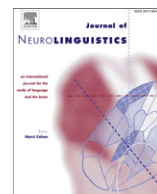




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The contribution of the frontal lobe to the perception of speech

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ABSTRACT

Classical models of language claim a clear-cut distinction between language production and perception, indicating for them a different localization in the brain, and limiting the involvement of the frontal lobe exclusively in motor functions. In this review we present empirical evidence pointing to a weaker separation between sensory and motor functions, showing that the motor system plays an important role also in perception. In particular, very recent neurophysiological literature shows that a selective alteration of neural activity in speech motor centers alters speech perception. This result not only confirms that the classical sensory versus motor separation has to be abandoned, but underlines the causal contribution of the frontal lobe to the perception of speech.

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1. Introduction

1.1. Broca's area and speech production

Although Marc Dax, during the first years of XIX century, already concluded that the loss of language was more frequently associated with damages to the left half of the brain, the French neurologist Paul Broca was the first in establishing that the posterior part of the left inferior frontal gyrus was of critical importance for language production. Broca's famous case, the patient "Tan" who was able to understand speech but was unable to speak, suffered from a lesion in an area, later named Broca's area,

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largely coincident with Brodmann areas 44 (pars opercularis) and 45 (pars triangularis) of the inferior frontal gyrus (see Amunts et al., 1999; Dronkers, Plaisant, Iba-Zizen, & Cabanis, 2007). Subsequently, the deficit associated with a lesion in Broca's area was defined as Broca's aphasia and described as a syndrome characterized by effortful speech production, impairment in melodic line and articulation, semantic and phonemic paraphasias, production of telegraphic sentences, reduced and abnormal grammatical form (Dronkers et al., 2007; McManus, 2002).

Modern textbooks consider Broca's 1861 paper as a landmark point for language localization research, as well as for the localizationist approach at large. No one would ever dare to contend that a lesion in that area causes production aphasia. However, many of Broca's contemporaries were reluctant in accepting his, often called, mosaic model (Freud, 1891; Jackson, 1874). In 1906 Pierre Marie, based on extensive clinico-anatomical studies showed that a given lesion location was not always associated to the same clinical picture (see Cole & Cole, 1971). However, fifty years later, the neurosurgeon Wilder Penfield experimentally demonstrated the direct involvement of Broca's region in speech production by electrically stimulating the frontal lobe in awake patients undergoing brain surgery. He reported that the stimulation of Broca's area, although with some individual variability, evoked the arrest of ongoing speech, thus definitely conferring a motor role to this region (Penfield & Roberts, 1959).

1.2. Broca's area and speech perception

From 1874, thanks to the work of Carl Wernicke, speech perception has been linked to the posterior part of the superior temporal gyrus (Wernicke's area) and the "classical model" of the neurobiological basis of language has started to emerge, based on the prominence of Broca's and Wernicke's regions in the left cerebral hemisphere, being considered expressive the first and receptive the second (see Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004). However, already in 1966, Luria had noted that **frontal lesioned** patients made language comprehension errors (Luria, 1966). Deficits are more evident when patients were tested with verbal material requiring syntactical understanding (Caramazza & Zurif, 1976). This description is in line with brain imaging studies indicating that in language comprehension Broca's area is activated when higher levels of linguistic processing are required (see Bookheimer, 2002 for a review). Furthermore, a series of cortical stimulation experiments demonstrated that Broca's area is implicated in both comprehension and production aspects of language (Burnstine et al., 1990; Ojemann, 1992; Ojemann, Ojemann, Lettich, & Berger, 1989). In particular, Schaffler, Luders, Dinner, Lesser, and Chelune (1993) reported on three patients, with intractable focal seizures arising from the language-dominant left hemisphere, that the electrical stimulation of Broca's area produced marked interference with language output functions as well as language comprehension deficits. These receptive deficits were predominantly in response to complex verbal instructions and in clear contrast with ability to process non-verbal material, not affected by the stimulation. Specifically, patients were tested using several different methods: 1) Patients were asked using multi-step commands such as "With your right hand touch your left ear, then close your eyes". 2) Patients were then asked questions such as "Where do you place food in the kitchen in order to keep it cold?" and if the patient was unable to answer, recognition was further evaluated by asking more specific questions. 3) Patients were also asked to point to various objects in the room. 4) Patients were administered with the Token test, and in detail to (a) pick up tokens specified by only one parameter; (b) pick up a token of a certain color, shape, and size from among 16 tokens; (c) pick up two tokens sequentially. 5) Patients were asked to match spoken sentences with appropriate pictures. Therefore, it seems plausible that anterior language areas are involved both in production and in several central language perception processes.

1.3. Fronto-parieto-temporal circuits and speech perception and production

While traditional models of language brain organization separated perceptual and production modules in distinct areas (Damasio & Geschwind, 1984; Gernsbacher & Kaschak, 2003), current models of language brain processing claim that several temporal, parietal and frontal areas interact in order to deliver the many features of language ability (Gow & Segawa, 2009; Mainy et al., 2008).

This position is supported by functional and anatomical results, showing that parallel circuits are working bidirectionally during speech processing. On the functional side, cortico-cortical evoked potentials demonstrate functional bidirectional connectivity between anterior and posterior language areas (Matsumoto et al., 2004). Anatomically speaking, the functional connection between anterior and posterior language areas is classically considered as mediated by the arcuate fasciculus. Recently the detailed anatomy of the arcuate fasciculus has been assessed by Diffusion Tensor Imaging showing both a direct and an indirect route passing through the inferior parietal lobule (Catani, Jones, & Ffytche, 2005).

However, Broca's area is not a homogenous area and can be subdivided according to different cytoarchitectonic features. Comparative cytoarchitectonics studies of the frontal cortex showed that, human pars opercularis (BA44, the posterior part of the classical Broca's area) is characterized by a rudimentary layer IV and no large cell bodies in layer III. More interestingly, this pattern is similar to that of monkey area F5, a typical premotor area, and human ventral premotor cortex (vPM). On the other hand, the pars triangularis (BA45, the anterior part of Broca's area) is characterized by an important granular layer IV and very large cell bodies in layer III, resembling human and monkey prefrontal cortices (Petrides, Cadoret, & Mackey, 2005). Therefore, according to cytoarchitectonical data, there seems to be an internal subdivision of human Broca's area, already present in the monkey brain, between a premotor-like (PM) and a prefrontal-like (PF) section.

Moreover, further evidence shows that these sectors of Broca's area have different connections with posterior language areas. The posterior aspect of Broca's area has shown a preferential connection with the anterior inferior parietal lobule whereas the anterior portion of Broca's area connects preferentially with the superior temporal gyrus (Frey, Campbell, Pike, & Petrides, 2008). This data is in good agreement with similar monkey results (Petrides & Pandya, 2009). However, an interesting research combining anatomical and functional measures indicated a slightly different connectivity pattern (Saur et al., 2008). More specifically, they show that PM connects with the inferior parietal lobule (IPL) and the entire superior temporal cortex (STG) whereas region PF is linked with the middle temporal gyrus (MTG). Nevertheless, these apparent discrepancies are well accounted by the differences in methods between the two studies. Frey et al. (2008) were concerned with mapping white matter fibers, whereas Saur et al. (2008) aimed at verifying the anatomical connection supporting a given function. As a matter of facts, Saur et al. (2008) showed that these two streams have a differential role in speech processing: Sublexical repetition of speech is subserved by the dorsal pathway (PM-IPL/STG), whereas higher-level language comprehension is mediated by the ventral pathway (PF-MTG).

Thus, sensory-motor mapping of sound to articulation, which might be generated by the co-occurrence of articulations and the perception of self-produced speech sounds, might be supported by the anatomo-functional connections outlined earlier. The correlated neuronal activity in motor and parieto-temporal areas could trigger long-term plastic processes based on Hebbian learning principles (Pulvermüller, 1999). In the evolving brain, the synaptic weights might indeed be tuned during a babbling phase in which random movements of the speech articulators provide tactile, proprioceptive, and auditory feedback signals that are used to learn the mappings between different neural representations (Garagnani, Wennekers, & Pulvermüller, 2008; Guenther, Ghosh, & Tourville, 2006).

2. Speech listening activates motor areas

Sensory-motor mapping of sound to articulation has gained more and more attention also due to the major change of perspective about the function of motor and premotor cortices. Once believed to be an output system driven by the perceptual brain, the motor system is now considered as an important component of perceptual and cognitive functions. This challenges the classical sensory vs motor separation (Young, 1970). The discovery that the agranular/disgranular frontal cortex is constituted of several distinct motor areas playing a role in motor control and in functions traditionally considered typical for higher order associative cortical areas, came from single cells recordings in the monkey brain. In these areas, different classes of visuo-motor neurons involved in sensorimotor transformation have been found, creating internal representations of actions (Rizzolatti & Craighero, 2004).

Several lines of research also in humans have suggested that these representations, in particular those linking action execution with action observation, may be used for various purposes, such as

action understanding and imitation. It has been suggested that this so-called “mirror neuron mechanism” may provide the brain with an implicit knowledge about the meaning of actions because seen actions are directly matched onto the observer's motor repertoire (see Rizzolatti & Craighero, 2004). Very interestingly, in humans, the core area of this mechanism is Broca's area (Binkofski et al., 1999; Buccino et al., 2001; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grèzes & Decety, 2001; Iacoboni et al., 1999; Nishitani & Hari, 2000).

Further, evidence indicates that action-related sensorimotor transformations are not restricted to visual information but concern also acoustic information. In the ventral premotor cortex of the monkey, sensory-motor neurons have been found which are active not only during action execution and action observation but also during the listening of the action-related sound (audio-visual mirror neurons, Kohler et al., 2002). This result has been considered evidence of the possibility to access to the motor representation of the action by means of every action-related information, indicating that this representation is multisensory or supra-sensory.

This finding has been extended to humans by a series of investigations involving different experimental techniques. Brain imaging experiments indicate that during the presentation of syllables and words, areas in the left inferior frontal and premotor cortex become active along with superior temporal areas (Siok, Jin, Fletcher, & Tan, 2003; Wilson, Saygin, Sereno, & Iacoboni, 2004; Zatorre, Evans, Meyer, & Gjedde, 1992). Also, magnetic-stimulation experiments suggest motor facilitation during speech perception (Fadiga, Craighero, Buccino, & Rizzolatti, 2002; Watkins & Paus, 2004; Watkins, Strafella, & Paus, 2003) supporting some of the claims of the Motor Theory of Speech Perception (MTSP), which postulated that the intended articulatory gestures, rather than sounds, are critical for both production and perception of speech (Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967; for a review see: Galantucci, Fowler, & Turvey, 2006). Specifically, in a TMS experiment (Fadiga et al., 2002) the authors started from the perspective that sounds conveying speech could be a vehicle of motor representations (articulatory gestures) shared by both the speaker and the listener, on which speech perception could be based upon. In other terms, the listener understands the speaker when his/her articulatory gestures representations are activated by verbal sounds. To test this hypothesis, normal subjects were requested to attend to an acoustically presented randomized sequence of disyllabic words and pseudo-words requiring or not important tongue movements when pronounced. The excitability of motor system in correspondence of tongue movements representation was assessed by using single pulse TMS and by recording motor evoked potentials (MEPs) from the anterior tongue muscles. The TMS stimuli were applied synchronously with the critical consonants. Results (see Fig. 1) showed that during speech listening there is an increase of motor evoked potentials recorded from the listeners' tongue muscles only when the listened word strongly involves tongue

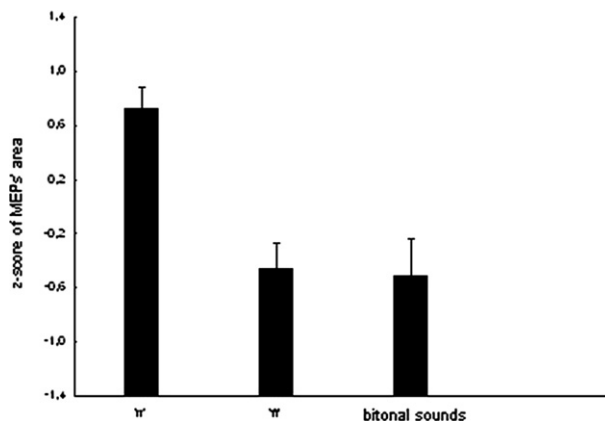


Fig. 1. The motor cortex is activated during speech perception. Listening to speech sounds activates corresponding motor representations necessary for the production of the same utterances. Fadiga et al. (2002) showed that listening to words or pseudo-words containing a double “r” sound induces larger MEPs elicited by the TMS stimulation of the tongue motor cortex.

movements, indicating that when an individual listens to verbal stimuli his/her speech related motor centers are specifically activated.

To investigate if specific motor structures, which are somatotopically organized to control different articulatory activities, are also differentially activated by incoming speech signals, an event-related functional MRI experiment was performed (Pulvermüller et al., 2006). The somatotopy of articulator gestures and articulations, was first mapped with a localizer task administered in the fMRI. Subjects had to move their lips or tongue and silently produce consonant–vowel syllables, starting with the lip-related [p] and tongue-related [t] phonemes. These tasks were performed by the same subjects who, in a different experiment, had listened to a stream of syllables that also started with [p] and [t]. Results showed the somatotopic distinction of motor regions in the precentral gyrus which reflect articulatory movements of the lips and tongue were also differentially activated in a somatotopic manner when participants listened to the lip- or tongue-related phonemes. This result shows that, during speech listening, specific motor circuits are recruited for the analysis of the speech sounds features, supporting a specific link between mechanisms for speech perception and production.

3. Causal role of motor areas in speech perception

A distinctive feature of action-perception-theories in general and in the domain of language specifically, is that motor areas are considered necessary for perception (Pulvermüller, 1999). Indeed, the aphasia literature already documents a necessary role of the inferior frontal cortex in speech perception, as lesions in this region lead to comprehension deficits (see Section 1.1 above). Neuro-computational lesion studies further show that the pattern of speech production and perception deficits seen in the different syndromes of aphasia, are best accounted for by models of functionally interwoven action-perception circuits (Pulvermüller & Preissl, 1991). 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 (Toni, de Lange, Noordzij, & Hagoort, 2008). In fact, the mere activation of motor areas during listening to speech might be caused by a corollary cortico-cortical connection that has nothing to do with the process of comprehension itself. Therefore, a possible solution might come from the selective alteration of neural activity in speech motor centers and the evaluation of effects on perception. Repetitive TMS (rTMS) was applied in the ventral premotor cortex in a series of speech discrimination tasks (Meister, Wilson, Deblieck, Wu, & Iacoboni, 2007; Möttönen & Watkins, 2009; Sato, Tremblay, & Gracco, 2009). The target area was that premotor region activated both during speech production and speech perception (Wilson et al., 2004). In Meister et al. (2007) participants were tested on a speech perception task involving discrimination of voiceless stop consonants in single syllables that were masked by white noise. Results showed that participants were impaired in this task but were unaffected in a control task matched in difficulty, task structure, and response characteristics. However rTMS effects spread uncontrollably to other areas, eventually resulting in a global functional reshaping of whole-brain dynamics.

Event-related TMS 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. Very recently in fact, a novel TMS experiment was designed by using a crossover design, orthogonalizing brain-phonology-concordance (D'Ausilio et al., 2009). Participants' had to recognize and classify phonemes produced by the tongue ([d] and [t]) or the lips ([b] and [p]). Double on-line TMS pulses were applied either to the lip or tongue motor representations of the precentral cortex, just prior to stimuli presentation. Results showed that participants' performance, both in terms of RT and accuracy, showed a double dissociation between stimulation site and stimulus categories (see Fig. 2): the stimulation of tongue motor representation reduced the reaction times in response to [d] and [t] and increased the number of errors for [b] and [p], while the stimulation of lips motor representation facilitated the response to [b] and [p] and made it worse for [d] and [t]. These results provide strong support for a specific functional role of motor system in the perception of speech sounds.

Computationally speaking, primary motor cortex stimulation might preactivate that specific sector, either representing tongue or lips movements, by increasing the excitability of neurons therein, that, in turn, might exert the facilitation of neurons located in premotor areas,

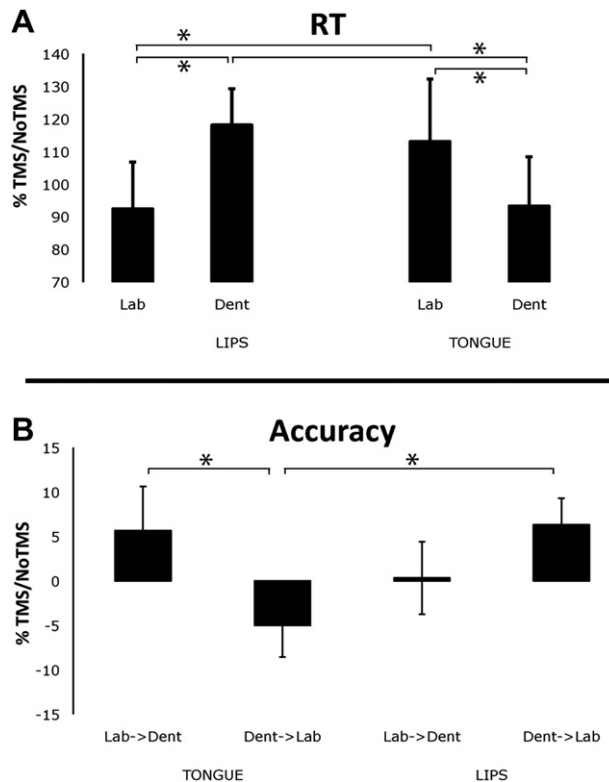


Fig. 2. The motor system is causally involved in speech perception. The motor system activity induced by listening to speech is necessary for the discrimination of the same sounds. D'Ausilio et al. (2009) showed that selective alteration of the activity in the motor system causes changes in reaction times (panel A) and accuracy (panel B) in a phoneme discrimination task.

somatotopically connected through bidirectional cortico-cortical links. The activation of the relative motor representation might favor one specific sensory hypothesis, leading to faster reaction times if the stimuli are functionally linked to the stimulated area, and reducing discrimination performance in the other class of stimuli. Neurocomputational studies confirm this postulate (Garagnani et al., 2008; Pulvermüller & Preissl, 1991).

The basic finding that activity in the motor system can alter speech discrimination is a direct evidence that sensory and motor processes interact during speech perception. Further indication for the existence of such an interaction is given both by an experiment showing that speech discrimination is biased by artificial facial tactile stimulations, simulating somatosensory afference during production (Ito, Tiede, & Ostry, 2009), and by a recent study that extracted the functional connectivity patterns in fMRI data, during listening to speech (Londei et al., 2007, in press). In the former study (Ito et al., 2009), participants listened to stimuli taken from a continuum between the words “head” and “had”, while their face was stretched to create patterns of facial skin deformation similar to those involved in the production of either the word “head” or “had”. Results showed that speech sound classification changed in a predictable way depending on the direction of skin stretch. This finding is considered evidence of the sensory-motor interaction during speech perception since somatosensory inputs associated with facial skin deformation are a primary source of sensory support for speech motor function owing to the lack of muscle proprioceptors in many orofacial muscles. The results of the latter study (Londei et al., 2007, in press) showed that only if the listened stimulus is pronounceable (i.e. a word or a phonologically legal pseudoword) an interconnected network of areas including inferior parietal, postcentral and precentral areas is activated. The somatosensory and motor components of

this network are functionally disconnected when listening to stimuli that are not pronounceable, such as during listening to time-reversed words.

4. Conclusions

The findings reviewed in the present paper indicate that areas in the frontal lobe involved in speech production are specifically contributing to speech perception, and that activity in the motor system can alter speech discrimination, directly indicating that sensory-motor processes interact during speech comprehension. The experimental evidence of a causal relationship between activity in motor areas and speech perception (D'Ausilio et al., 2009; Meister et al., 2007) provide evidence that activation of motor areas during listening to speech is NOT the consequence of a corollary cortico-cortical connection (as erroneously proposed by Toni et al., 2008) but reflects the sensory-motor nature of perceptual representations.

In conclusion, there is growing experimental evidence indicating that perceptual regions are not sufficient alone for the perception of action-related sensory-information, and that the contribution of the motor system in the frontal lobe is essential to access the implicit knowledge about actions. Furthermore, this mechanism might be applied also to speech perception. This mechanism is applicable to speech perception and recognition defined as the identification of spoken phonemes and word forms as unique articulatory-acoustic entities.

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References

- Amunts, K., Schleicher, A., Bürgel, U., Mohlberg, H., Uylings, H. B., & Zilles, K. (1999). Broca's region revisited: cytoarchitecture and intersubject variability. *Journal of Comparative Neurology*, 412, 319–341.
- Binkofski, F., Buccino, G., Posse, S., Seitz, R. J., Rizzolatti, G., & Freund, H. A. (1999). Fronto-parietal circuit for object manipulation in man: evidence from an fMRI-study. *European Journal of Neuroscience*, 11, 3276–3286.
- Bookheimer, S. (2002). Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience*, 25, 151–188.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *European Journal of Neuroscience*, 13, 400–404.
- Burnstine, T. H., Lesser, R. P., Hart, J., Jr., Uematsu, S., Zinreich, S. J., Krauss, G. L., et al. (1990). Characterization of the basal temporal language area in patients with left temporal lobe epilepsy. *Neurology*, 40, 966–970.
- Caramazza, A., & Zurif, E. B. (1976). Dissociation of algorithmic and heuristic processes in language comprehension: evidence from aphasia. *Brain and Language*, 3, 572–582.
- Catani, M., Jones, D. K., & Ffytche, D. H. (2005). Perisylvian language networks of the human brain. *Annals of Neurology*, 57, 8–16.
- Cole, M. F., & Cole, M. (1971). *Pierre Marie's papers on speech disorders*. New York: Hafner Press.
- D'Ausilio, A., Pulvermüller, F., Salmas, P., Bufalari, I., Begliomini, C., & Fadiga, L. (2009). The motor somatotopy of speech perception. *Current Biology*, 19, 381–385.
- Damasio, A. R., & Geschwind, N. (1984). The neural basis of language. *Annual Review of Neuroscience*, 7, 127–147.
- Damasio, H., Tranel, D., Grabowski, T., Adolphs, R., & Damasio, A. (2004). Neural systems behind word and concept retrieval. *Cognition*, 92, 179–229.
- Dronkers, N. F., Plaisant, O., Iba-Zizen, M. T., & Cabanis, E. A. (2007). Paul Broca's historic cases: high resolution MR imaging of the brains of Leborgne and Lelong. *Brain*, 130, 1432–1441.
- Fadiga, L., Craighero, L., Buccino, G., & Rizzolatti, G. (2002). Speech listening specifically modulates the excitability of tongue muscles: a TMS study. *European Journal of Neuroscience*, 15, 399–402.
- Freud, S. (1891). *Zur auffassung der aphasien*. Leipzig: Deuticke.
- Frey, S., Campbell, J. S., Pike, G. B., & Petrides, M. (2008). Dissociating the human language pathways with high angular resolution diffusion fiber tractography. *Journal of Neuroscience*, 28, 11435–11444.
- Galantucci, B., Fowler, C. A., & Turvey, M. T. (2006). The motor theory of speech perception reviewed. *Psychonomic Bulletin Review*, 13, 361–377.
- Garagnani, M., Wennemers, T., & Pulvermüller, F. (2008). A neuroanatomically-grounded Hebbian learning model of attention-language interactions in the human brain. *European Journal of Neuroscience*, 27(2), 492–513.
- Gernsbacher, M. A., & Kaschak, M. P. (2003). Neuroimaging studies of language production and comprehension. *Annual Review of Psychology*, 54, 91–114.
- Gow, D. W., Jr., & Segawa, J. A. (2009). Articulatory mediation of speech perception: a causal analysis of multi-modal imaging data. *Cognition*, 110, 222–236.

- Grafton, S. T., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Experimental Brain Research*, 112, 103–111.
- Grèzes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. *Human Brain Mapping*, 12, 1–19.
- Guenther, F. H., Ghosh, S. S., & Tourville, J. A. (2006). Neural modeling and imaging of the cortical interactions underlying syllable production. *Brain and Language*, 96, 280–301.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 286, 2526–2528.
- Ito, T., Tiede, M., & Ostry, D. J. (2009). Somatosensory function in speech perception. *Proceedings of the National Academy of Sciences U S A*, 106, 1245–1248.
- Jackson, J. H. (1874). On the nature of the duality of the brain. *Medicine Press Circular*, 1, 63.
- Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: action representation in mirror neurons. *Science*, 297, 846–848.
- Lieberman, A., Cooper, F., Shankweiler, D., & Studdert-Kennedy, M. (1967). Perception of the speech code. *Psychological Review*, 74, 431–461.
- Londei, A., D'Ausilio, A., Basso, D., Sestieri, C., Del Gratta, C., Romani, G., et al. (2007). Brain network for passive word listening as evaluated with ICA and granger causality. *Brain Research Bulletin*, 72, 284–292.
- Londei, A., D'Ausilio, A., Basso, D., Sestieri, C., Del Gratta, C., Romani, G., et al. *Sensory-motor brain network connectivity for speech comprehension*, in press. DOI: [10.1002/hbm.20888](https://doi.org/10.1002/hbm.20888).
- Luria, A. (1966). *The higher cortical function in man*. New York: Basic Books.
- Mainy, N., Jung, J., Baci, M., Kahane, P., Schoendorff, B., Minotti, L., et al. (2008). Cortical dynamics of word recognition. *Human Brain Mapping*, 29, 1215–1230.
- Matsumoto, R., Nair, D., LaPresto, E., Najm, I., Bingaman, W., Shibusaki, H., et al. (2004). Functional connectivity in the human language system: a cortico-cortical evoked potential study. *Brain*, 127, 2316–2330.
- McManus, C. (2002). *Right hand, left hand: The origins of asymmetry in brain, bodies, atoms, and cultures*. Cambridge, MA: Harvard University Press.
- Meister, I. G., Wilson, S. M., Deblieck, C., Wu, A. D., & Iacoboni, M. (2007). The essential role of premotor cortex in speech perception. *Current Biology*, 17, 1692–1696.
- Möttönen, R., & Watkins, K. E. (2009). Motor representations of articulators contribute to categorical perception of speech sounds. *Journal of Neuroscience*, 29, 9819–9825.
- Nishitani, N., & Hari, R. (2000). Temporal dynamics of cortical representation for action. *Proceeding of the National Academy of Sciences USA*, 97, 913–918.
- Ojemann, G. (1992). Localization of language in frontal cortex. *Advances in Neurology*, 57, 361–368.
- Ojemann, G., Ojemann, J., Lettich, E., & Berger, M. (1989). Cortical language localization in left, dominant hemisphere. An electrical stimulation mapping investigation in 117 patients. *Journal of Neurosurgery*, 71, 316–326.
- Penfield, W., & Roberts, L. (1959). *Speech and brain mechanisms*. Princeton: Princeton University Press.
- Petrides, M., Cadoret, G., & Mackey, S. (2005). Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature*, 435, 1235–1238.
- Petrides, M., & Pandya, D. N. (2009). Distinct parietal and temporal pathways to the homologues of Broca's area in the monkey. *PLoS Biology*, 7, e1000170.
- Pulvermüller, F. (1999). Words in the brain's language. *Behavioral & Brain Science*, 22, 253–279.
- Pulvermüller, F., Huss, M., Kherif, F., Moscoso del Prado Martin, F., Hauk, O., & Shtyrov, Y. (2006). Motor cortex maps articulatory features of speech sounds. *Proceedings of the National Academy of Sciences U S A*, 103, 7865–7870.
- Pulvermüller, F., & Preissl, H. (1991). A cell assembly model of language. *Network: Computation in Neural Systems*, 2, 455–468.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192.
- Sato, M., Tremblay, P., & Gracco, V. L. (2009). A mediating role of the premotor cortex in phoneme segmentation. *Brain & Language*. doi:10.1016/j.bandl.2009.03.002.
- Saur, D., Kreher, B. W., Schnell, S., Kummerer, D., Kellmeyer, P., Vry, M. S., et al. (2008). Ventral and dorsal pathways for language. *Proceedings of the National Academy of Sciences U S A*, 105, 18035–18040.
- Schaffler, L., Luders, H., Dinner, D., Lesser, R., & Chelune, G. (1993). Comprehension deficits elicited by electrical stimulation of Broca's area. *Brain*, 116, 695–715.
- Siok, W. T., Jin, Z., Fletcher, P., & Tan, L. H. (2003). Distinct brain regions associated with syllable and phoneme. *Human Brain Mapping*, 18, 201–207.
- Toni, I., de Lange, F. P., Noordzij, M. L., & Hagoort, P. (2008). Language beyond action. *Journal of Physiology – Paris*, 102, 71–79.
- Watkins, K., & Paus, T. (2004). Modulation of motor excitability during speech perception: the role of Broca's area. *Journal of Cognitive Neuroscience*, 16, 978–987.
- Watkins, K. E., Strafella, A. P., & Paus, T. (2003). Seeing and hearing speech excites the motor system involved in speech production. *Neuropsychologia*, 41, 989–994.
- Wilson, S. M., Saygin, A. P., Sereno, M. I., & Iacoboni, M. (2004). Listening to speech activates motor areas involved in speech production. *Nature Neuroscience*, 7, 701–702.
- Young, R. M. (1970). *Mind, brain and adaptation in the nineteenth century. Cerebral localization and its biological context from Gall to Ferrier*. Oxford: Clarendon Press.
- Zatorre, R. J., Evans, A. C., Meyer, E., & Gjedde, A. (1992). Lateralization of phonetic and pitch discrimination in speech processing. *Science*, 256, 846–849.