessions, all stimuli were practiced with both left and right hands. Due to the constraints of the surgical procedure, S.T. was instructed that in the operating room he would be responding with his left hand. It should be noted that handedness is not lexically contrastive in ASL. In addition, routinely in the course of daily activities, deaf signers often use their nondominant hand for signing, as in the case of carrying a bag of groceries or holding a child, etc., while conversing; thus signing with either the right or the left hand is not considered unnatural.

Anatomical Localization

During the CSM procedure, sites of stimulation were identified by sterile number tickets laid on the cortex. Following testing, these locations were photographed. A three-dimensional model of S.T.'s brain was created by combining a T-1-weighted 3-D MR volume of the brain with a 2-D MR venogram and a 3-D MR arteriogram. Coregistration of the intraoperative number markers onto this three-dimensional model was accomplished through reference to patterns of cortical veins and arteries (Modayur *et al.,* 1997; Hinshaw and Brinkley, 1997).

Imaging parameters were as follows: 3-D structural brain image, SPGR (29/5/1/45°) (TR/TE/NEX/flip angle), 22-cm FOV, 256 × 192 matrix, 124 1.2-mm sagittal partitions; 2-D TOF MR venogram (45/9/1/60°), 22-cm FOV, 256 × 192 matrix, 100 contiguous 1.5-mm axial images; 3-D MOTSA MR angiogram (RAMP excitation, GE Medical Systems, Milwaukee, WI), four overlapping slabs of 16 partitions each (36/6.9/1/25°), flow compensation, 22-cm FOV, 256 × 256 matrix, 64 axial slices at 0.9-mm spacing.

RESULTS

Motor / Sensory Mapping

Stimulation of the cortical sites numbered 1 and 2 resulted in mouth and lip movements, site 3 elicited jaw movement, and sensation in the lips was reported with stimulation of sites 4 and 6. Sensation of the right hand was elicited with stimulation of site 5 (Fig. 1). There were no motor or sensory responses at any other site. This mapping establishes the location of the Rolandic cortex, with its familiar pattern of sensory cortex lying posterior to motor cortex, and face/mouth cortex lying inferior to hand representation.

Language Mapping

Stimulation of several sites within the left hemisphere exposure led to significant left-handed signing errors. The anatomical locations of the sites and nature of the resulting errors are discussed below.

Object Naming

Nine of 23 sites tested led to object naming errors (Table 1). Two sites were particularly prone to naming

disruption. An isolated frontal opercular site (B) evoked repeated object naming disruption. A site in the parietal opercular region (Po) also resulted in robust object naming errors. Moderate naming disruption was also observed in sites surrounding site Po (Fig. 2). Occasional errors were also observed in the midtemporal lobe region. No object naming errors occurred under nonstimulation conditions. Importantly, the nature of the errors at the frontal opercular, parietal opercular, and midtemporal lobe sites was qualitatively different.

As seen in Fig. 1, site B lies at the posterior portion of the third left frontal convolution, immediately in front of sites evoking face motor responses. This site corresponds to the posterior aspect of Broca's area, Brodmann area (BA) 44. Site Po is the supramarginal gyrus (BA 40), as confirmed by an in-depth planar reconstruction. S.T.'s parietal opercular area is consistent with the anatomical type 1 pattern described in Steinmetz *et al.* (1990). Midtemporal sites stimulated included superior and middle temporal gyri and correspond to BA 22 and BA 21.

Stimulation of anterior site B resulted in errors involving the motor execution of signs. These errors are characterized by a laxed articulation of the intended
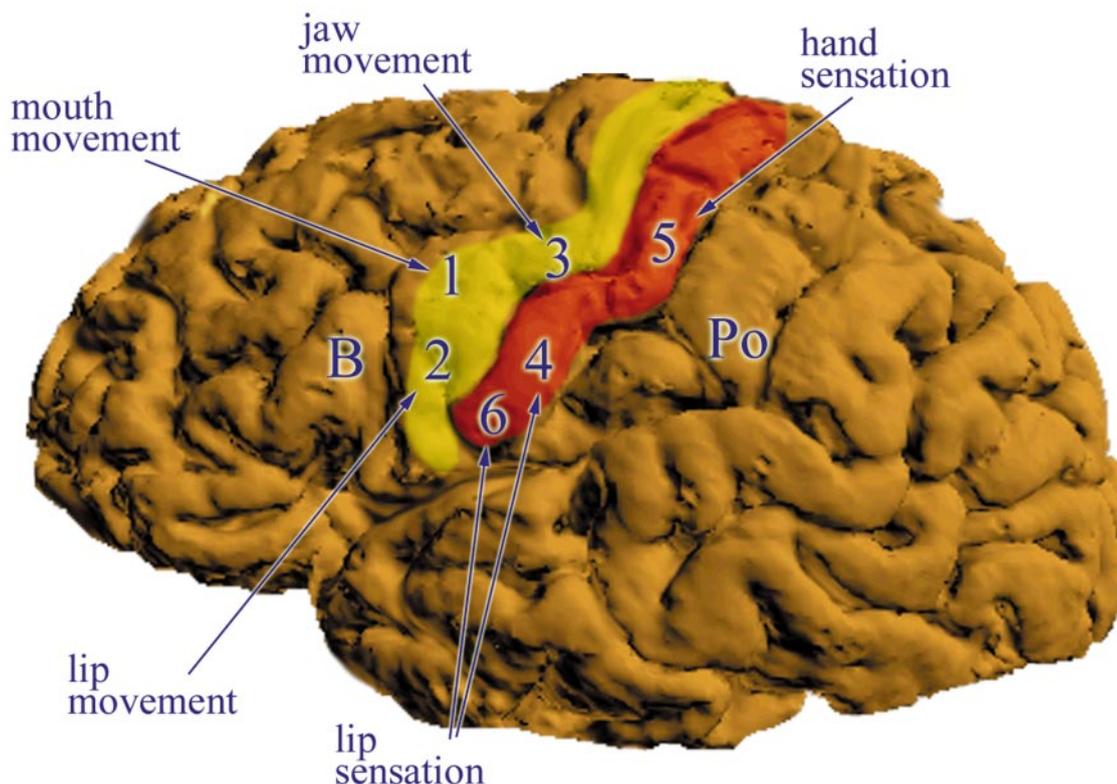

Figure 1

FIG. 1. Three-dimensional reconstruction of S.T.'s brain, showing sites of motor (1, 2, 3), sensory (4, 5, 6), and language (B, Po) representation.

sign, with nonspecific movements (repeated tapping or rubbing) and a reduction in hand shape configurations to a laxed-closed fist hand shape. For example, without stimulation S.T. correctly signed COW with a "Y" hand shape (outstretched thumb and little finger, all other fingers closed), with the thumb anchored on the temple and two downward twists of the wrist (Fig. 3a). During stimulation of site B, S.T.'s attempt at signing COW resulted in a closed fist hand shape with a repeated laxed tapping of this incorrect hand shape at the cheekbone (Fig. 3c). Without stimulation, S.T. correctly signed SHIRT with the fingertips of the "F" hand shape touching the chest twice (Fig. 3b). Under stimulation, S.T. instead produced a closed fist hand shape and made small rubbing motions at the chest (Fig. 3d). As illustrated by these examples, during stimulation of site B the articulatory integrity of the intended signs was consistently compromised. Interestingly, there was no effort on the part of S.T. to self-correct these imperfect forms.
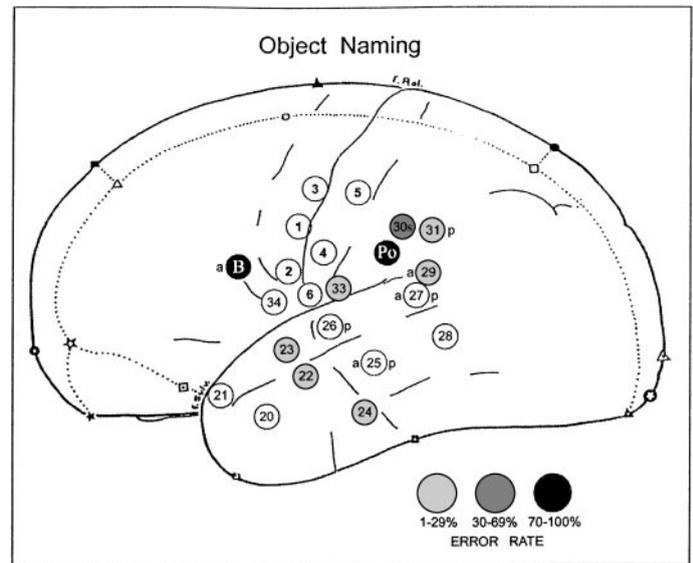

FIG. 2. Object naming stimulation results.

The sign errors observed with stimulation of Po are qualitatively different. S.T. produced both formational and semantic errors. Formational errors are characterized by repeated attempts by the subject to distinctly articulate the intended targets; often his signing exhibited successive formational approximations of the correct sign. For example, the sign PEANUT is normally signed with a closed fist and outstretched thumb, and with a movement composed of an outward wrist rotation (the thumb flicking off the front of the teeth). Under stimulation, this sign began as an incorrect, but clearly articulated, "X" hand shape (closed fist with a protruding bent index finger) articulated at the correct location, but with an incorrect inward rotation movement. In two successive attempts to correct this error, the subject first corrected the hand shape and then went on to correct the movement as well. A second example is illustrated in Figs. 4a and 4b. In its correct form, the sign SCISSORS is iconic; the index and middle fingers emulate the action of scissor blades opening and closing (Fig. 4a). Under stimulation to site Po, S.T.'s attempts to correctly articulate the sign take the following form (Fig. 4b): he starts with the correct "V" hand shape but produces no scissoring movement, bends the fingers of this hand shape, switches to a "Y" hand shape, and executes a movement with a repeated wrist twist, switches back to the correct "V" hand shape, but then proceeds to incorrectly bend these two fingers downward repeatedly rather than "scissor" them as required, and ultimately, he gives up. Notably, we do not find the laxed and reduced articulations characteristic of signing under conditions of stimulation to frontal site B. Instead, as these examples illustrate, under stimulation to site Po, the subject's signing exhibits problems involving the selection of the indi-
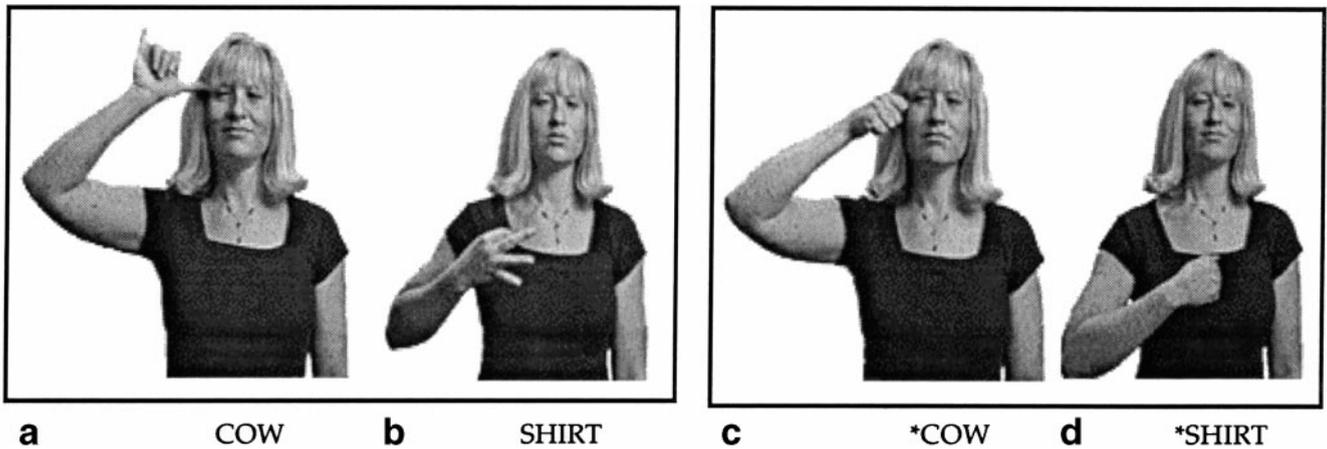
TABLE 1

Language Mapping Results

Object naming			Sign repetition		
Site/location	Stimulus trials	Errors	Site/location	Stimulus trials	Errors
Frontal operculum					
B	8	7	B	3	3
32a	5	0	32a	2	0
34	4	0	34	2	0
Parietal operculum					
P0	12	10	P0	4	0
30s	2	1	30s	3	0
31	7	2	31	2	0
33	7	2	33	2	1
Posterior temporal lobe					
27	3	0	27	2	0
27a	4	0	27a	—	
27p	1	0	27p	—	
28	3	0	28	2	0
29	7	2	29	3	0
29a	2	0	29a	—	
Midtemporal lobe					
22	5	1	22	4	0
22p	—		22p	1	0
23	5	1	23	6	0
24	4	1	24	3	0
25	6	0	25	4	0
25a	1	0	25a	—	
25p	1	0	25p	—	
26	5	0	26	2	0
26p	5	0	26p	2	0
Anterior temporal lobe					
20	4	0	20	2	0
21	5	0	21	4	0

FIG. 3. Site B object naming responses. (a) Correct articulation of the sign COW. (b) Correct articulation of the sign SHIRT. (c) Under stimulation to site B, S.T.'s inaccurate articulation of the sign COW. (d) Under stimulation to site B, S.T.'s inaccurate articulation of the sign SHIRT.

vidual components of sign forms (i.e., hand shape, movement, and to a lesser extent, location) (Corina and Sandler, 1993).

Semantic errors were also observed under stimulation to site Po, and the form of these errors is particularly noteworthy. Specifically, all of these errors involve semantic substitutions that are formationally quite similar to the intended targets. For example, the stimulus picture "pig" elicited the sign FARM, the stimulus picture "bed" was signed as SLEEP, and the stimulus picture "horse" was signed as COW. In ASL, these semantic errors contain considerable formational overlap with their intended targets; for example, the signs PIG and FARM differ in movement, but share an identical articulatory location (the chin) and each are made with similar hand shapes; the signs BED and SLEEP share hand shape and are both articulated

about the face; finally, the signs COW and HORSE differ only in hand shape. In English these mistakes might be similar to uttering "lobster" when one intended to say "oyster," or "plane" when one intended to say "train"; that is, these errors share both semantic and formational properties. As discussed below, the occurrence of these unusual semantic–formational blends is of significant theoretical interest.

Formational and semantic errors were occasionally observed at three sites proximal to site Po. Stimulation to sites 29, 30s, and 31 resulted in formational selection errors, while stimulation to sites 29 and 31 resulted in a semantic–formational error (ELEPHANT for RAT) and a semantic intrusion (CAT (correct) followed by the fingerspelling of #D-O-G (intrusion)). Finally, at site 33 two additional errors were observed: in one error S.T. appears to be groping to articulate the lexical sign
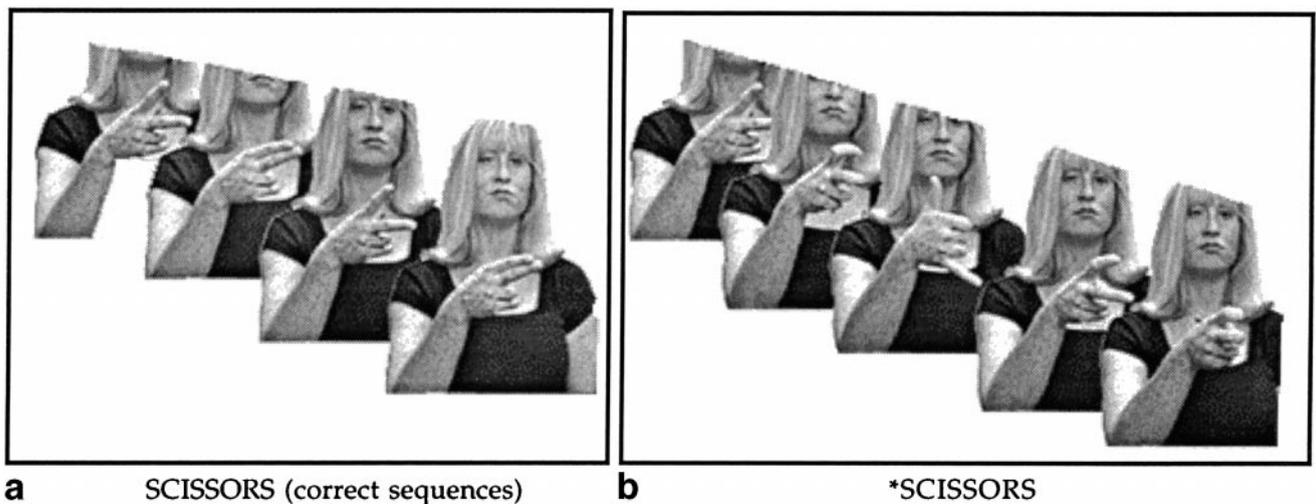

FIG. 4. Site Po object naming responses. (a) Correct articulation of the sign SCISSORS. (b) Under stimulation to site Po, S.T.'s formationally inaccurate articulation of the sign SCISSORS.

SUN; a second error resulted in a perseverative response from the previous trial.

Three sites in the midtemporal region produced isolated naming errors. Stimulation of sites 23 and 22 (superior and middle temporal gyri) resulted in semantic substitutions (DRINK-LIQUOR for MILK, and CIGAR for CIGARETTE). Stimulation to site 24 (inferior middle temporal gyrus) resulted in a perseverative response from the previous trial.

In summary, the analysis of these object naming errors shows that, following stimulation to anterior frontal site B, we find an impairment in the global implementation of signs. Overall, these errors showed laxed articulation (not unlike "mumbling" in spoken language) and were not corrected by the signer (see Table 2). In contrast, stimulation at parietal opercular site Po resulted in errors affecting the selection of the individual formational components of a sign, as well as errors involving semantic–formational blends. Characteristically, successive approximations of the target

sign were attempted. The movements and hand shapes observed during these attempts tended to be complex and varied (in contrast to the reduced inventory of forms observed with stimulation to B) (see Table 3). From these findings it appears that stimulation to the frontal site B has a global effect on the motor output of signing, whereas stimulation to parietal opercular site Po disrupts the correct selection of the linguistic components (including both phonological and semantic elements) required in the service of naming. Infrequent semantic naming errors were also observed in midtemporal lobe regions.

Sign Repetition

The data from the sign repetition tasks permit further insight into the specificity of function at cortical sites B and Po. Strikingly, stimulation to anterior frontal site B produced reliable errors in sign repetition

TABLE 2

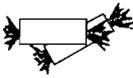Summary of Naming Errors That Occurred with Stimulation to Broca's Area

STIMULUS	HANDSHAPE		MOVEMENT		LOCATION	
	✓ TARGET	✘ PRODUCED	✓ TARGET	✘ PRODUCD	✓ TARGET	✓ PRODUCED
			closing	✘ tapping	mouth	✓ mouth
			twisting	✘ tapping	temple	✓ temple
			away	✘ rubbing	chest	✓ chest
			closing	✘ tapping	nose	✓ nose
			twisting	✘ closing	neutral	✓ neutral
			brushing	✘ tapping	chin	✓ cheek
			brushing	✘ tapping	cheek	✓ cheek

Summary of Naming Errors That Occurred with Stimulation to the Supramarginal Gyrus (SMG)

STIMULUS	HANDSHAPE		MOVEMENT		LOCATION	
	✓ TARGET	✗ PRODUCED	✓ TARGET	✗ PRODUCED	✓ TARGET	✗ PRODUCED
			touch (2x)	✗ bending	cheek	✗ face
			brushing	✗ tap→ away → wiggle	chin	✓ chin
			bending	✗ brushing	chin	✓ chin
			closing	✗ bend → twist → bend	neutral	✓ neutral
			bending	✓ bending	temple	✓ temple
			away	✗ touch → away	mouth	✓ mouth
			bending	✓ bending	chin	✓ chin
			touch (2x)	✗ circle → touch (2x)	cheek	✓ cheek

(3/3). No errors were observed in sign repetition with stimulation to any of the temporal lobe or posterior-parietal opercular sites. An isolated repetition error was observed at site 33 (see Fig. 5).

The sign repetition errors resulting from stimulation to site B evidenced a laxed and imprecise articulation similar to that observed in the naming task. For example, during nonstimulated trials, the sign PUZZLED was produced with an index finger hand shape that bends at the second joint as it is brought toward the bridge of the nose (Fig. 6a). Under stimulation to site B, the hand shape is laxed and the movement is incorrect, reduced to rubbing and tapping on the nose (Fig. 6b).

The data from the nonsign repetition tasks are consistent with the sign repetition data. During stimulation to site B, S.T. made clear errors on nonsign repetition trials, while no nonsign repetition errors

were observed with stimulation to site Po. Unfortunately, during the intraoperative procedure S.T. "regularized" many of the nonsign targets (i.e., he viewed a nonsign trial and produced a formationally similar actual ASL sign). These performance errors occurred during both stimulated and nonstimulated trials. The presence of these regularization errors limited the number of valid nonsign repetition data points available for analysis. Conservatively, scoring only those nonsign trials in which S.T. correctly preformed the task, we found that stimulation of site B resulted in 4/4 nonsign repetition errors, while stimulation to site Po resulted in no errors (though we were limited to only a single trial at Po using the available data). A clustering of single nonsign repetition errors was also found at posterior temporal sites 27, 28, and 29 and a single error at anterior temporal site 21.
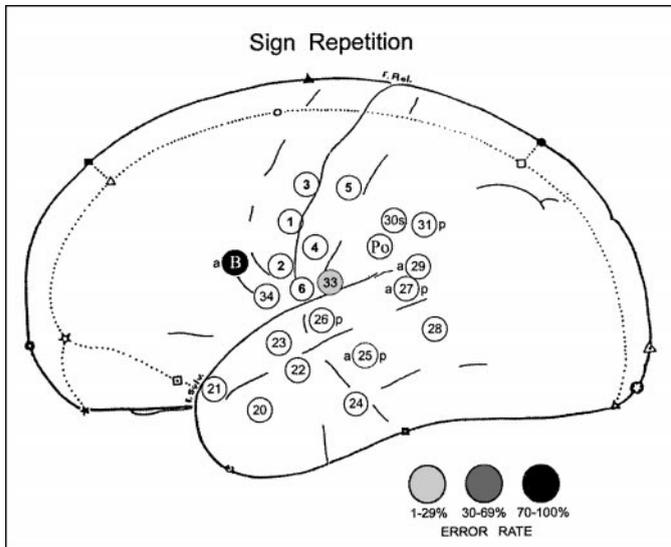
FIG. 5.   Sign repetition stimulation results.

Focusing our discussion on the two regions that showed robust and repeated naming errors, B and Po, our data provide further evidence that the frontal opercular site is involved in the execution of the motoric aspects of signs and is agnostic as to whether sign forms are derived from self-generation (as in naming) or from copying another signer's rendition of these forms. Though the nonsign repetition data are limited, it would appear that the motor output affects complex sign formation independent of lexical–semantic content.

In contrast, the posterior opercular site appears highly specialized; disruption was found only in the context of a task in which S.T. was required to translate a picture of an object into a lexical sign name for that object. When the formational components of the sign are available to the subject (as in the case of copying

another individual's sign and nonsign forms), even under stimulation to site Po, the subject is able to combine these observed sign elements into coherent and accurate gestures for reproduction.

DISCUSSION

Linguistic Specificity of Broca's Area

In our study, stimulation to the posterior portion of Broca's area consistently affected the articulatory integrity of the sign and resulted in laxed and imperfect formation of the underlying sign target. The effects of motor execution on language output were observed for both object naming and sign repetition tasks. In addition, nonsign repetition was also compromised, thus ruling out the effects of lexical–semantic content in the observed disruptions.

Our results are consistent with the characterization of the posterior portion of Broca's area as participating in the motoric execution of complex articulatory forms, especially those underlying the phonetic level of language structure. Significantly, our sign language findings provide new insights into the functional specificity of posterior Broca's region. As noted, researchers have suggested that speech difficulties associated with damage to Broca's area may be related to the anatomical proximity of face and mouth cortex (Goodglass, 1993). As such, it is particularly informative that we observed these errors in sign language, a language that makes use of the hands and arms as the primary articulators. When we examine the stimulation map for motor and sensory function in this subject, it is evident that while Broca's area shares the expected anatomical proximity to mouth cortex, the site of hand representation is anatomically distant (Fig. 1). Thus, it is remarkable that stimulation of Broca's area leads to impairment in sign language execution, as these sign language errors cannot be accounted for by the proximity of Broca's area
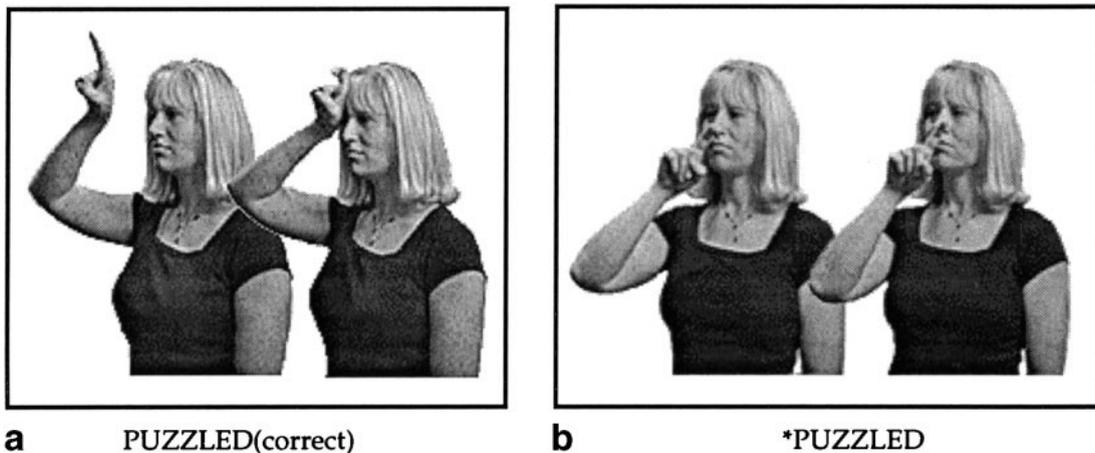

FIG. 6.   Site B sign repetition responses. (a) Correct repetition of the sign PUZZLED. (b) Under stimulation to site B, S.T.'s inaccurate repetition of the sign PUZZLED.

to the hand-motor representations within the Rolandic cortex. Taken together with previous findings, our data suggest that Broca's area may be participating in aspects of motor control that underlie the complex movements of the articulators used in the service of language, both spoken and signed. Though lacking the regional specificity of the present study, case studies of deaf signers with lesions including Broca's area corroborate this finding (Poizner *et al.,* 1987; Hickok *et al.,* 1996b).

It is interesting to note that recent functional imaging studies in hearing individuals have reported Broca's area activation during tasks outside the linguistic domain, specifically during tasks involving the perception of hand movements (Shulag *et al.,* 1994; Decety *et al.,* 1997; Grafton *et al.,* 1996). For example, Decety *et al.* (1997) reported significant activation of BA 45 during a PET study in which subjects watched meaningful pantomime. However, activation was not observed when subjects watched meaningless gestures. Grafton *et al.* (1996) reported activation of BA 45 when subjects observed the grasping of common objects, and activation of BA 44 was prominent when subjects were asked to imagine themselves grasping objects.

These findings have led some to argue that Broca's area function includes representational capacities related to action/recognition of oro-facial and brachio-manual behaviors (Rizzolatti and Arbib, 1998). Our results might be viewed as being consistent with this broader, more general characterization of Broca's area function. However, we believe the role of verbal mediation during imaging tasks involving observation of meaningful gestures requires further evaluation.

While the involvement of Broca's area in the perception of gestures has been explored, the contribution of frontal opercular regions to the motor *production* of complex hand movements has not been well established. In an early PET imaging study, Frith *et al.* (1991) reported activation in dorso-lateral prefrontal cortex that was attributed to "willed-action." This region was found to be active in cases when a subject chose to move one of two fingers on the right hand relative to a stimulus specified finger movement. In addition, this general region was found to be active during a verbal generation task relative to a verbal repetition task. Frith *et al.* (1991) interpreted this region as a modality-independent locus of willed action. More recent studies have questioned the modality independence of these data (Kapur *et al.,* 1994; Hyder *et al.,* 1997). For example, Hyder *et al.* (1997), using fMRI, have reported a locus of activity for a willed sensorimotor task (i.e., finger movement) in the middle frontal gyrus (BA 46) and a separate locus (BA 45) for a willed verbal task (i.e., verbal fluency).

It is unlikely that the production problems observed with stimulation of Broca's area in this subject reflect a deficit in the initiation of action. Anatomically, the locus of stimulation that disrupts signing is posterior and inferior to middle frontal gyrus activations observed in willed sensorimotor tasks (see Hyder *et al.,* 1997 for discussion). In addition, rather than a cessation of motor activity, S.T. produces goal directed movements to locations associated with the correct target sign, though, as reported, the articulatory details of the sign formation are compromised.

Finally, it is noteworthy that the deficits in sign production are evidenced in the *left* signing hand following stimulation to the left frontal opercular region; thus these output errors do not reflect primary motor or sensory deficits. Taken together these data clearly implicate a role for Broca's area in left-hand articulations of *linguistic* movement in this deaf signer.

SMG and Linguistic Feature Binding

In our study we localized stimulation of the SMG to the inferior portion of the sulcus lying between the posterior ascending ramus of the sylvian fissure and the inferior portion of the postcentral sulcus. Under stimulation to this portion of the SMG, our subject showed great selectional difficulties with hand postures and movements associated with individual signs. One important question concerns whether these errors are apraxic or aphasic in nature.

Left-hemisphere parietal lesions often are associated with limb apraxia—the impairment of the ability to carry out voluntary movement in the absence of sensory loss, paresis, or motor weakness. There is a wide range of symptomology that is associated with apraxic disorders and the literature is replete with inconsistent definitions. Apraxic symptoms can range from frank disorders of object use (which often fall under the rubric of ideational apraxia) to extremely subtle impairments, such as the inability to imitate meaningless gestures and hand postures (an impairment often associated with ideomotor apraxia).

In the present case of S.T., there are several indications that the deficits in signing observed with stimulation to the SMG reflect linguistic rather than apraxic impairment. For example, imitation of meaningless (and meaningful) movements is often used as a diagnostic measure of the ideomotor form of apraxia (De Renzi *et al.,* 1980). However, S.T. did not show impairments when asked to imitate nonsign or sign gestures—impairments were observed only during a task in which object naming was required. This precludes an analysis of these errors as stemming from an ideomotor apraxic deficit.

In the context of the naming task the predominant formational errors involve selectional difficulties with hand postures and movements. It is important to note that the hand shapes and movements that comprise these errors are chosen from the inventory of formational elements of American Sign Language. These affected formational elements (hand shape and move-

ment) correspond to two central parameters of ASL sign phonology and can be characterized as collections of distinctive features within a phonological representation (Corina and Sandler, 1993; Chomsky and Halle, 1968). These errors are not random selections of movements or hand shapes, but are constrained by the phonotactics of ASL. Taken together these data support an interpretation of the deficit following stimulation to the SMG as indicative of a linguistic, rather than an apraxic, impairment.

The finding that ASL selectional difficulties are observed with stimulation of the SMG is interesting in light of recent imaging and behavioral studies that have implicated parietal cortices in motor response selection (Rushworth *et al.,* 1997; Deiber *et al.,* 1991, 1996). Rushworth *et al.* (1997), for example, have suggested that impairment in selection of motor actions may underlie the sequencing deficits characteristic of ideational apraxics. Ideational apraxics may misorder, omit, or perseverate components of an action that is composed of a sequence of movements; for example, when asked to post a letter, a patient may properly fold the letter, but then seal the envelope before having put the letter inside. The proper completion of a complex action requires careful orchestration of the subcomponents of the overall task. In the case of S.T., with stimulation to the SMG we observe selectional difficulties involving the phonological subcomponents of a complex linguistic action. Thus, the SMG may be participating in a highly specialized form of response selection, one that is specific to language function.

In addition to the incorrect selection of phonological information, we observed semantic errors. Importantly, these semantic errors demonstrated considerable phonological overlap with their intended targets. In spoken language speech error data, semantic–phonological blends have been of significant theoretical interest in that they have been analyzed as evidence for a model of lexical representations in which semantic and phonological stages of lexical processing interact (Martin *et al.,* 1996; Dell and O'Seaghdha, 1992).

Taken together our data indicate that the SMG may play a critical role in the selection of phonological feature information and the association of this information with semantic representations in the service of language production. Lexical–semantic representations, like phonological representations, are often understood as collections of primitive semantic features (Katz, 1972). Additionally, a stage of processing in which lexical–semantic information (e.g., lemma representations) and phonological information are associated is well attested in influential models of language production (Garret, 1998; Levelt, 1989). The errors observed in S.T.'s signing during stimulation to this parietal opercular region may indicate a disjunction in the binding of lexical–semantic and phonological fea-

tures. Sign language semantic and phonological paraphasias (including semantic–formational blends) have been reported in case studies of aphasic deaf signers with lesions that include the SMG (Corina, 1998).

It is interesting to note that the anatomical locus of the SMG, the area that has given rise to these disjunctions in sign language, lies just above the posterior third of the superior temporal sulcus, a region often referred to as Wernicke's area. A recent MEG study of picture naming has implicated Wernicke's area (in particular the posterior third of the superior temporal gyrus) and the tempo-parietal junction as being involved in phonological encoding for spoken language and possibly participating in temporally adjacent processes (e.g., lemma selection, articulatory encoding) (Levelt *et al.,* 1998). The convergence of the current CSM study and the MEG study is notable; both reveal a stage of processing whereby phonological information and semantic information are associated during language production in response to a picture naming task. The question of whether the differences in anatomical location implicated across these two studies (i.e., SMG versus Wernicke's area) reflect normal variation, methodological differences, or language modality differences awaits further study.

CONCLUSION

The unusual case of S.T. provides important data that help to constrain and foster interpretation of the anatomical–functional relationships underlying human language. Our findings suggest that, as we seek to further specify the general functional nature of perisylvian language areas, it will be worthwhile to make use of the differences in human language as tools to clarify the regional specificities common to all languages.

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