Listening to speech activates motor areas involved in speech production

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To examine the role of motor areas in speech perception, we carried out a functional magnetic resonance imaging (fMRI) study in which subjects listened passively to monosyllables and produced the same speech sounds. Listening to speech activated bilaterally a superior portion of ventral premotor cortex that largely overlapped a speech production motor area centered just posteriorly on the border of Brodmann areas 4a and 6, which we distinguished from a more ventral speech production area centered in area 4p. Our findings support the view that the motor system is recruited in mapping acoustic inputs to a phonetic code.

Language depends on the maintenance of parity between acoustic and articulatory representations: there must be a common phonetic code[1]. Phonemes are organized in terms of distinct features that are primarily defined by articulatory properties; for instance, /p/ is a voiceless bilabial stop consonant. If the common phonetic code has motor properties, then the motor system could be involved in perceiving speech, as a transformation must be made from the acoustic signal to a phonetic representation. Recent work on mirror neurons has revitalized interest in the idea that motor areas are involved in perceptual processes[2]. Most neuroimaging studies of speech perception, however, have focused on characterizing the strong responses consistently observed in the superior temporal lobe[3,4]. Frontal areas have sometimes been reported to be activated by passive listening to speech[3,5] and are often responsive during audiovisual speech perception[6], but the potential motor properties of the areas found in these studies have not been investigated. Although Broca's area is frequently implicated in studies involving phonological tasks or syntactic comprehension, it is presumed to be important for higher levels of linguistic processing[7]. Two studies using transcranial magnetic stimulation (TMS) have reported facilitation of tongue[8] and lip[9] muscles when subjects listened to speech; however, the precise brain areas involved are not known owing to limitations of spatial localization with TMS.

We used fMRI to examine whether passive listening to meaningless monosyllables activates motor areas involved in producing speech. Ten subjects listened to 16-s blocks, each containing 23 repetitions of a meaningless monosyllable. During the same scanning sessions, subjects were cued to produce the same syllables. The motor tasks lasted only 3 s; to avoid movement artifacts, we discarded volumes acquired during actual motor activity and analyzed subsequent volumes in which the delayed hemodynamic response occurred. Eight of the ten subjects also listened to blocks of control nonspeech stimuli: a burst of white noise or a bell, and carried out a bimanual motor task. Details are provided in **Supplementary Methods** online.

In all ten subjects, regions in the precentral gyrus, extending into the anterior bank of the central sulcus, were significantly activated by listening to speech, as compared to rest (**Fig. 1**). These activations were
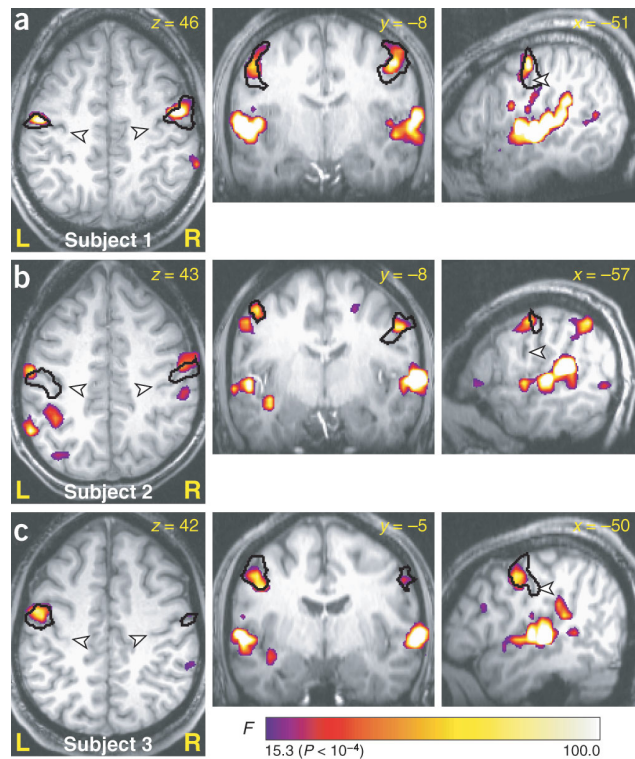

Figure 1 Areas activated by passive listening to meaningless monosyllables in three representative subjects. Individual activation maps were thresholded at $P < 10^{-4}$ (uncorrected) for listening conditions or $P < 10^{-12}$ for motor conditions, with a minimum cluster size of 300 mm^3. Mean Montreal Neurological Institute (MNI) coordinates for centers of mass of areas activated by listening to speech were (–50, –6, 47; left) and (55, –3, 45; right). The regions outlined in black show premotor and primary motor cortical activity while producing the same syllables. Other areas were also activated in the motor conditions, but are not shown. Arrowheads show the location of the central sulcus. Motor areas activated by both speech perception and production were observed in every subject. Extensive activations in the superior temporal gyrus and surrounding areas were also observed in all subjects. All participants gave informed consent, and the study was approved by the UCLA and UCSD institutional review boards.

located primarily in the superior part of ventral premotor cortex (PMv), extending toward primary motor cortex (see below). Activations were bilateral in four subjects, left-lateralized in two and right-lateralized in four. At lower thresholds or with reduced minimum cluster sizes, however, responses were bilateral for all subjects. Other activated areas are reported in **Supplementary Table 1** online.

Motor areas activated by production of the same syllables are shown in **Figure 1** (outlined in black; see also **Supplementary Table 1**). Motor responses were bilateral in all subjects. Comparison of the regions activated by listening to and producing the syllables showed substantial overlap for all subjects. Across subjects, $73 \pm 7\%$ of voxels in precentral gyrus and central sulcus regions activated by listening to speech were also activated by speech production. We defined regions of interest for each subject as clusters of voxels in the precentral gyrus or central sulcus that were responsive to either listening to speech or listening to

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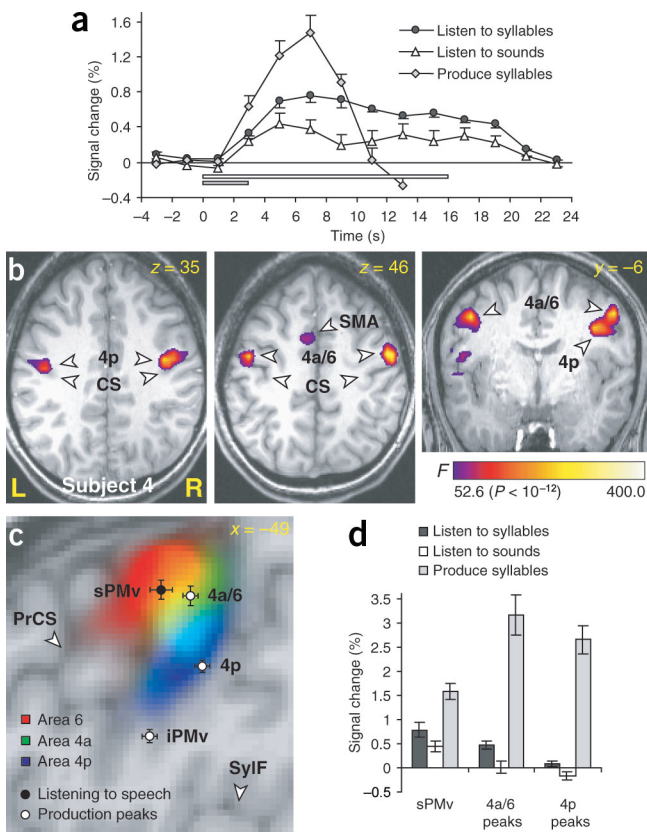
Figure 2 Characterization of the relationships between listening and motor areas. (**a**) Hemodynamic responses in motor regions that were responsive to listening to either speech or nonspeech ($P < 10^{-4}$). The bars show the time periods during which auditory stimuli were presented (16 s) and during which subjects were producing speech (3 s). Error bars here and in other panels represent s.e.m. (**b**) Motor areas for speech production in areas 4p and 4a/6 in a representative subject. In the coronal view, two distinct peaks can be seen in the right hemisphere, but in the left hemisphere, area 4p cannot be seen as it is posterior to the plane. Across subjects, the mean MNI coordinates of the 4p peaks were (–45, –13, 34; left) and (48, –10, 35; right), and of the 4a/6 peaks (–51, –11, 46; left) and (56, –8, 44; right). CS, central sulcus; SMA, supplementary motor area. (**c**) The locations of listening and production peaks overlaid on probabilistic cytoarchitectonic maps of areas 4a, 4p and 6 in the left hemisphere. The peaks lay close to the plane shown ($x = -49$). The map for the right hemisphere was similar. sPMv, superior PMv; iPMv, inferior PMv; PrCS, precentral sulcus; SylF, Sylvian fissure. (**d**) Maximum percent signal change by condition for three of the peaks in panel **c**.

4p in motor imagery[13]. The bimanual task allowed us to confirm that these motor areas are specific to the mouth. Finger/hand motor areas responsive to the bimanual task were located medial, posterior and superior to the regions activated for listening to and producing speech (**Supplementary Table 1**).

These findings are consistent with the view that speech perception involves the motor system in a process of auditory-to-articulatory mapping to access a phonetic code with motor properties[1]. Whether or not the superior PMv region we identified is necessary for normal speech perception is not known. Frontal lesions can severely compromise speech perception[14], but which lesions in particular lead to perception deficits is not clear. In addition to responding robustly to speech, the superior PMv region also showed diminished responses to nonspeech sounds. Premotor cortex is involved in coding attended environmental features, including auditory stimuli, in a body-based but highly abstract form[15], and the level of activity in this region may reflect the extent to which an articulatory representation can be obtained for any acoustic input.

Note: Supplementary information is available on the Nature Neuroscience website.

nonspeech sounds, and then plotted the mean time course (**Fig. 2a**). A robust response to speech production confirmed the motor properties of these listening-responsive voxels, and activity was much greater for speech than for nonspeech sounds.

Closer examination of speech production–related activity revealed several distinct peaks within each cluster. In 16 of 20 hemispheres, we observed a ventral peak with $30 \leq z \leq 39$ and a dorsal peak with $40 \leq z \leq 50$ (except in two hemispheres where this peak was a few millimeters more dorsal). The ventral peaks were located deep in the central sulcus, whereas the dorsal peaks lay more laterally on the anterior lip of the sulcus (**Fig. 2b**); activations always spanned the central sulcus, but distinct sensory peaks were never observed. Based on probabilistic cytoarchitectonic maps[10,11], the ventral peaks were located in Brodmann area 4p, whereas the dorsal peaks lay on the border of areas 4a and 6 (**Fig. 2c**). Previous imaging studies of speech production have not distinguished two areas and generally report group-averaged peak coordinates that lie between the two peaks we observed[12].

In relation to these peaks for speech production, the mean center of mass for listening to speech was located 4.5 ± 0.7 mm anterior to the area 4a/6 production peak ($P = 0.0005$) but not significantly medial, lateral, superior or inferior to it (all Ps > 0.05). This slightly anterior location means that it falls most likely in area 6, in the superior portion of PMv[2] (**Fig. 2c**). Note that an inferior region of PMv is also involved in speech production[12] (see location in **Fig. 2c**), but this region did not respond to listening to speech. We next examined listening responses in peak production voxels (**Fig. 2d**). Peak area 4a/6 voxels responded to listening to speech but not nonspeech sounds, suggesting that the area activated by listening to speech may extend into the most anterior part of primary motor cortex. In contrast, peak area 4p voxels did not respond in either listening condition. This functional distinction may be analogous to the recently reported greater involvement of area 4a than

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