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Brief reports

Role of left posterior superior temporal gyrus in phonological processing for speech perception and production

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Abstract

Models of both speech perception and speech production typically postulate a processing level that involves some form of phonological processing. There is disagreement, however, on the question of whether there are separate phonological systems for speech input versus speech output. We review a range of neuroscientific data that indicate that input and output phonological systems partially overlap. An important anatomical site of overlap appears to be the left posterior superior temporal gyrus. We then present the results of a new event-related functional magnetic resonance imaging (fMRI) experiment in which participants were asked to listen to and then (covertly) produce speech. In each participant, we found two regions in the left posterior superior temporal gyrus that responded both to the perception and production components of the task, suggesting that there is overlap in the neural systems that participate in phonological aspects of speech perception and speech production. The implications for neural models of verbal working memory are also discussed in connection with our findings. © 2001 Cognitive Science Society, Inc. All rights reserved.

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1. Introduction

Models of both speech perception and speech production typically postulate a processing level that involves some form of phonological processing, that is, accessing/assembling

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segmental and syllabic information. There is disagreement, however, on the question of whether there are separate phonological systems for perception versus production (Dell, Schwartz, Martin, Saffran & Gagnon, 1997; Levelt, Roelofs & Meyer, 1999), or whether a single system participates in phonological processing for both the input and output of speech (Allport, 1984; MacKay, 1987; Coleman, 1998). Clues relevant to this issue can be found in neuropsychological and neurophysiological studies, both old and new. Specifically, data from a variety of experiments converge on the view that there is a cortical region in the left posterior superior temporal lobe that participates in phonemic aspects of both speech perception and speech production (Coleman, 1998; Hickok, 2000; Hickok & Poeppel, 2000). In what follows, we review the evidence and then discuss a functional magnetic resonance imaging (fMRI) study that was designed to test this hypothesis directly.

An early hypothesis about the relation between speech perception and production processes, and their neural basis, comes from Wernicke (1874/1977). Based on his observation that sensory aphasics (today called Wernicke's aphasics) have fluent but disordered speech production alongside their poor auditory comprehension, Wernicke hypothesized that the left superior temporal gyrus plays an important role in both speech perception and speech production. In particular, he argued that the same "auditory word images" that are activated in the perception of speech are also activated during the production of speech. Wernicke believed that the activation of the auditory representation of words during production helped constrain the selection of the appropriate "motor word image." When these auditory word images are disrupted, as in sensory aphasia, or when the anatomical pathway connecting auditory and motor systems is disrupted, as he assumed in the case of conduction aphasia, the selection of motor word images is no longer appropriately constrained, and disordered (i.e., paraphasic) speech output is the result.

Wernicke's observation that damage to the left superior temporal lobe produces both deficits in speech comprehension and speech production has been repeatedly confirmed in modern clinical aphasiology (Damasio, 1992; Goodglass, 1993). Despite these observed parallels between perception and production deficits, however, psycholinguistic models have not uniformly embraced the idea that there is overlap in systems involved in phonemic aspects of speech perception and production. Nor has the relation between perception and production been a prominent topic of investigation in research on the neuroanatomy of phoneme-level processing: with only a few exceptions (e.g., Price et al., 1996; Papathanassiou et al., 2000), most current work focuses independently on either speech perception or speech production. But an examination of the neuroscience literature in these two domains reveals that *both* lines of investigation have identified the left posterior superior temporal lobe as a region that participates in phonemic-level processes (although it is not the only region).

On the perceptual side, functional imaging studies using a variety of methodologies have consistently found activation of the posterior superior temporal gyrus (in fact, *bilateral activation*; see below) (Binder et al., 1994; Dhankhar et al., 1997; Gage, Poeppel, Roberts & Hickok, 1998; Kuriki, Okita & Hirata, 1995; Mazoyer et al., 1993; Petersen, Fox, Posner, Mintun & Raichle, 1988; Poeppel et al., 1996; Price et al., 1996; Schlosser, Aoyagi, Fulbright, Gore & McCarthy, 1998; Zatorre, Meyer, Gjedde & Evans, 1996). Although other areas have been implicated in phonemic-level aspects of speech perception, the posterior

superior temporal gyrus (pSTG) is the most consistently observed area of activation in functional imaging studies (Hickok & Poeppel, 2000). Cortical stimulation of the pSTG, but not the anterior STG or middle temporal gyrus, has been found to interrupt speech perception (Boatman, Lesser & Gordon, 1995), and intraoperative single unit recordings in the STG (also bilaterally) have revealed cells that respond selectively to speech stimuli (Creutzfeldt, Ojemann & Lettich, 1989). Finally, pure word deafness, a syndrome that appears to reflect a profound low-level deficit in speech perception (Bachman & Albert, 1988), is most commonly associated with lesions involving the STG (again bilaterally) (Buchman, Garron, Trost-Cardamone, Wichter, & Schwartz, 1986).

On the production side, a major source of evidence for the involvement of the pSTG comes from conduction aphasia (Hickok, 2000). Conduction aphasia is a disorder characterized by good auditory comprehension, fluent production punctuated by predominantly phonemic paraphasias, and naming difficulty (Damasio, 1992). Verbatim repetition of heard speech is also impaired, but although this symptom has gained clinical prominence in the diagnosis of conduction aphasia, speech-production difficulties are not limited to repetition tasks (Goodglass, 1992). Classically, conduction aphasia is thought to result from a disconnection of anterior and posterior language areas caused by damage to a white matter fiber bundle, the arcuate fasciculus (Geschwind, 1965), but recent work has suggested that conduction aphasia is a disorder of cortical dysfunction, rather than a disconnection syndrome (Anderson et al., 1999; Hickok, 2000). There are two lesion patterns associated with conduction aphasia. The pattern referred to most often in discussions of conduction aphasia is that involving the left supramarginal gyrus and underlying white matter, which includes the arcuate fasciculus. But conduction aphasia can also be caused by damage involving the left posterior superior temporal gyrus with the supramarginal gyrus and arcuate fasciculus completely spared (Damasio & Damasio, 1980). In fact, a recent study has shown that conduction aphasia-like symptoms, including phonemic paraphasias, can be induced by direct electrical stimulation of the lateral surface of the posterior superior temporal gyrus (Anderson et al., 1999). The fact that a defining symptom of conduction aphasia is a predominance of phonemic paraphasias—some authors view conduction aphasia as a disorder of phonemic encoding for production (Wilshire & McCarthy, 1996)—and that conduction aphasia can be caused by lesions involving the pSTG suggests that this cortical region is involved in phonemic aspects of speech production. In addition, the observation that naming problems in conduction aphasia often resemble tip-of-the-tongue states (Goodglass, Kaplan, Weintraub & Ackerman, 1976) is also supportive of a link between conduction aphasia and the phonological encoding stage of speech production because tip-of-the-tongue phenomena have been linked to breakdowns in phonological encoding (Vigliocco, Antonini & Garrett, 1998).¹

There is converging evidence from other sources that suggests a role for the pSTG in aspects of speech production. A transcranial magnetic stimulation study showed that picture naming can be facilitated by delivering a stimulation pulse to the left (but not right) pSTG region 500 to 1000 ms before picture presentation (Töpper, Mottaghy, Brüggemann, Noth & Huber, 1998). Functional imaging studies have reported activation in the pSTG in tasks that have a speech-production component (overt or covert), including reading (Price et al., 1996), word generation (Wise et al., 1991), object naming (Bookheimer, Zeffiro, Blaxton, Gaillard

& Theodore, 1995; Hickok et al., 1999), and syllable rehearsal (Paus, Perry, Zatorre, Worsley & Evans, 1996). Moreover, a recent study with magnetoencephalography (MEG) suggests that the activation of the pSTG during speech production has a time course consistent with the phonological encoding stage (Levelt, Praamstra, Meyer, Helenius & Salmelin, 1998). On the basis of an extensive review of functional imaging studies of word production, Indefrey & Levelt (2000) conclude that the left pSTG is part of a network important for phonological code retrieval. They also suggest that the region may play a similar function for speech comprehension.

To sum up so far, there is evidence pointing to the left pSTG generally as a site important for phonemic-level aspects of both speech perception and production. But are the same cortical fields involved in both perception and production as Wernicke claimed? Or are the systems involved in perception and production supported by distinct subfields within the pSTG? At least one study that looked, within subject, at the overlap of activations associated with speech perception and speech production indeed suggests that the same areas are involved in both processes. Papathanassiou et al. (2000) examined overlap in activations associated with speech-perception (listening to stories) and speech-production (generating verbs associated with heard nouns) tasks. They identified a large region of overlap centered on the pSTG (as well as some additional areas).

The goal of the present experiment was to test further the hypothesis that the left pSTG participates in both the perception and production of speech. Toward this end, we used an event-related fMRI paradigm and tasks that involved speech perception and speech production, as well as working memory (Baddeley, 1992).

2. Methods

2.1. *Subjects and task*

Seven right-handed subjects between the ages of 20 and 29 years (four female, three male) participated in the study and gave informed written consent. Subjects were studied in an event-related fMRI paradigm (Buckner et al., 1996; Hickok, Love, Swinney, Wong & Buxton, 1997) using a task that involved both speech-perception and speech-production components. Specifically, subjects were presented with 24 trials that comprised the following sequence of events: Three multisyllabic pseudowords were presented auditorily at a rate of one per second. Subjects then rehearsed the list silently for 27 s; subjects were cued to stop rehearsing by a tone of 500-ms duration. The tone was followed by an 18-s rest period, and then a new trial was initiated. A different set of three multisyllabic pseudowords was used in each trial. We used multisyllabic pseudowords to maximize the load on phonological processing systems. The rather long duration of the rehearsal period was selected so that we could be sure that activation during that period was associated with the rehearsal and not merely lingering activation secondary to the perceptual phase of the task.

We predicted three activation patterns: (1) A perceptual-dominant response pattern in which activation levels would increase during the auditory stimulation but not during the motor component; (2) a motor-dominant response pattern in which activation levels would

increase during the rehearsal phase; and (3) a perceptual-motor response pattern in which activation levels would remain active during both the perceptual and motor phases of the task. We expected perceptual-dominant responses in early auditory cortical fields bilaterally, motor-dominant responses in left frontal cortex, and combined perceptual-motor responses in the left pSTG. Cells responsive to auditory stimuli have been documented in monkey frontal cortex, particularly when those sensory inputs are of behavioral significance (Watanabe, 1992), raising the additional possibility that we might also observe combined responses in some left frontal regions in our study.

2.2. *Imaging procedures*

Scanning was conducted at 1.5 Tesla on a Siemens Vision MRI scanner and used a gradient-echo echo-planar imaging (EPI) sequence with the following parameters: echo time = 40, repetition time = 3 s, field of view = 256 mm, matrix = 64 h 64, voxel dimensions = 6 h 4 h 4 (mm). Sixteen (6 mm thick) contiguous axial slices were acquired so as to easily cover brain regions relevant to the study. Before scanning, subjects were fitted with magnet-safe headphones connected by plastic air tubes to the delivery system (Macintosh Powerbook) set up in the control room. Subjects were then scanned in three 7-min intervals, each of which consisted of eight trials and 133 image acquisitions per slice. The first five image volumes for each scanning session were not task related and served to allow the signal to reach steady state. Following the three experimental sessions, all subjects received a high-resolution (180 sagittal slices, voxel dimensions = 1 mm, 1 mm, 1 mm) MP-RAGE (magnetization-prepared rapid gradient echo) scan for use as an anatomically detailed background for statistical activation maps.

For each subject, the entire sequence of EPI image volumes was realigned to the first of the session using a six-parameter rigid-body three-dimensional motion-correction algorithm (Woods, Grafton, Holmes, Cherry & Mazziotta, 1998). Next, a high-pass filter with a window size of 25 time steps was applied to each functional time series to remove temporal drift and slowly recurring sources of noise in the BOLD (blood oxygenation level determination) signal. A low-pass filter (finite impulse response, filter width = 1.5 time steps) was then used to remove high-frequency artifacts such as those introduced by respiration. Both filters and their parameters were chosen on the basis of results obtained by Kruggel, von Cramon, & Descombes (1998) in their comparison of a variety of signal-restoration procedures for fMRI data analysis. Finally, after coregistration of the EPI images to the MP-RAGE structural MRI, both sets of images were transformed into standardized Talairach-Tournoux (Talairach & Tournoux, 1988) space using a 105 parameter nonlinear warping algorithm (Woods, Grafton, Watson, Sicotte & Mazziotta, 1998).

2.3. *Statistical analysis*

To test the hypothesis that a single brain area would sustain its activation across two temporally continuous, but qualitatively different, components of the task, we used a series of regression models to search for the linear combination of regressors that best explained the variance in a given voxel. A separate predictor variable was generated for each component

of the task that was expected to elicit a BOLD response, namely, (1) the hearing of the three pseudowords, (2) the silent repetition phase, and (3) the 500-ms burst of noise. A model of the approximate hemodynamic response was generated for each component by convolving its dummy variable representation (on = 1, off = 0) over the trial epoch with a Gaussian model of the hemodynamic response function using experimentally derived values (dispersion = 1.8 s, delay = 4.8 s) (Clark, Maisog & Haxby, 1998). The validity of the preceding procedure rests on the assumption that the hemodynamic response to a sequence of impulses (or a stimulus of extended duration) is linearly additive (Boynton, Engel, Glover & Heeger, 1996; Dale & Buckner, 1997), and that the shape of a Gaussian density function is a fair match for the BOLD response (Rajapakse, Kruggel, Maisog & von Cramon, 1998). The generated models were then used as independent variables and entered into a stepwise multiple regression algorithm (Neter, 1985) that searched for the weighted sum of the variables that best fit the obtained time series. Those predictors for which inclusion in the model yielded a regression coefficient with $p < .0001$ (uncorrected) were determined to be significant.

For every subject, statistical probability maps (SPM) were created for each of the three task components, using the t score of the regression coefficient to represent the magnitude of significance for each brain voxel. An F map was then created that showed the model significance for those voxels with significant regression coefficients for *both* components one and two (pseudoword presentation + articulation) of the task, thus delineating areas that are best modeled by a linear combination of the first two regressors. The third component of the task, the noise burst, though included in the regression analysis, played a purely functional role in the experiment, and therefore its independent statistical contribution was not systematically examined.

3. Results

Very clear perceptual-dominant responses were seen bilaterally in regions that appear to correspond to primary auditory cortex and surrounding fields, as well as some frontal and parietal regions. Motor-dominant responses were also observed in a variety of areas, predominantly in the left hemisphere, which in various subjects included lateral premotor cortex and inferior frontal cortex, as well as temporal lobe regions. (See Fig. 1 for sample data from a single subject.) Of primary interest for the present study, however, was the observation in each participant of regions in the left pSTG that showed a combined perceptual-motor response pattern (Figs. 1 and 2). Six of the seven participants showed two clearly distinct posterior superior temporal lobe sites (the remaining subject showed a larger activation that encompassed both regions, although there were separate peaks within that larger activation). One site was centered in the superior temporal sulcus (STS) and/or lateral pSTG; the other was on the dorsal pSTG/parietal operculum (PO). The location of the dorsal pSTG foci was centered in the depths of the Sylvian fissure at its posterior-most extent at the boundary between the temporal and parietal lobes. Some subjects also showed the STS activation in the right hemisphere; no subject, however, showed the dorsal pSTG/parietal operculum activation in the right hemisphere. As expected, we also noted combined perceptual-motor

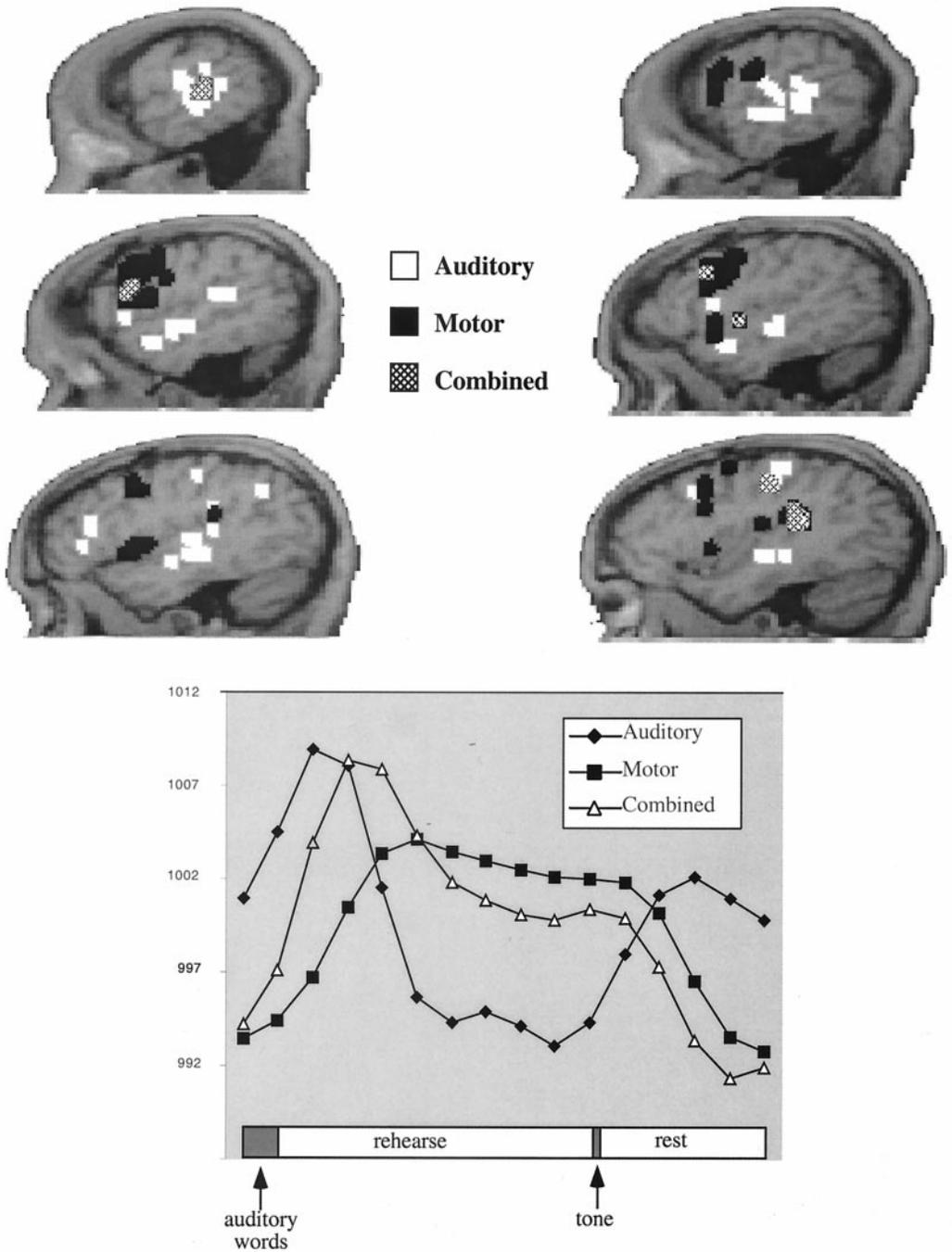


Fig. 1. Data from a single participant showing the distribution of voxels in six left hemisphere sections which showed a perceptual-dominant response (white), motor-dominant response (black), and a combined perceptual-motor response pattern (hatched). The graph shows samples of the temporal response for the three patterns.

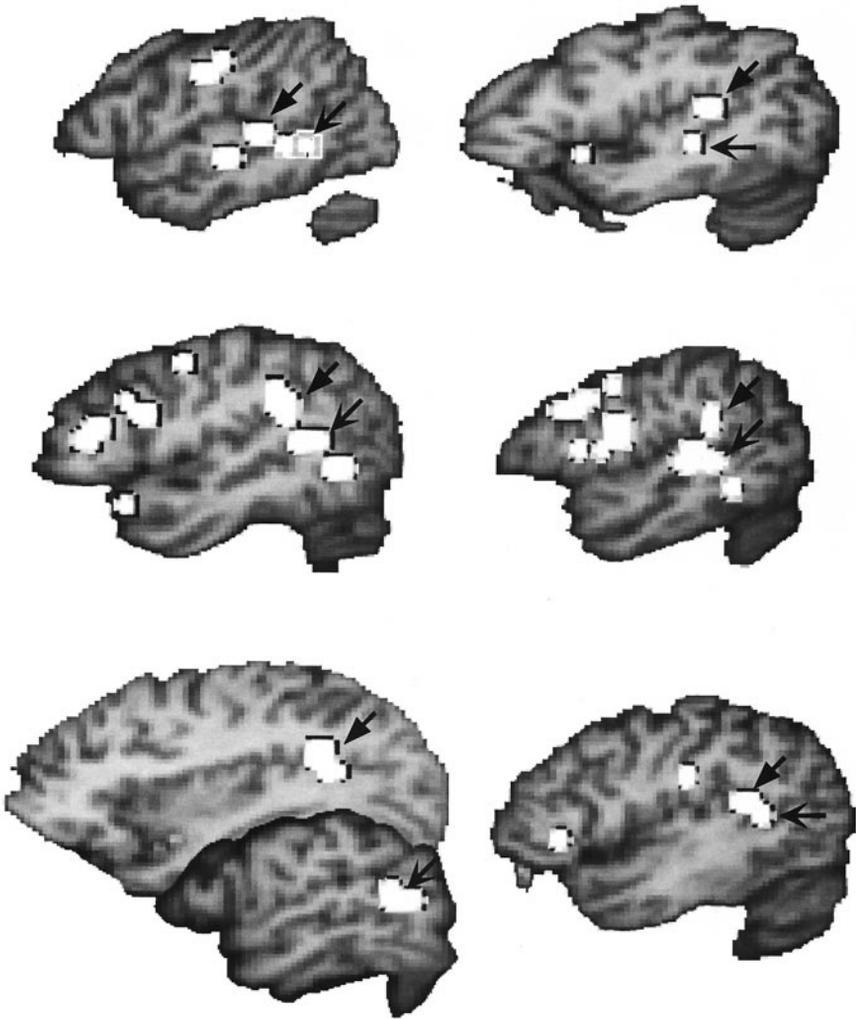


Fig. 2. Left hemisphere sagittal sections from each participant showing the distribution of combined perceptual-motor responses. Note the presence of a dorsal posterior superior temporal gyrus (pSTG) site (solid arrows) and a more ventral posterior superior temporal sulcus (pSTS) site (open arrows) in each subject.

response patterns in left frontal cortex. Two sites were activated in every subject: a lateral premotor site, and an inferior frontal site roughly corresponding to Broca's area.

Visual inspection of the time course of activation in the two posterior sites suggested subtle differences. To explore the possibility of different activation patterns in the dorsal and ventral pSTG sites, we examined the averaged time course of activated pixels from each of these two clusters in six of the seven participants (the remaining subject did not show a clear differentiation of the two regions). Fig. 3 (left panel) shows a sample of the activation sites in one subject and the time course of activation in both regions averaged across subjects. Notice that the STS site tended to show a more robust auditory activation than did the dorsal pSTG/PO site (this held true for four of the six subjects but did not reach significance; $p =$

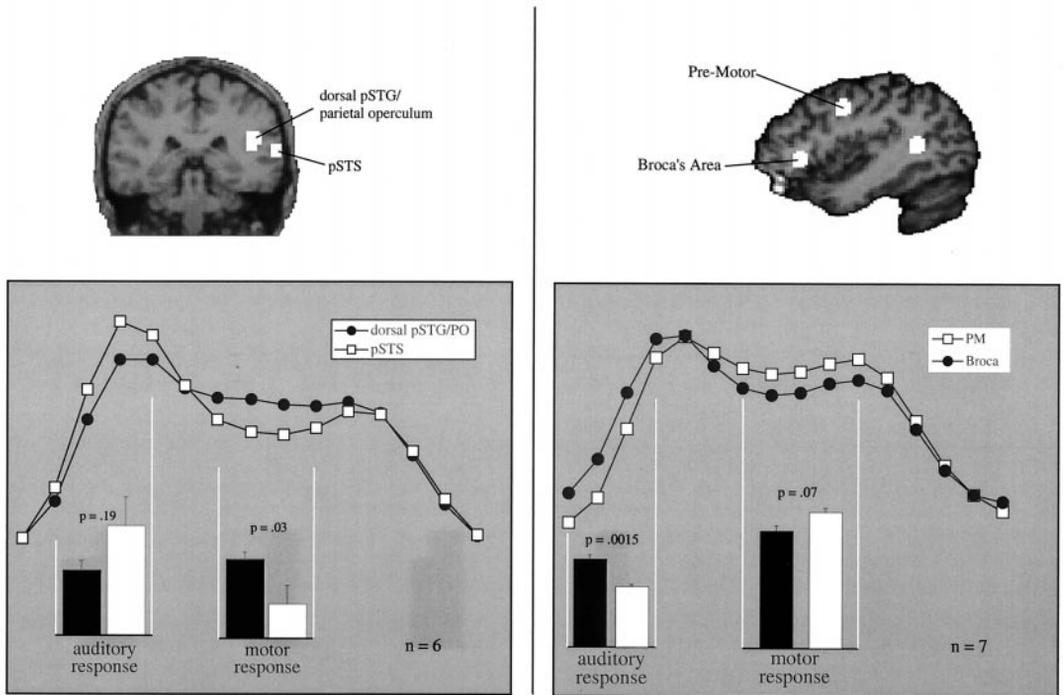


Fig. 3. Different temporal response patterns between the two left-temporal lobe (left panel) regions and between the two left-frontal lobe (right panel) regions that showed a combined perceptual-motor response. The temporal response data are averaged across subjects. Bar graphs represent the mean amplitude, and standard error, of the response of the two regions averaged over several acquisition time points indicated by the white vertical lines. Sample locations (top of each panel) are from an individual subject.

.19, two-tailed), whereas the dorsal pSTG/PO site showed a more robust activation during the rehearsal phase of the trial (this held for every subject and was statistically reliable; $p = .03$, two-tailed).

The two frontal sites that showed a combined auditory-motor response also appeared to differ somewhat in their response pattern on visual inspection. We examined these differences by taking the average time course of activated pixels from each of these two clusters in each of the seven participants. Fig. 3 (right panel) shows a sample of the activation sites in one subject and the time course of activation in both regions averaged across subjects. Broca's area demonstrated an earlier response in the auditory phase of the task than did the premotor site (seven of seven subjects; $p = .0015$, two-tailed), whereas the premotor site tended to be more active during the motor phase of the task (six of seven subjects; $p = .07$, two-tailed).

For comparison, Fig. 4 presents the time course of activation for the four combined response regions. The pSTS and premotor sites are at the extremes in their activation patterns—pSTS showing the most vigorous auditory response and weakest motor response, and premotor showing the reverse pattern—with pSTG/PO and Broca's area falling in between with very similar response patterns. Table 1 presents a correlation matrix reflecting

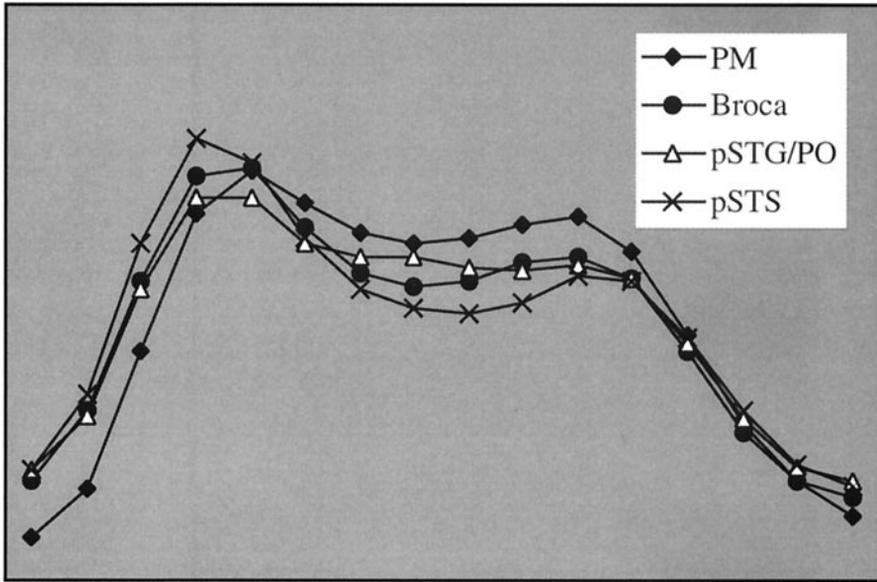


Fig. 4. Group-averaged response patterns in each of four left hemisphere regions. Note the diverging responses of the perceptual-motor (PM) and posterior superior temporal sulcus (pSTS) regions, and the similarity of response patterns between Broca's area and posterior superior temporal gyrus (pSTG)/parietal operculum (PO).

the relation between the four regional activation patterns pictured in Fig. 4. As Fig. 4 indicates, the pSTS and premotor activation patterns are the least correlated, whereas the pSTG/PO and Broca's area activations are very tightly coupled: r value > 0.99 .

4. Discussion

Results from a variety of studies, including the present experiment, suggest the existence of cortical fields in the left pSTG that participate both in speech perception and in speech production. Although we cannot, on the basis of the present experiment alone, determine the nature of the computational operations involved in this joint perception/production activation, evidence from other sources suggests that the pSTG is involved in phonological

Table 1

Correlation matrix between the four regions showing a combined perceptual-motor response pattern

	Broca	pSTG/PO	pSTS
PM	0.951	0.970	0.880
Broca		0.992	0.977
pSTG/PO			0.955

PM, premotor; Broca, Broca's area; pSTG, posterior superior temporal gyrus; PO, parietal operculum; pSTS, superior temporal sulcus.

processing of some sort (reviewed in section 1). We therefore hypothesize that the joint activation found in the present study in the pSTG reflects the activity of cortical systems involved in some aspect of phonological processing. This result, therefore, supports psycholinguistic models that posit overlap in the phonological input and output systems.

We do not believe, however, that there is complete overlap in the phonological input/output systems. For example, a host of findings make the case for *bilateral* involvement in speech perception (Hickok & Poeppel, 2000). Relevant findings include observations that phonemic perception is not profoundly impaired by damage to the left pSTG (or, in fact, to left perisylvian cortex more generally), that the isolated right hemisphere can process phonemic information fairly accurately, and that physiological indices record largely bilateral and symmetric pSTG activations in response to auditorily presented speech. These observations suggest that there are systems in the right pSTG that can support phonological processing in the reception of speech, but play a lesser role in the production of speech. Likewise, there appear to be left frontal regions that play a greater role in speech production than they do in speech perception. Broca's area, for example, is traditionally associated with output processes yet probably plays a lesser role in phonemic aspects of speech perception (Hickok & Poeppel, 2000), and there is evidence from lesion (Dronkers, 1996) and functional imaging studies (Wise, Greene, Büchel & Scott, 1999) indicating that the anterior insula is associated with speech production, which may include phonological aspects. In fact, Indefrey and Levelt (2000) have suggested that access to phonological codes may be supported by the left pSTG, whereas processes such as syllabification may be supported by left frontal structures.

Different activation patterns were observed in the two left temporal lobe regions, which showed a combined perceptual-motor response. In particular, the left dorsal pSTG/PO site consistently showed a stronger activation during the rehearsal phase of the task than did the left pSTS site. The pSTS site, on the other hand, tended to show a more robust response during the perceptual phase of the task. One interpretation of these functional differences is that the pSTS site is part of a ventral processing stream involved in processing speech information for the purpose of comprehension, whereas the pSTG/PO site is part of a dorsal processing stream involved in auditory-motor integration in speech. Hickok & Poeppel (2000) have argued for such a dorsal-ventral distinction in speech processing and have suggested that verbal working memory tasks (as in the present experiment) draw on the resources of both streams. The argument goes as follows. Verbal working memory is a system in which articulatory mechanisms (articulatory rehearsal) are used to keep sensory information (phonological storage) active during a retention period. A prominent view of the neuroanatomy of this system is that the articulatory rehearsal mechanism involves a left frontal circuit (Broca's area and prefrontal cortex), whereas the phonological store component involves the inferior parietal lobe (Jonides et al., 1998). Hickok & Poeppel (2000), however, have suggested a different interpretation of the parietal activation in verbal working memory tasks. They suggest that the parietal activation is not the phonological store, per se, but rather a sensory-motor integration system (analogous to similar parietal lobe systems in the visuo-motor domain) that mediates between frontal-articulatory systems and temporal lobe sensory systems in which phonological information is represented. The present result is consistent with this view because activation was noted both in a dorsal temporal/inferior

parietal site and in a more ventral STG site. The tendency of the ventral STG region to show a more strongly perceptual-weighted response is consistent with this interpretation. Also consistent with this proposal is the demonstration in the visual domain that both dorsal and ventral streams play a role in working memory. Single units in the both the ventral (Fuster & Jurvey, 1981) and dorsal (Murata, Gallese, Kaseda & Sakata, 1996) streams have been found to have short-term memory properties, responding not only to sensory stimulation but also during a subsequent delay in delayed response tasks. More directly, Milner & Goodale (1995) have argued from neuropsychological data for an interaction between dorsal and ventral streams in a delayed grasping task.

As single unit data led us to predict, combined perceptual-motor responses were also consistently observed in two left frontal regions, Broca's area and a premotor region. The activation patterns in these two frontal regions differed, however, with the premotor region producing a more sluggish response to the auditory stimulation, but a more robust response during the rehearsal phase. Both Broca's area and more dorsal frontal activation sites have been reported in verbal working memory tasks (Awh et al., 1996). The relative roles of these two frontal regions are not yet clear, but the pattern of activation in the present experiment—in particular, the very high correlation between Broca's area and the pSTG/PO activation time course—suggests that there is a tighter functional relation between posterior superior temporal regions and Broca's area than between posterior temporal regions and premotor cortex. Histological data support this interpretation. The posterior superior temporal lobe regions showing combined perceptual and motor responses in the present study correspond to area Tpt (Galaburda & Sanides, 1980), a region that shares cytoarchitectonic features with Brodmann Area 44 (Broca's area). In a review of this evidence, Galaburda (1982) states that area Tpt “. . .exhibits a degree of specialization like that of Area 44 in Broca's region. It contains prominent pyramids in layer IIIc and a broad lamina IV. . . . Thus 44 and Tpt are equivalent transitional areas between the paramotor and the generalized cortices of the prefrontal area, and between parakoniocortex and the temporoparietal occipital junction areas, respectively. . . the intimate relationship and similar evolutionary status of Areas 44 and Tpt allow for a certain functional overlap. In fact, architectonic similarities between anterior or posterior language areas, and the overlap in their connective organization make it a somewhat surprising finding that lesions in either region produce such different aphasic syndromes” (Galaburda, 1982). The nearly identical response patterns found between pSTG/PO and Broca's area in the present study are consistent with Galaburda's observations.

In summary, findings in the present experiment, together with those in a host of studies using a variety of methodologies, suggest that the left pSTG contains subfields that participate in phonological aspects of both speech perception and production. The evidence also indicates that the overlap between phonological input and output systems is partial. This arrangement, with overlapping, but nonidentical systems, may explain why previous work has found evidence both for shared input/output phonemic-level systems and for separable input/output systems. This work also suggests functional distinctions between pSTG regions that may correspond to divergent dorsal and ventral processing streams in speech and language (Hickok & Poeppel, 2000). The dorsal stream appears to involve cortex in the

dorsal pSTG/PO and likely projects to Broca's area, which itself is part of a frontal network involving more dorsal structures; this frontoparietal network serves to interface sound-based representation of speech with motor-based representations of speech. The ventral stream is less lateralized (particularly upstream in the processing hierarchy) and involves cortex in pSTS, which may project posteriorly to temporal-parietal-occipital structures involved in interfacing sound-based representations with conceptual representations. Both of these superior temporal lobe regions play a role in phonemic aspects of speech production, although probably serving different functions.

Notes

1. Psycholinguistic characterizations of conduction aphasia typically implicate only phonemic aspects of speech *production*. We are suggesting, however, that the region damaged in (at least one form of) conduction aphasia also plays a role in speech perception. If this region is involved in both perception and production, why is auditory comprehension in conduction aphasia largely preserved? Hickok & Poeppel (2000) have argued, on the basis of a range of data, that speech-perception systems are largely bilaterally organized, whereas speech-production systems are more strongly lateralized to the left hemisphere. This hypothesis explains the dissociation between perception and production in conduction aphasia (Hickok, 2000).

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