

The Motor Somatotopy of Speech Perception

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Summary

Listening to speech recruits a network of fronto-temporo-parietal cortical areas [1]. Classical models consider anterior (motor) sites to be involved in speech production whereas posterior sites are considered to be involved in comprehension [2]. This functional segregation is challenged by action-perception theories suggesting that brain circuits for speech articulation and speech perception are functionally dependent [3, 4]. Although recent data show that speech listening elicits motor activities analogous to production [5–9], it's still debated whether motor circuits play a causal contribution to the perception of speech [10]. Here we administered transcranial magnetic stimulation (TMS) to motor cortex controlling lips and tongue during the discrimination of lip- and tongue-articulated phonemes. We found a neurofunctional double dissociation in speech sound discrimination, supporting the idea that motor structures provide a specific functional contribution to the perception of speech sounds. Moreover, our findings show a fine-grained motor somatotopy for speech comprehension. We discuss our results in light of a modified “motor theory of speech perception” according to which speech comprehension is grounded in motor circuits not exclusively involved in speech production [8].

Results

Recent years have seen a major change in views about the function of motor and premotor cortex [11]. Once believed to be an output system, slavishly following the dictate of the perceptual brain, the motor brain is now recognized as critical component of perceptual and cognitive functions. This challenges the classical sensory versus motor separation [12]. Similarly, traditional models of language brain organization separated perceptual and production modules in distinct areas [1, 2]. However, a large amount of data is accumulating against the reality of such a strict anatomic-functional segregation [5–9, 13, 14]. The motor theory of speech perception

(MTSP) [3], an early precursor of a new zeitgeist, most radically postulated that the articulatory gestures, rather than sounds, are critical for both production and perception of speech (see [4]). On neurobiological grounds, fronto-temporal circuits are thought to play a functional role in production as well as comprehension of speech. The coactivation of motor circuits and the concurrent perception of self-produced speech sounds during articulations might lead to correlated neuronal activity in motor and auditory systems, triggering long-term plastic processes based on Hebbian learning principles [15–17]. The postulate of a critical role of actions in the formation of speech circuits is paralleled in more general action-perception theories emphasizing a critical role of action representations in action-related perceptual processes [18]. However, a majority of researchers are still skeptical toward a general role of motor systems in speech perception, admitting, if at all, only a subsidiary role of motor areas and reserving the critical role to superior temporal and inferior parietal cortices [19].

A recent series of studies directly investigated the activities in motor areas during speech perception. Passive listening to phonemes and syllables was shown to activate motor [5–8] and premotor [9] areas. Interestingly, these activations were somatotopically organized according to the effector recruited in the production of these phonemes [5, 6, 8] and in accordance with motor activities in overt production [8, 9]. A distinctive feature of action-perception theories in general and in the domain of language specifically is that motor areas contribute to perception [4, 16, 20]. However, all the above mentioned studies are inherently correlational, and it has been argued that in absence of a stringent determination of a causal role played by motor areas in speech perception, no final conclusion can be drawn in support of motor theories of speech perception [10]. The only empirical evidence in favor of this view is represented by a recent repetitive TMS study suggesting that ventral premotor cortex (PMv) may play some role in phonological discrimination [21]. In our view, however, this study fails to offer a convincing proof of the causal influence that motor areas may exert. Because of the spread and the variety of possible effects elicited by a 15 min TMS stimulation, such an offline rTMS protocol might have indeed modified the activity of a larger network of areas, possibly including posterior receptive language centers [22]. Moreover, there is no evidence of an effector-specific effect, i.e., that stimulating tongue representation induced specific deficits in the perception of tongue-related phonemes.

Here, we set out to investigate the functional contributions of the motor-articulatory systems to specific speech-perception processes. To this end, a cross-over design orthogonalizing the effect of brain-phonology concordance with those of linguistic stimuli and TMS loci was chosen. Phonemes produced with different articulators (lip-related: [b] and [p]; tongue-related: [d] and [t]) were presented in a phoneme-discrimination task. The effect of TMS to lip and tongue representations in precentral cortex, as previously described by fMRI [8], was investigated. Double TMS pulses were applied just prior to stimuli presentation to selectively prime the cortical activity specifically in the lip (LipM1) or tongue

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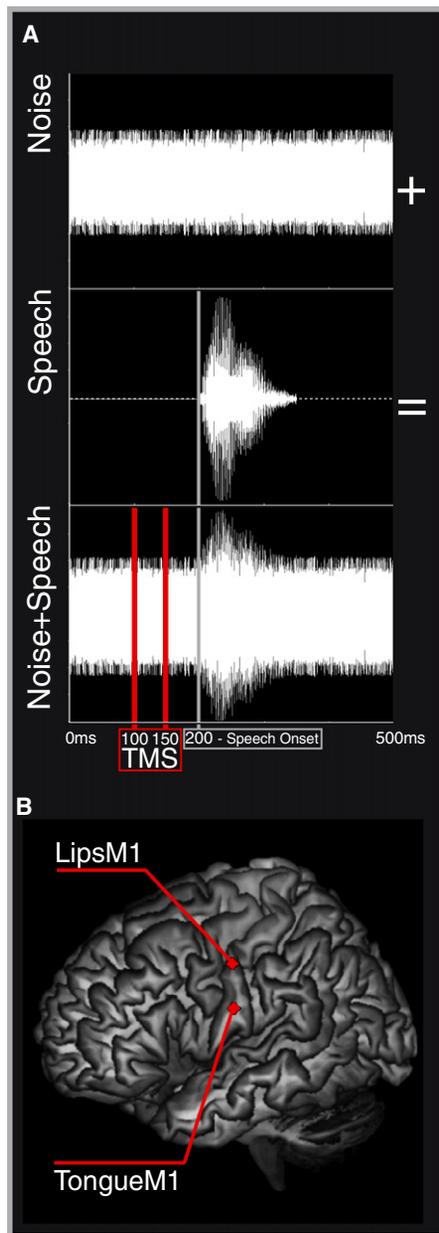


Figure 1. Stimuli, TMS Timing, and Regions of Stimulation
(A) Noise, speech sound, and experimental stimulus waveforms. Noise and speech recordings were mixed into a single trace. TMS (vertical red lines) was applied in double pulses 100 and 150 ms after noise onset. Speech sounds started 200 ms after noise onset (gray vertical line).
(B) LipM1 and TongueM1 normalized mean coordinates are projected on a standard template [8, 34].

(TongueM1) area (Figure 1). We hypothesized that focal stimulation would facilitate the perception of the concordant phonemes ([d] and [t] with TMS to TongueM1), but that there would be inhibition of perception of the discordant items ([b] and [p] in this case). Behavioral effects were measured via reaction times (RTs) and error rates.

RT performance showed a behavioral double dissociation between stimulation site and stimulus categories (Figure 2). RT change of phonological decisions induced by TMS pulses to either the TongueM1 or LipM1 showed opposite effects for tongue- and lip-produced sounds. The interaction of the

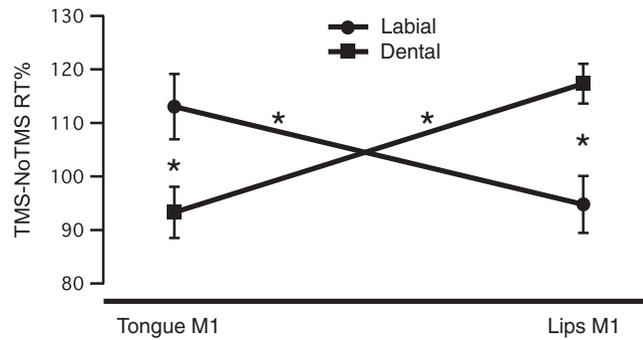


Figure 2. Reaction Times during Speech Discrimination
Effect of TMS on RTs show a double dissociation between stimulation site (TongueM1 and LipM1) and discrimination performance between class of stimuli (dental and labial). The y axis represents the amount of RT change induced by the TMS stimulation. Bars depict SEM. Asterisks indicate significance ($p < 0.05$) at the post-hoc (Newman-Keuls) comparison.

phoneme type and stimulation site factors was significant ($F[1,36] = 17.578$; $p < 0.0005$), and the post-hoc analysis evidenced a significant difference between labial ([b], [p]) and dental ([d], [t]) phonemes for each of the stimulation sites. As hypothesized, recognition of lip-produced phonemes was indeed faster than that of tongue-produced ones when stimulating the LipM1 (labial = $94.8\% \pm 5.3\%$ SEM; dental = $117.3\% \pm 3.7\%$ SEM; $p = 0.009$), and the stimulation of the TongueM1 induced the reverse pattern (labial = $113.6\% \pm 6.4\%$ SEM; dental = $93\% \pm 5.1\%$ SEM; $p = 0.024$). In addition, labial and dental stimuli recognition was faster when stimulating their concordant M1 representation compared with that to the discordant stimulation locus (labial, $p = 0.015$; dental, $p = 0.009$). Therefore, the stimulation of a given M1 representation led to better performance in recognizing speech sounds produced with the concordant effector compared with discordant sounds produced with a different effector. These results provide strong support for a specific functional role of motor cortex in the perception of speech sounds.

In parallel, we tested whether TMS was able to modulate the direction of errors (Figure 3). Errors were grouped in two classes: lip-phoneme errors (L-Ph-miss) and tongue-phoneme errors (T-Ph-miss). The ANOVA showed a significant interaction effect ($F[1,36] = 4.426$; $p < 0.05$). Post-hoc comparisons

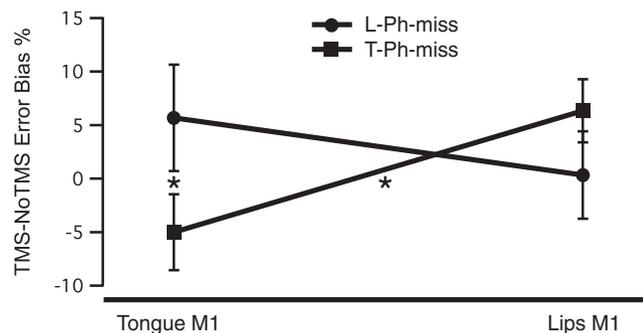


Figure 3. Accuracy Results
We tested whether TMS was able to modulate the direction of errors, i.e., if the stimulation of the TongueM1 increases the number of labial sounds erroneously classified as dental and vice versa. After TMS, a dissociation between stimulation site (TongueM1 and LipM1) and kind of errors (L-Ph-miss, T-Ph-miss) was found. The y axis represents the amount of error change induced by the TMS stimulation. Other conventions as in Figure 2.

revealed more L-Ph-miss than T-Ph-miss errors when stimulating the TongueM1 representation ($p = 0.049$), and also more T-Ph-miss errors when stimulating the LipM1 relative to the TongueM1 ($p = 0.012$). Therefore, the error pattern confirmed the dissociation already seen in the RT data. As a matter of fact, the stimulation of a given motor representation led to a perceptual bias in favor of speech sounds concordant with the stimulation site. Stimulation of the tongue area made lip sounds tend to be perceived as dentals and, vice versa, lip area TMS made [d] and [t] sound like bilabials.

Discussion

The double dissociation we found in the present work provides evidence that motor cortex contributes specifically to speech perception. As shown by both RTs and errors, the perception of a given speech sound was facilitated by magnetically stimulating the motor representation controlling the articulator producing that sound, just before the auditory presentation. Inhibitory effects were seen for discordant speech sounds. Computationally speaking, our stimulation might preactivate, or prime, a given M1 sector by increasing the excitability of neurons therein. This higher excitability might lead to faster RTs if that area contributes to a task. The reduction of performance observed in the other class of stimuli can be explained by mechanisms of lateral inhibition between competing representations. Similarly, TMS-induced priming of one specific representation may bias the system toward activating the already preactivated representation, leading to the observed error pattern. The direction of our effects suggests that our TMS protocol is enhancing the activity in M1 locally, in agreement with other results reported in TMS literature [23–25] and with the work by Pulvermüller and colleagues [26] describing a similar effect at the semantic level. Two factors might have caused facilitation of subjects' behavioral performance: (1) TMS timing and (2) basal cortical activity. In fact, a single TMS pulse disrupts cortical processing for a limited time window, by synchronizing neuronal activities. Animal models actually hold that inhibition turns into facilitation after a short time window depending on pulse strength [27]. Alternatively, the direction of effects can be accounted by cortical state dependency. It's well known that motor thresholds vary according to the cortico-spinal basal activity (i.e., muscle contraction). Analogously, the recent work of Silvanto and colleagues [28, 29] showed that TMS induces both behavioral facilitation and inhibition according to the basal activity of the target cortical area. Although both explanations are equally probable, the double dissociation we found is the strongest proof to support our central hypothesis. It should be stressed, however, that our finding does not prove that M1 is directly involved in speech perception. A possible explanation for the facilitation of the perception of phonemes motorically congruent with the stimulated site is that the synchronous excitation of M1 neurons induced by TMS may have exerted in turn the facilitation of neurons located in premotor areas, somatotopically connected with M1 through bidirectional cortico-cortical links.

Biologically grounded models of speech and language have previously postulated a functional link between motor and perceptual representations of speech sounds [8, 30]. We demonstrate here for the first time a specific causal link for features of speech sounds. The relevant areas in motor cortex seem to be also relevant for controlling the tongue and lips, respectively. As mentioned, the MTSP [3, 4] had postulated

a critical role of articulatory phonetic gestures for the perception of speech. However, this theory also claimed a modular status of the linguistic phoneme system, which was thought to be functionally dissociated from the nonlinguistic motor system. This position is difficult to reconcile with the finding of congruency between cortical areas for speech perception, articulation, and nonlinguistic movements of tongue or lips [8]. Here we therefore provide only partial support for the MTSP, and we propose that the motor gestures critical for speech perception are processed by the same brain parts and circuits involved also in the production of other, nonlinguistic, movements. We are not suggesting, however, that the motor cortex is an area for phonological discrimination per se; rather, we favor the idea that it might be part of a larger network. This latter claim is also supported by a large number of studies showing an integrated brain network for speech processing as opposed to a single localized module [1, 13, 14, 16, 19, 31]. We propose that TMS of M1 might have unbalanced the network dynamics of action-perception circuits, likely involving motor, premotor, and temporo-parietal areas.

The present results might be of potential interest in the rehabilitation of aphasia. Current experimental protocols, showing initial exciting results, are indeed evaluating the possible benefit of repeated TMS (rTMS) application in these patients [31]. TMS is typically used to trigger (or inhibit) plastic processes in conjunction with standard rehabilitation protocols. However, rTMS effects spread uncontrollably to other areas, eventually resulting in a global functional reshaping of whole-brain dynamics. Event-related TMS, such as the one presented in our study, might be potentially more spatially selective and thus more effective. Single pulses or short trains might in fact be more efficient in triggering local plastic processes in selected neuronal populations. We therefore propose that innovative rehabilitation programs based on recent neuroscientific findings about action-perception circuits [13, 16], such as the intensive language-action therapy [32], in conjunction with event-related TMS protocols might be more effective also at chronic stages of aphasia.

Experimental Procedures

Subjects

Ten healthy right-handed subjects volunteered after giving informed consent and were paid for their participation (mean age, 26.07; SD, 2.91; 6 female). None had any history of neurological disease, trauma, or psychiatric syndrome and all had normal hearing. Procedures were approved by the local ethical committee.

Stimuli

Subjects listened to one out of four stimuli in each trial: [b], [p], [d], and [t] spoken before a [œ] sound, through headphones. [b] and [p] are labial sounds, requiring the critical lip movement for their production, whereas [d] and [t] are dental sounds that require a significant tongue movement. Each stimulus was the vocal recording of an actor. In order to avoid ceiling effects in the phoneme identification task, we immersed vocal recordings in 500 ms of white noise. Each vocal stimulus was presented 200 ms after the beginning of white noise. The noise/stimulus ratio was set in a pilot experiment (11 subjects) to let subjects respond correctly $\approx 75\%$ of cases. Task RT and accuracy, grouped into labial (mean RT, 839 ± 59.95 ms SEM; mean accuracy, $77.58\% \pm 5.36\%$ SEM) and dental (mean RT, 815 ± 53.11 ms SEM; mean accuracy, $75.76\% \pm 5.78\%$ SEM) sounds did not differ significantly in the pilot experiments (RT, $t(10) = 1.249$; $p = 0.24$; accuracy, $t(10) = 0.234$; $p = 0.82$).

Task

Subjects were asked to listen and recognize the consonants and respond as fast as possible with a four-button pad. Buttons were configured in a diamond shape and the relative position, with associated consonant letters,

was shown during the experiment on a screen in front of them. Responses were given with the left index finger. Response recording, stimuli presentation, and TMS triggering were controlled by a custom-made Basic script running under the MS-DOS environment to warrant timing accuracy.

TMS

TMS stimulation was delivered through a figure-of-eight 40 mm coil and a Magstim Rapid stimulator (Magstim, Whitland, UK). The 25 mm coil was used to allow a more focal stimulation. First *Dorsal Interosseus* (FDI) mapping and resting motor threshold (rMT) evaluation was assessed by using standard protocols [33]. Motor-evoked potentials (MEP) were recorded by using a standard tendon-belly montage with Ag/Cl electrodes. Signal was band-pass filtered (50–1000 Hz) and digitized (5 kHz). TongueM1 and LipM1 localization were, instead, based on standardized coordinates with respect to the functionally defined best stimulation site of the FDI muscle. Specifically, for lip and tongue area stimulation, we chose the mean MNI coordinates corresponding to the peak motor cortex activation probability (t-values), during lip and tongue movements and articulation, revealed by a previous fMRI study (lips: –56, –8, 46; tongue: –60, –10, 25; Figure 1A; [8]). In parallel, also FDI MNI coordinates were taken from the literature (–37, –25, 58; [34]). In the following step, MNI coordinates (FDI, TongueM1, and LipM1) were first transformed into the 10–20 EEG system space (Münster T2T-Converter: <http://wwwneuro03.uni-muenster.de/ger/t2tconv/conv3d.html>) and then the distance between FDI/tongue and FDI/lip were calculated in the same standard space. Therefore, TongueM1 and LipM1 were located according to differential 10–20 EEG coordinates centered on the functionally defined FDI location. In each subject, the FDI was first functionally mapped, and then TongueM1 and LipM1 were located according to the differential 10–20 EEG coordinates (lips: 6.6% of *nasion-inion* distance in the anterior direction and 5.8% of the inter-tragus distance in the lateral direction—FDI mean distance: 5.5 cm; tongue: 8.6% anterior and 11.6% lateral—FDI mean distance: 3.35 cm; mean distance between lips and tongue: 2.15 cm). In the stimulated trials, two pulses with 50 ms interval were delivered at 110% of the FDI rMT. Coil orientation was maintained at 45° with respect to the interhemispheric fissure. Pulses were given 100 ms and 150 ms after noise onset; thus, the last TMS pulse occurred 50 ms prior to consonant presentation (see Figure 1).

Procedure

Subjects first completed a block of trials with no TMS intervention, to train participants and to test their ability to accomplish the task up to our criteria ($\approx 75\%$ of correct trials; a total of 60 trials, 15 each stimulus category). Upon successful completion of this learning phase, they were entered in the TMS mapping block. The right FDI primary motor representation was located and marked on the left hemisphere, and the rMT was measured. LipM1 and TongueM1 representations were marked on the scalp with respect to the functionally defined FDI spot (for the procedure see the TMS section). After the mapping session, two blocks were presented in succession separated by a 2 min interval. TMS stimulation over LipM1 and TongueM1 was delivered in different blocks, whose order was counterbalanced across subjects. In each block, subjects had to complete 80 trials, 60 with TMS and 20 random catch trials. Random catch trials were exactly the same as the TMS trials except that no TMS was applied. Catch trials were used as a reference to evaluate the effect induced by TMS on behavior.

Measures and Analysis

Experimental measures included RTs and errors. RTs were calculated from the beginning of consonant sound presentation (200 ms after noise onset). The RT data were collapsed into two categories: labial and dental sounds. Preliminary analyses showed that there were no significant differences between the voiced ([b], [d]) and unvoiced ([p], [t]) phonemes. Subjects' performance was normalized by computing the percentage of variation of mean RT in TMS-stimulated trials with respect to trials without TMS. Errors were considered as the amount of responses erroneously attributed to the other category (misses). Errors were collapsed in two categories according to their falling in the other group of stimuli (L-Ph-miss and T-Ph-miss). Single subjects' error scores were expressed as the percentage of change between stimulated trials and TMS-free ones. Separate analyses of variance (ANOVA) were conducted on RT and error data, including the factors phoneme type (labial versus dental or, in the error analysis, L-Ph-miss versus T-Ph-miss) and stimulation site (LipM1 versus TongueM1). Significant interactions were further investigated with Newman-Keuls post-hoc comparisons ($\alpha = 0.05$).

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