

The Essential Role of Premotor Cortex in Speech Perception

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Summary

Besides the involvement of superior temporal regions in processing complex speech sounds, evidence suggests that the motor system might also play a role [1–4]. This suggests that the hearer might perceive speech by simulating the articulatory gestures of the speaker [5, 6]. It is still an open question whether this simulation process is necessary for speech perception. We applied repetitive transcranial magnetic stimulation to the premotor cortex to disrupt subjects' ability to perform a phonetic discrimination task. Subjects were impaired in discriminating stop consonants in noise but were unaffected in a control task that was matched in difficulty, task structure, and response characteristics. These results show that the disruption of human premotor cortex impairs speech perception, thus demonstrating an essential role of premotor cortices in perceptual processes.

Results

When we say that we speak a language, we imply that we also understand it. This obvious fact reveals an important constraint on linguistic representations: Language requires the maintenance of “parity” between acoustic and articulatory representations for input and

output, respectively [5, 6]. Although each of these peripheral representations interfaces with a common conceptual core, their structural properties are very different: one representation involves an acoustic signal with rich temporal and spectral structure, whereas the other representation involves intricate motor programs coordinating more than one hundred muscles. The necessary close relationship between acoustic and articulatory forms raises the possibility that the motor system might play a role not only in producing speech but also in perceiving it. This idea is controversial [7] but theoretically important in that it assumes a role for motor mechanisms in perception. Recent neuroimaging [1, 2] and single-pulse transcranial magnetic stimulation (TMS) studies [3, 4] have demonstrated neural activity in speech motor regions during passive speech perception. However, it is not known whether activity in motor areas is causally linked to the perception of speech.

To directly test the hypothesis that premotor regions are crucial for phonetic perception, we used functional magnetic resonance imaging (fMRI) to localize a left premotor cortical region (PMC) that is activated both during speech production and speech perception (Figure 1 and Table 1) [1]. We then temporarily disrupted the activity of this region and of the left superior temporal gyrus (STG) with repetitive TMS (rTMS). This safe and painless method provides direct insight into the causal role of a given brain area in human behavior [8, 9]. Subjects were tested on a speech perception task and two control tasks. The speech perception task involved discrimination of voiceless stop consonants in single syllables that were masked by white noise. All subjects also were tested in a color discrimination task, whereas a subgroup of subjects was tested also in a tone discrimination task. Difficulty across tasks was equated, and the tasks had the same structure and required the same response (button press).

The average percentage of correct responses in the baseline condition was $78.9\% \pm 1.6\%$ (SEM) for the speech perception task and $76.6\% \pm 2.6\%$ for the color perception task; these did not differ if compared with a Student's paired t tests ($p = 0.45$).

Repeated-measures analysis of variance (ANOVA) with the main factors “task” (speech perception, color discrimination) and “TMS condition” (no TMS [baseline], TMS to PMC, TMS to STG) showed a significant task \times TMS condition interaction ($p = 0.015$).

Pairwise comparisons with a Student's paired t test showed a highly significant decrease of the percentage of correct responses for the speech task after TMS stimulation of the PMC site compared to baseline (correct response rate after TMS to PMC $70.6\% \pm 2.0\%$, $p = 0.00097$, all t test results are reported two tailed; effect size: Cohen's d : 1.04), whereas the color perception task was unaffected ($76.5\% \pm 2.6\%$ correct responses, $p = 0.97$). For the speech task, the rate of correct responses after PMC TMS was also significantly lower than after TMS to STG ($p = 0.033$; Cohen's d : 0.45); the

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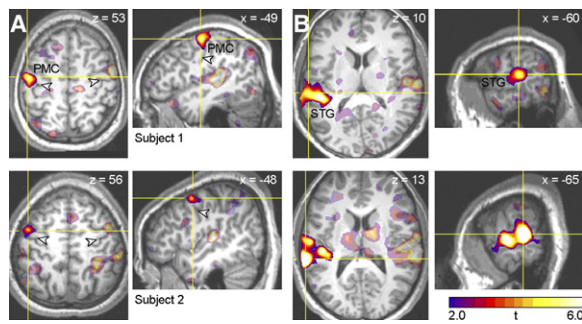


Figure 1. Representative fMRI Activation Peaks for Speech Perception for Two Subjects

Regions selected for stimulation are shown in bright colors; peak coordinates in these regions were used as targets for TMS in the main experiment. Other activated regions are shown in faded colors. (A) shows the left premotor cortex (PMC). Arrowheads indicate the location of the central sulcus. (B) shows the left superior temporal gyrus (STG).

same comparison for the color perception task showed no difference ($p = 0.59$).

There was no effect of TMS to STG on correct response rate both for the speech and the color perception tasks ($74.7\% \pm 2.2\%$ [speech, $p = 0.12$], $75.4\% \pm 2.4\%$ [color, $p = 0.52$] correct responses). Taken together, the results of this experiment show that TMS over the left premotor cortex affected speech perception but not color perception in a task matched for structure, number of responses, and difficulty (Figure 2).

In a subgroup of participants ($n = 12$), the effect of TMS over the left premotor cortex was additionally tested in a tone perception task, requiring recognition of pitch changes. ANOVA of this subgroup of subjects with the main factors “task” (speech, tone discrimination) and “TMS” (baseline, TMS to PMC, TMS to STG) revealed a main effect of TMS ($p = 0.026$) as the only significant effect. Therefore, we combined data from

Table 1. MNI Coordinates of Voxels that Were Targeted for Application of Transcranial Magnetic Stimulation over the Superior Temporal Gyrus and the Premotor Cortex

Subjects	STG			PMC		
	x	y	z	x	y	z
Subj1	-58	-30	12	-52	-8	48
Subj2	-54	-28	6	-44	-4	46
Subj3	-68	-26	4	-52	0	46
Subj4	-66	-24	4	-48	-4	50
Subj5	-66	-24	4	-56	-6	50
Subj6	-62	-24	10	-58	2	46
Subj7	-64	-28	12	-52	-10	50
Subj8	-66	-24	4	-50	-4	54
Subj9	-66	-24	6	-54	-8	52
Subj10	-64	-30	10	-52	0	48
Subj11	-66	-22	10	-58	-6	48
Subj12	-66	-28	8	-58	0	48
Subj13	-66	-28	10	-56	-2	48
Subj14	-62	-30	10	-54	-10	48
Subj15	-52	-26	4	-54	-4	46

These coordinates were voxels showing peak activation in an fMRI experiment that involved on speech perception and that was done prior to the TMS experiment (functional MRI localizer).

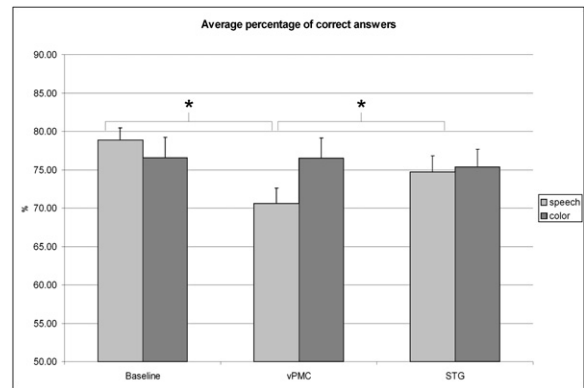


Figure 2. Percentage Rate of Correct Answers for Each Task and Each TMS Site

The tasks included phonetic discrimination and color discrimination. TMS was applied to PMC and STG; in addition, a baseline experiment without TMS was done. Error bars show SEM. TMS over PMC induced significant decrease of correct responses in the phonetic discrimination task, whereas TMS had no effect on the control task of color discrimination. TMS to STG did not affect performance of either task.

the speech and tone task and subsequently performed post hoc *t* tests. These analyses revealed a significant decrease of correct response rate after TMS to PMC compared to baseline ($p = 0.002$; Cohen’s *d*: 0.71) and after TMS to STG compared to baseline ($p = 0.047$; Cohen’s *d*: 0.47).

Further pairwise *t* tests showed a decrease of correct responses for the speech task after TMS to PMC compared to baseline ($p = 0.02$; Cohen’s *d*: 0.55), but not after TMS to STG compared to baseline ($p = 0.45$) (baseline $80.6 \pm 1.9\%$, PMC $72.4 \pm 1.8\%$, STG $77.6 \pm 2.5\%$ correct responses).

For the tone task, a significant decrease of the correct response rate was noted for TMS to STG compared to baseline ($p = 0.02$) but not for TMS to PMC (baseline $85.5\% \pm 2.5\%$, PMC: $80.74\% \pm 3.33\%$, STG: $79.07\% \pm 4.17\%$) (Figure 3). Color discrimination in the subgroup of 12 subjects was not affected by TMS applied to PMC and STG (baseline $76.36\% \pm 3.15\%$, PMC $76.57\% \pm 3.33\%$, STG $74.34\% \pm 3.21\%$ all $ps > 0.48$ for Student’s *t* tests). The comparisons of correct response rates between the TMS conditions revealed a strong trend toward a decrease of performance after TMS to PMC compared to TMS to STG for the speech condition ($p = 0.057$), in line with the result of the entire group, but no difference for the tone condition ($p = 0.583$). Taken together, these results indicate that TMS to both PMC and STG induce varying degrees of impairment in performance for perception of speech stimuli and nonspeech auditory stimuli. The TMS effect on speech perception was more pronounced after TMS to PMC, whereas the TMS effect on tone perception was more pronounced after TMS to STG.

Reaction times for the speech perception task showed a slight, nonsignificant increase compared to baseline both after TMS over left PMC and left STG, indicating that there was no speed-accuracy tradeoff for the speech perception task (average reaction time baseline: 1081.3 ± 39.1 ms (SEM), after PMC TMS: 1125.6 ± 46.5 ms, after

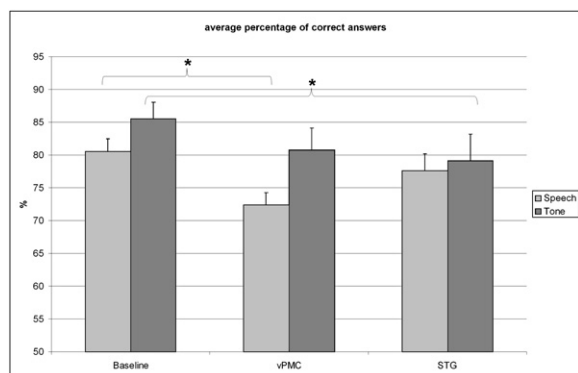


Figure 3. Percentage Rate of Correct Answers for Each Task for a Subgroup Performing an Additional Tone Perception Task

The TMS sites were the same as in the main group (baseline, PMC, STG). Error bars show SEM. Like in the entire group of subjects, TMS over PMC induced significant decrease of correct response rate in the phonetic discrimination task but not in the tone discrimination task. In contrast, TMS over the superior temporal gyrus induced a decrease of performance in the tone perception task. However, ANOVA analysis of the subgroup data revealed a main effect of TMS condition but no significant task \times TMS condition interaction, indicating that both regions play a role in the auditory-perception processes tested.

STG TMS: 1101.7 ± 41.4 ms). Reaction times for the color discrimination task showed no significant differences across TMS conditions as well. ANOVA analysis of the reaction-time data for the speech task and color task with the main factors “task” and “TMS” (baseline, PMC TMS, STG TMS) showed a significant main effect of task ($p < 0.001$) because reaction times for the color task were faster than for the speech task (average reaction time all speech conditions: 1102.9 ± 30.4 ms, all color conditions: 920.6 ± 34.3 ms).

We performed additional analyses to rule out possible order effects. One-way ANOVA on the experimental results grouping the error rates and reaction times according to session order and additional pairwise comparisons of these data with paired Student’s *t* test showed no effects on accuracy or reaction time. Statistical analyses testing the order of experimental conditions within a given TMS session showed no significant effects.

Discussion

To the best of our knowledge, this is the first evidence showing that rTMS over motor areas affects any kind of perceptual process. We demonstrate that the left premotor cortex is crucially involved in speech perception but not in a color discrimination control task that was matched in difficulty, task structure, and response characteristics. The role of motor areas in speech perception has been previously suggested on the basis of theoretical considerations [5, 6]. Recent imaging and TMS data have supported the involvement of motor areas in speech perception [1–4]. However, none of the previous studies tested the causal relationship between activity in motor areas and speech perception. The present results provide evidence that the congruency of sensory and motor activation in this area is not epiphenomenal.

Rather, activity in the premotor cortical area stimulated here is essential for speech perception. The TMS-induced decrease in syllable discrimination performance cannot be due to a general effect on response selection, which is a classical function of prefrontal cortex [10], because the color discrimination task, also requiring response selection, was unaffected by TMS. Furthermore, we found not only a decrease of performance in the speech perception task after TMS to PMC compared to baseline but also a decrease relative to TMS to STG. Therefore it is highly unlikely that the behavioral effects observed after stimulating the premotor cortex reflect merely an indirect modulation of temporal auditory areas via functional connections between frontal and temporal regions [11].

Instead, these data suggest that phonetic discrimination crucially depends not only on auditory processes in posterior perisylvian regions but also on activity in the motor system. The results presented here are in line with a recent behavioral study that related the degree of phonemic awareness to individual motor skills [12], suggesting a common cortical architecture for development of motor abilities and discrimination of complex articulatory sound patterns. Furthermore, aphasia after lesions in left prefrontal regions can include deficits in phonemic perception as well [13–16]. Additional support comes from studies that involve direct electrical stimulation of the cortex [17] and that have demonstrated the importance of frontal regions for speech perception as well as speech production.

What is the role of the left premotor cortex within the cortical network mediating speech perception? According to a recently proposed framework of speech perception, the premotor cortex is the anterior part of the “dorsal stream,” which provides auditory-motor mapping [18]. It is anatomically and functionally connected to superior temporal regions [11, 19, 20] and might be involved in phonetic discrimination, thereby facilitating the mapping of perceived speech sounds onto internal motor representations of articulatory gestures [2–6]. Broca’s area, which is located more ventrally, has tight functional connections with premotor cortex and might also be involved in the process [21]. A recent fMRI study found that activation of both superior temporal and PMC areas is higher for perception of foreign-language phonemes, which do not have a pre-existing phonetic cortical representation resulting from language acquisition, compared the native-language phonemes [11]. The authors proposed that the premotor cortex generates forward models of native phonemes that are compared within the superior temporal cortex with the results from initial acoustic-speech analysis. This hypothesis is supported by previous studies suggesting that the premotor cortex provides top-down information that facilitates speech perception in circumstances such as when the acoustic signal is degraded [22] or when explicit conscious access is required to phonetic form [18].

The lack of STG TMS effect on speech perception might be due to a larger auditory network for speech perception than tone perception; functional imaging studies have shown that initial stages of speech processing within the temporal cortex are represented bilaterally in areas specialized for voice processing [23, 24]. Data from split-brain patients and individuals

with word deafness support this view [18]. Speech perception is a complex process that requires not only auditory-signal analysis but also phonetic analysis, thus involving a wide bilateral network within the superior temporal cortex [24, 25]. Because TMS was applied only to the left STG, speech perception probably was preserved because of compensatory processes within the contralateral temporal cortex.

The involvement of premotor cortex in perception more generally has been motivated by a large body of work comprising electrophysiological investigations in monkeys and neuroimaging studies in humans [26]. There is evidence from functional imaging studies that there is a superordinate function of premotor cortex, and this function, exceeding motor planning, also mediates attentional, intentional, and perceptual integration of motor acts across modalities [27, 28]. Located between sensory areas that provide multimodal representations of surrounding environment in the posterior part of the brain and anterior higher-order areas that provide long-term planning and action selection, the premotor cortex is associated with both motor control and motor awareness [29] and is also involved in attentional processes related to action [27]. "Mirror neurons" have been described in macaque monkeys; these neurons respond not only to the production of actions but also to the sight [29] or sound [30] of actions. Such a mirroring mechanism, by coupling action and perception, might hold the key to the maintenance of parity between senders and receivers of all sorts of messages, obviously including the ones more directly relevant to language. The present results demonstrate that the involvement of the premotor cortex in perception is not merely epiphenomenal and suggest that sensory regions are not sufficient alone for human perception. Rather, the perceptual representations of speech sounds, and perhaps sensory stimuli more generally, are fundamentally sensory motor in nature.

Experimental Procedures

Participants

Nineteen healthy subjects, with an age of 26.9 ± 2.2 (SE) years (all right handed; 11 males), and with normal or corrected to normal vision, participated in this experiment and were tested in speech and color perception. A subgroup of 12 subjects (mean age 26.6 ± 3.2 years, six males) was also tested on tone perception. All participants gave informed consent and the study was approved by the UCLA Institutional Review Board.

Experimental Procedures

The experiment took place in a quiet, shaded room. In each subject, the thresholds for phonetic discrimination and color discrimination tasks were determined with two separate adaptive procedures.

In the phonetic task, each trial consisted of presentation of a consonant-vowel syllable in noise, which the subject would identify as pa, ta, or ka by pressing one of three keys. Syllables were synthesized with a Klatt synthesizer and standard parameter values for a male speaker [31]. The syllable durations were 170 ms. They were embedded in the center of a 600 ms Gaussian white-noise mask. Stimuli were presented with MATLAB (Mathworks, Natick, MA) and the Psychophysics toolbox [32, 33]. A 1-up-2-down adaptive staircase procedure was used. We determined thresholds by taking the average of the last four reversals.

In the visual task, a circle of diameter 23 mm subtending 2.2° visual angle was presented for 600 ms against a black background. The circle was gray, but tinged with red, green, or blue, and subjects would attempt to identify the color by pressing one of three keys.

The brightness of each channel (red, green, blue) was 50%, except for the target channel that was increased by 3.5% initially, with a step size of 1.2% for the first three reversals and 0.4% thereafter.

The tone task was performed by a subset of subjects ($n = 12$). It was identical to the speech task except that instead of syllables, tones were presented consisting of sine waves (1000 Hz, 1250 Hz, 1500 Hz; duration 200 ms). In the adaptive procedure, the same initial SNR and step size was used as in the speech task.

Subjects then were tested under the following conditions: baseline and after rTMS to the PMC or STG, as described below. The order of the experimental conditions was counterbalanced across subjects, and the interval between sessions was at least 60 min. Experiments with comparable rTMS parameters have shown that effects of magnetic stimulation last up to 20 min [34, 35]; thus, carryover effects among the different TMS stimulation sessions after the chosen intersession time intervals were highly unlikely. In each condition, there were 60 phonetic discrimination trials and 60 color discrimination trials.

Individual error rates and averaged reaction times were analyzed for all experimental conditions. A repeated-measures ANOVA model with the main factors "task" (speech perception, color perception) and "TMS condition" (no TMS, TMS to PMC, TMS to STG) was employed. Post hoc comparisons were performed with Student's *t* tests.

Transcranial Magnetic Stimulation

TMS was applied with a Magstim Rapid Stimulator (Magstim, Spring Gardens, UK) with a figure-of-eight coil. Motor threshold was determined in the right first dorsal interosseus muscle and defined as the minimum stimulus intensity required for eliciting motor-evoked potentials (MEP) in at least five of ten trials. Stimulation intensity was 90% of individual resting motor threshold, with a maximum possible TMS intensity of 60% of maximum stimulator output. Mean stimulation intensity was $57.9\% \pm 0.7\%$ (SEM) for the main experiment and $56.9\% \pm 0.9\%$ for the subgroup of the control experiment. For each of the sites stimulated, 900 pulses were applied at a frequency of 1 Hz (train duration 15 min). 1Hz rTMS stimulation has been shown to produce inhibitory modulation of cortical excitability over various cortical areas (i.e., [34, 36]).

The stimulation sites were located with frameless stereotaxy (BrainSight, Rogue Research, Montreal, Canada) at the beginning of the session. In 15 out of 19 subjects, individual activation peaks for speech perception were obtained with fMRI as described below (Table 1). In the remaining four subjects, we used the average peak coordinates for left PMC and STG obtained from our previous speech perception study [1]. None of the subjects reported side effects of TMS.

Functional MRI Localizer

Prior to the main TMS study, an MPRAGE structural volume MRI was acquired for registration purposes in all subjects (TR = 2300 ms; TE = 2.93 ms; flip angle = 8° ; 160 sagittal slices; $1.33 \times 1.33 \times 1.5$ mm resolution; field of view = $256 \times 256 \times 240$ mm).

Additionally, we scanned 15 of the 19 subjects with fMRI in order to individually localize frontal and temporal regions involved in speech perception. Functional images were acquired on a 3 T Siemens Allegra scanner. Two different experimental paradigms were used as follows: In ten subjects, the functional run was 128 s and composed of five blocks (16.5 s) of listening to the syllable (pa) at a rate of 1.33 Hz, interleaved with five blocks of rest (15.5 s). A total of 64 EPI images were acquired (TR = 2000 ms; TE = 25 ms; flip angle = 90° ; 36 axial slices with interleaved acquisition; $3 \times 3 \times 4$ mm resolution; field of view = $192 \times 192 \times 144$ mm) plus two initial images that were discarded. In five subjects, an experimental design involving the same EPI sequence was done with the following experimental conditions: perception or self-paced utterance of meaningless syllables (/pa/, /ta/, /ka/), viewing of a video showing both index fingers of a person tapping two pushbuttons, and self-paced fingertapping with both index fingers. The functional run was 830 scans. During assessment of the threshold for motor-evoked potentials prior to the main experiment, the PMC site was stimulated in all subjects with an intensity of 120% of motor threshold. No motor evoked potentials could be elicited in the contralateral hand in any of the subjects.

A standard analysis was carried out with SPM2 (<http://www.fil.ion.ucl.ac.uk/spm>). Superior temporal and premotor regions were activated during speech perception in every subject. The premotor region of interest is located posteriorly in the precentral gyrus, and it is activated in every subject listening to speech [1, 11].

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