



# The role of premotor cortex in speech perception: Evidence from fMRI and rTMS

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## ABSTRACT

This article discusses recent functional magnetic resonance imaging (fMRI) and repetitive Transcranial Magnetic Stimulation (rTMS) data that suggest a direct involvement of premotor cortical areas in speech perception. These new data map well onto psychological theories advocating an active role of motor structures in the perception of speech sounds. It is proposed that the perception of speech is enabled – at least in part – by a process that simulates speech production.

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## 1. Introduction

The premotor cortex is classically considered to be concerned with the planning, preparation, selection, and initiation of movements (Wise, 1985). Recent data, however, have suggested that the human premotor cortex may actually be directly involved in the perception of speech. These data revived a theory that called for an active role of motor structures in speech perception.

Several years ago, at the Haskins laboratory in Yale, New Haven, Alvin Liberman and his colleagues were working on reading devices for war veterans that had lost sight. Their idea was to build devices that would transform text into spoken words so that blind veterans could read books and newspapers. To their dismay, Liberman and colleagues found that the veterans' perception of the device's speech output was unbearably slow. Much slower of even distorted human speech. This observation inspired Liberman and colleagues to propose a theory of speech perception according to which speech sounds are understood not so much as sounds, but rather as *articulatory gestures*, as the intended motor plans necessary to speak (Liberman et al., 1957, 1967; Liberman and Mattingly, 1985; Liberman and Whalen, 2000). This theory – called the *motor theory of speech perception* – basically suggests that the way our brain perceives other people talking is by simulating that we are doing the talking ourselves. Although differing in a number of important aspects, also the *direct realist theory of speech perception* emphasizes that the key functional aspect of perceiving speech sounds has to do more with retrieving the articulatory gestures that emit those sounds than with the analysis of the acoustic signal (Fowler and Rosenblum, 1991).

Both the *motor theory* and the *direct realist theory* of speech perception were inspired by the observation that the acoustic cues for each phoneme tend to be highly contextually dependent. How do

phonetic representations become invariant then? The hypothesis of the *motor theory* and of the *direct realist theory* of speech perception is that the phonetic representations become invariant at the level of motor control structures.

Some data from brain damaged patients were in support of an involvement of motor structures in speech perception. Patients that produce phonemic jargon are more impaired in phonemic discrimination than patients that produce semantic jargon (Alajouanine et al., 1964). In his seminal book *Higher Cortical Functions in Man*, Luria also proposed that silent articulation was necessary to process speech sounds, on the basis of the observation that speech perception was impaired in patients with articulatory deficits (Luria, 1966).

The most important empirical evidence in support of a role of motor structures in speech perception, however, was considered the phenomenon called *categorical perception*. This term refers to the fact that stop consonants in particular can only be perceived categorically. Changes in voice onset time (VOT) and formant frequency are typically not perceived by listeners, until they cross a categorical boundary between two phonemes (Liberman et al., 1957). Interestingly, stop consonants can also be produced only in some sort of categorical fashion. It is indeed impossible to emit a sound that is halfway through two stop consonants. This functional similarity between perception and production suggested that perception was ultimately an articulatory phenomenon. However, other empirical evidence challenged this reasoning. Indeed, categorical perception was demonstrated in infants well before they began to speak (Eimas et al., 1971). Even more devastatingly for the role of categorical perception in support of the motor theory of speech perception, was the demonstration that chinchillas, animals that do not speak, also have categorical perception (Kuhl and Miller, 1975).

The discovery of mirror neurons, premotor neurons of the macaque brain that fire when the monkey performs an action

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and when it observes somebody else performing it (di Pellegrino et al., 1992; Gallese et al., 1996), revived the hypothesis that motor structures may be concerned with perceptual processes (Rizzolatti and Craighero, 2004). Mirror neurons were originally discovered in area F5 of the ventral premotor cortex of the macaque brain. Indirect evidence of human mirror neuron areas has been provided by Transcranial Magnetic Stimulation (TMS), (see for instance, among many others, Fadiga et al., 1995; Strafella and Paus, 2000; Aziz-Zadeh et al., 2002) and functional magnetic resonance imaging (fMRI) (see for instance, among many others Iacoboni et al., 1999, 2005; Grèzes et al., 2003).

One of the appealing aspects of the discovery of mirror neurons with respect to theories positing a role for motor structures in speech perception, is the fact that these cells, by firing during both production and perception of similar actions, embody the concept of parity between action and perception, a concept that Liberman proposed as the key functional aspect of successful communication between the sender and the receiver of a message (Liberman and Mattingly, 1985). In the motor theory of speech perception, the parity between articulatory codes and acoustic representations is considered the common code between the speaker and the listener. Indeed, immediately after mirror neurons were discovered in Parma, Giacomo Rizzolatti told Luciano Fadiga that the properties of those neurons reminded him of the motor theory of speech perception of Alvin Liberman (Luciano Fadiga, personal communication).

## 2. Motor cortices and speech perception: TMS and fMRI

This remark must have inspired Fadiga to use TMS to test the motor theory of speech perception (Fadiga et al., 2002). In this experiment, Fadiga and his colleagues stimulated the sector of the motor cortex that control tongue muscles while recording the tongue muscle twitches induced by the brain stimulation. Subjects were listening to words through earphones. Fadiga and colleagues used two main types of words. One type required strong tongue movements when produced (double “r”, such as “terra”, which means *ground* in Italian). The other type required only a slight tongue movement when produced (double “f”, such as “baffo”, which means *moustache* in Italian). The motor theory of speech perception predicts that while subjects listen to words that require strong tongue movements such as “terra”, the stimulation over the tongue motor cortex should produce stronger muscular twitches in the tongue compared to listening to words such as “baffo”. This hypothesis was confirmed by the experimental data (Fadiga et al., 2002). This TMS experiment demonstrates that while listening to other people talking, the listeners mirror the speaker with their tongues! Other labs have confirmed the basic phenomenon (Watkins et al., 2003; Watkins and Paus, 2004).

Following these TMS experiments, an fMRI study looked at brain activation while subjects speak and while they listen to other people speaking. In this fMRI experiment, subjects listened to syllables through earphones while they were in the magnetic resonance scanner and also said aloud a series of syllables. In every subject studied, it was observed that the same speech motor area that was activated while speaking, was also activated while listening to other people speaking (Wilson et al., 2004). Notably, this area was located – according to probabilistic cytoarchitectonic maps (Geyer et al., 1996; Geyer, 2004) – at the border between Brodmann area 6 and Brodmann area 4a, well within classical ‘motor’ territory and well outside classical frontal lobe language areas for speech production and perception, which tend to be located more ventrally, between Brodmann area 44 and ventral area 6. An independent, subsequent study substantially confirmed and even refined this phenomenon (Pulvermüller et al., 2006).

Follow up studies on this premotor/motor area for speech production and perception that fulfills at least one prediction of the motor theory of speech perception<sup>1</sup> have provided further information on its properties. A recent fMRI study has investigated the time-varying characteristics of this area while subjects were listening to audio-clips of a narrator that described a series of Warner Bros cartoons (Wilson et al., 2008). Each subject was scanned during two fMRI runs of approximately 12 min each, such that subjects could watch and listen to the narratives of five Warner Bros cartoons. Model-free inter-subject correlation analyses were used to test whether this brain area is systematically modulated by the input. The reasoning behind this approach is that voxels which tend to respond similarly across subjects reveal neural activity that varies in time following stimulus properties (Hasson et al., 2004), such as dynamic changes in phonology, syntactic and semantic structure. Inter-subject correlation analyses during continuous narrative speech comprehension demonstrated that this area responds systematically to the time-varying properties of narrative speech (Wilson et al., 2008). This is a typical feature of a perceptual area (Hasson et al., 2004). These recent fMRI data reinforce the notion that this human brain area at the border between premotor and primary motor cortex is not only concerned with speech production, but also with speech perception.

The functional properties of this human premotor area that activates during both speech production and speech perception were further tested during a fMRI study that investigated the relationships between producibility of speech sounds and brain activity (Wilson and Iacoboni, 2006). Subjects first performed a behavioral task, in which they had to produce non-native phonemes. Subsequently, subjects were studied with fMRI while they listened to both native and non-native phonemes. In a separate imaging scan, subjects were also studied while they produced native phonemes. Both the superior temporal cortex (a classical auditory brain region) and the human premotor area previously identified as responsive to speech sounds (Wilson et al., 2004) were activated while subjects were listening to both native and non-native phonemes. Furthermore, both superior temporal cortex and premotor cortex discriminated between native and non-native phonemes, with lower activity for native phonemes. Moreover, functional connectivity analyses demonstrated that the premotor area for speech production and perception was functionally connected with the superior temporal cortical regions responsive to speech sounds. The connectivity analyses demonstrated equivalent functional connections both when the superior temporal cortex was used as ‘seed’ area, and when the premotor area for speech production and perception was the ‘seed’ area (Wilson and Iacoboni, 2006). These results suggested that the flow of information between superior temporal and premotor/motor areas was largely bidirectional. However, when brain activity while listening to non-native phonemes was correlated with the behavioral performance during the task that required subjects to produce non-native phonemes, only the superior temporal activity was found to correlate with producibility. The activity in the premotor cortical area did not correlate with producibility of non-native phonemes (Wilson and Iacoboni, 2006).

The seemingly paradoxical result here is that activity in a sensory area correlates with a production task, whereas the activity in a premotor area does not. However, the activity in the premotor area still demonstrated (1) a response to listening to speech sounds, (2) a discrimination between native and non-native speech sounds, and (3) functional connectivity with the superior temporal auditory cortices. Taken together, these fMRI data suggest that

<sup>1</sup> The motor theory of speech perception also makes assumptions of nativism and modularity that are irrelevant here and that the studies reviewed here cannot support or reject.

while the superior temporal cortex transforms acoustic signal to phonetic code, the premotor area responsive to both production and perception of speech sounds may be responsible for the generation of forward models (Haruno et al., 2001) of phonemic categorization, which would be intrinsically motor. These forward models, predicting the acoustic consequences of the motor phonemic categorization, would then be compared to the acoustic input in superior temporal cortex. Here, an 'error' signal, that is, the discrepancy between the acoustic input and the prediction of the acoustic consequence of the motor plan, would be generated, producing the correlation between activity in an auditory area and producibility of the speech sounds (Wilson and Iacoboni, 2006). The error signal, then, would be used to correct the phonemic categorization in premotor cortex. Thus, if this account is correct, speech perception is neither a purely sensory nor a purely motor phenomenon, but rather requires the integration of sensory and motor information in a recursive sensory-motor process involving both superior temporal and premotor cortex (Fig. 1).

Obviously, this account implies an active and causal role of the motor system in speech perception. Since fMRI can only provide correlative information about activated brain areas, only a TMS 'virtual lesion' experiment can demonstrate such active and causal role. Indeed, a recent repetitive TMS (rTMS) study has provided such evidence (Meister et al., 2007). In this study subjects performed a phonetic discrimination task, a tone discrimination task, and a color discrimination task. Task difficulty was equated using 1-up-2-down adaptive staircase procedures. Low frequency rTMS was applied over the left premotor area for speech production and perception, and over the left superior temporal cortex. The model described in Fig. 1 predicts higher TMS-induced deficits in the tone task when rTMS is applied to the superior temporal cortex and higher TMS-induced deficits in the speech perception task when rTMS is applied to the premotor cortex. Indeed, the results of this recent rTMS study fit quite well this predicted pattern of activity (Meister et al., 2007). In the tone discrimination task, there was a significant decrease in correct responses after TMS over the left superior temporal cortex, but not after TMS over the left premotor area responding to speech sounds. In contrast, there was a significant decrease of correct responses in the phonetic discrimination task after TMS over the left premotor area but not after TMS over the left superior temporal cortex. Finally, the color discrimination task was not affected by TMS over the premotor and the superior temporal cortex (Meister et al., 2007). These data clearly support the hypothesis of an interplay between superior temporal and premotor areas in speech perception, with superior temporal areas providing an acoustic analysis of the input and pre-

motor areas providing a phonemic categorization of the heard speech sound. Furthermore, to the best of my knowledge, these data are the first empirical demonstration of a causal link between a premotor area and any form of human perception.

### 3. Concluding remarks

This article has discussed recent fMRI and rTMS evidence suggesting an active role of premotor areas in speech perception. This new evidence fits well previous psychological models of speech perception that invoked an active role of motor structures in the perception of speech sounds (Liberman et al., 1957, 1967; Liberman and Mattingly, 1985; Liberman and Whalen, 2000; Fowler and Rosenblum, 1991). While the data clearly point to functional interactions between classical auditory areas, such as the superior temporal cortex, and premotor areas in speech perception, a likely role that premotor areas may have in speech perception is to provide an internal motor simulation of the perceived phonemes.

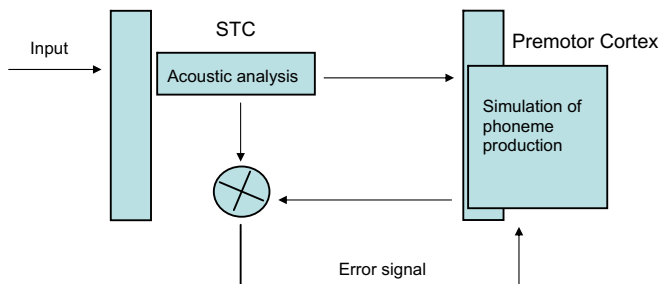
In evolutionary terms, the mechanism of simulation has been likely selected within the motor system in order to solve motor control problems due to slow re-afferent feedback (Haruno et al., 2001). This mechanism has been probably later co-opted to facilitate other functions, a phenomenon known in biology as exaptation (Gould and Vrba, 1982). Under this framework, simulation motor mechanisms for action control would have been co-opted to implement forms of communication between individuals that eventually became human language (Meister and Iacoboni, 2007).

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**Fig. 1.** According to a recent model (Wilson and Iacoboni, 2006), the superior temporal cortex (STC) would implement acoustic analysis while the premotor cortex would implement a simulation (forward model) of phoneme production. This forward model would allow the prediction of the acoustic consequences of phoneme production that would be compared in the superior temporal cortex with the acoustic analysis of the heard speech sounds. This comparison would generate an error signal to be sent back to premotor cortex, which would generate a corrected phoneme production simulation to be used for phoneme categorization.

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