

HAND ACTIONS AND SPEECH REPRESENTATION IN BROCA'S AREA

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ABSTRACT

This paper presents data and theoretical framework supporting a new interpretation of the role played by Broca's area. Recent brain imaging studies report that, in addition to speech-related activation, Broca's area is also significantly involved during tasks devoid of verbal content. In consideration of the large variety of experimental paradigms inducing Broca's activation, here we present some neurophysiological data from the monkey homologue of Brodmann's areas (BA) 44 and 45 aiming to integrate on a common ground these apparently different functions. Finally, we will report electrophysiological data on humans which connect speech perception to the more general framework of other's action understanding.

Key words: hand action, speech, Broca's area, mirror neurons, neurophysiology, transcranial magnetic stimulation

A series of studies on the brain correlates of the verbal function demonstrate the involvement of Broca's region (Brodmann's area – BA 44) during both speech generation (see Liotti et al., 1994 for review) and speech perception (see Papathanassiou et al., 2000 for a review of recent papers). Recently, however, several experiments have shown that Broca's area is involved also in very different cognitive and perceptual tasks, not necessarily related to speech. Brain imaging experiments have highlighted the possible contribution of BA 44 in "pure" memory processes (Mecklinger et al., 2002; Ranganath et al., 2003), in calculation tasks (Gruber et al., 2001), in harmonic incongruity perception (Maess et al., 2001), in tonal frequency discrimination (Muller et al., 2001) and in binocular disparity (Negawa et al., 2002). Another important contribution of BA 44 is certainly found in the motor domain and motor-related processes. Gerlach et al. (2002) found an activation of BA 44 during a categorization task only if performed on artifacts. Kellenbach et al. (2003) found a similar activation when subjects were required to answer a question concerning the action evoked by manipulable objects. Several studies reported a significant activation of BA 44 during execution of grasping and manipulation (Binkofski et al., 1999a, 1999b; Gerardin et al., 2000; Grèzes et al., 2003; Hamzei et al., 2003; Lacquaniti et al., 1997; Matsumura et al., 1996; Nishitani and Hari, 2000). Moreover, the activation of BA 44 is not restricted to motor execution but spreads over to motor imagery (Binkofski et al., 2000; Gerardin et al., 2000; Grèzes and Decety, 2002).

From a cytoarchitectonical point of view (Petrides and Pandya, 1997), the monkey's frontal area which closely resembles human Broca's region is a premotor area (area F5 as defined by Matelli et

al., 1985). Single neuron studies (see Rizzolatti et al., 1988) showed that hand and mouth movements are represented in area F5. The specificity of the goal seems to be an essential prerequisite in activating these neurons. The same neurons that discharge during grasping, holding, tearing, manipulating, are silent when the monkey performs actions that involve a similar muscular pattern but with a different goal (i.e., grasping to put away, scratching, grooming, etc.). All F5 neurons share similar motor properties. In addition to their motor discharge, however, a particular class of F5 neurons discharges also when the monkey observes another individual making an action in front of it ('mirror neurons'; Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996a). There is a strict congruence between visual and motor properties of F5 mirror neurons: e.g., mirror neurons motorically coding whole hand prehension discharge during observation of whole hand prehension performed by the experimenter but not during observation of precision grasp. The most likely interpretation for the visual response of these visuomotor neurons is that, at least in adult individuals, there is a close link between action-related visual stimuli and the corresponding actions that pertain to monkey's motor repertoire. Thus, every time the monkey observes the execution of an action, the related F5 neurons are addressed and the specific action representation is "automatically" evoked. Under certain circumstances it guides the execution of the movement, under others, it remains an unexecuted representation of it, that might be used to understand what others are doing.

Transcranial magnetic stimulation (TMS) (Fadiga et al., 1995; Strafella and Paus, 2000) and brain imaging experiments demonstrated that a mirror-neuron system is present also in humans:

when the participants observe actions made by human arms or hands, motor cortex becomes facilitated (this is shown by TMS studies) and cortical activations are present in the ventral premotor/inferior frontal cortex (Rizzolatti et al., 1996b; Grafton et al., 1996; Decety et al., 1997; Grèzes et al., 1998, 2003; Iacoboni et al., 1999; Decety and Chaminade, 2003). Grèzes et al. (1998) showed that the observation of meaningful but not that of meaningless hand actions activates the left inferior frontal gyrus (Broca's region). Two further studies have shown that observation of meaningful hand-object interaction is more effective in activating Broca's area than observation of non goal-directed movements (Hamzei et al., 2003; Johnson-Frey et al., 2003). Similar conclusions have been reached also for mouth movement observation (Campbell et al., 2001). In addition, direct evidence for an observation/execution matching system has been recently provided by two experiments, one employing functional magnetic resonance imaging (fMRI) technique (Iacoboni et al., 1999), the other using event-related magnetoencephalography (MEG) (Nishitani and Hari, 2000), that directly compared in the same subjects action observation and action execution.

The evidence that Broca's area is activated during time perception (Schubotz et al., 2000), calculation tasks (Gruber et al., 2001), harmonic incongruity perception (Maess et al., 2001), tonal frequency discrimination (Muller et al., 2001), prediction of sequential patterns (Schubotz and von Cramon, 2002a) as well as during prediction of increasingly complex target motion (Schubotz and von Cramon, 2002b), suggest that this area could have a central role in human representation of sequential information in several different domains (Lieberman, 1991). This could be crucial for action understanding, allowing the parsing of observed actions on the basis of the predictions of their outcomes. Others' actions do not generate only visually perceivable signals. Action-generated sounds and noises are also very common in nature. In a very recent experiment Kohler et al. (2002) have found that 13% of the investigated F5 neurons discharge both when the monkey performed a hand action and when it heard the action-related sound. Moreover, most of these neurons discharge also when the monkey observed the same action demonstrating that these 'audio-visual mirror neurons' represent actions, independently of whether they are *performed*, *heard* or *seen*. The presence of an audio-motor resonance in a region that, in humans, is classically considered a speech-related area, prompts the Liberman's hypothesis on the mechanism at the basis of speech perception (motor theory of speech perception; Liberman et al., 1967; Liberman and Mattingly, 1985; Liberman and Wahlen, 2000). This theory maintains that the ultimate constituents of speech are not sounds but articulatory gestures

that have evolved exclusively at the service of language. Speech perception and speech production processes could thus use a common repertoire of motor primitives that, during speech production, are at the basis of articulatory gesture generation, and during speech perception are activated in the listener as the result of an acoustically evoked motor "resonance". According to Liberman's theory (Lieberman et al., 1967; Liberman and Mattingly, 1985; Liberman and Wahlen, 2000), the listener understands the speaker when his/her articulatory gestures representations are activated by the listening to verbal sounds. Although this theory is not unanimously accepted, it offers a plausible model of an action/perception cycle in the frame of speech processing.

To investigate if speech listening activates listener's motor representations, Fadiga et al. (2002) administered TMS on cortical tongue motor representation, while subjects were listening to various verbal and non-verbal stimuli. Motor evoked potentials (MEPs) were recorded from subjects' tongue muscles. Results showed that during listening of words formed by consonants implying tongue mobilization (i.e., Italian 'R' vs. 'F') MEPs significantly increased. This indicates that when an individual listens to verbal stimuli, his/her speech related motor centers are specifically activated. Moreover, words-related facilitation was significantly larger than pseudo-words related one.

The presence of "audio-visual" mirror neurons in the monkey and the presence of "speech-related acoustic motor resonance" in humans, suggests that, independently of the sensory nature of the perceived stimulus, the mirror-neuron resonant system retrieves from the action vocabulary (stored in the frontal cortex) the stimulus-related motor representations. It is however unclear if the activation of the motor system during speech listening is causally related to speech perception, or if it is a mere epiphenomenon due, for example, to an automatic compulsion to repeat without any role in speech processing. One experimental approach to answer this question could be to interfere with speech perception by applying TMS on speech-related motor areas. Although classical theories consider the inferior frontal gyrus as the "motor center" for speech production, cytoarchitectonical homologies with monkey area F5, and brain imaging and patients studies (among more recent publications see Watkins and Paus, 2004; Dronkers et al., 2004, Wilson et al., 2004) suggest that this region may play a fundamental role in perceived speech processing. Broca's area was therefore selected as the best candidate for our study.

In order to investigate a possible role of Broca's area in speech perception, both at the lexical and at the phonological level (Fadiga et al., 2002 showed that both these speech-related properties influence motor resonance) we selected a priming paradigm. Priming experiments, in general, demonstrate that

TABLE I
Example of the stimuli used in the experiment

	Rhyming	Not-rhyming
Word/word	zucca (pumpkin) – mucca (cow)	fiume (river) – scuola (school)
Word/pseudo-word	freno (brake) – preno	strada (street) – terto
Pseudo-word/pseudo-word	losse – tosse (cough)	stali – letto (bed)
Pseudo-word/pseudo-word	polta – solta	brona – dasta

whenever a word (target) is preceded by a somehow related word (prime) it is processed faster than when it is preceded by an unrelated word. The prime can therefore have either a semantic or phonologic relation with the target. Our starting aim was to test the possibility to modulate this facilitation by interfering on Broca's activity with TMS. A magnetic stimulus delivered immediately after the listening of the prime, on a functionally-related brain region, should impair prime processing, resulting in a modification in the priming effect. In our experiment we used the paradigm by Emmorey et al. (1989) in which subjects are requested to perform a lexical decision on a target preceded by a rhyming or not rhyming prime. By manipulating the lexical content of both the prime and the target stimuli (Emmorey et al., 1989, used only word prime), in addition to the rhyming effect we tested also the role of Broca's area at the lexical level. Single pulse TMS was administered to Broca's region in 50% of the trials while subjects were submitted to a lexical decision task on the target. Subjects had to respond by pressing one of two keys with their left index finger. TMS was administered during the 20 msec pause between prime and target acoustic presentation (interstimulus interval – ISI). The click

of the stimulator never overlapped with the acoustic stimuli. The pairs of verbal stimuli could pertain to four categories which differed for presence of lexical content (words vs. pseudo-words) in the prime and in the target (Table I).

From data analysis on trials without TMS (see Figure 1) an interesting (and unexpected) finding emerged: lexical content of the stimuli modulates the phonological priming effect. No priming effect was found in the pseudo-word/pseudo-word condition in which neither the target nor the prime was an element of the lexicon. In other words, in order to have a phonological effect it is necessary to have the access to the lexicon. In trials during which TMS was delivered, a TMS-dependent effect was found only in pairs where the prime was a word and the target was a pseudo-word, and consisted in the abolition of the phonological priming effect. Thus, TMS on Broca's area made the pairs word/pseudo-word similar to the pseudo-word/pseudo-word ones.

This finding suggests that the stimulation of the Broca's region might have affected the priming effect not because it interferes with phonological processing but because it interferes with lexical categorization of the prime. In support to this

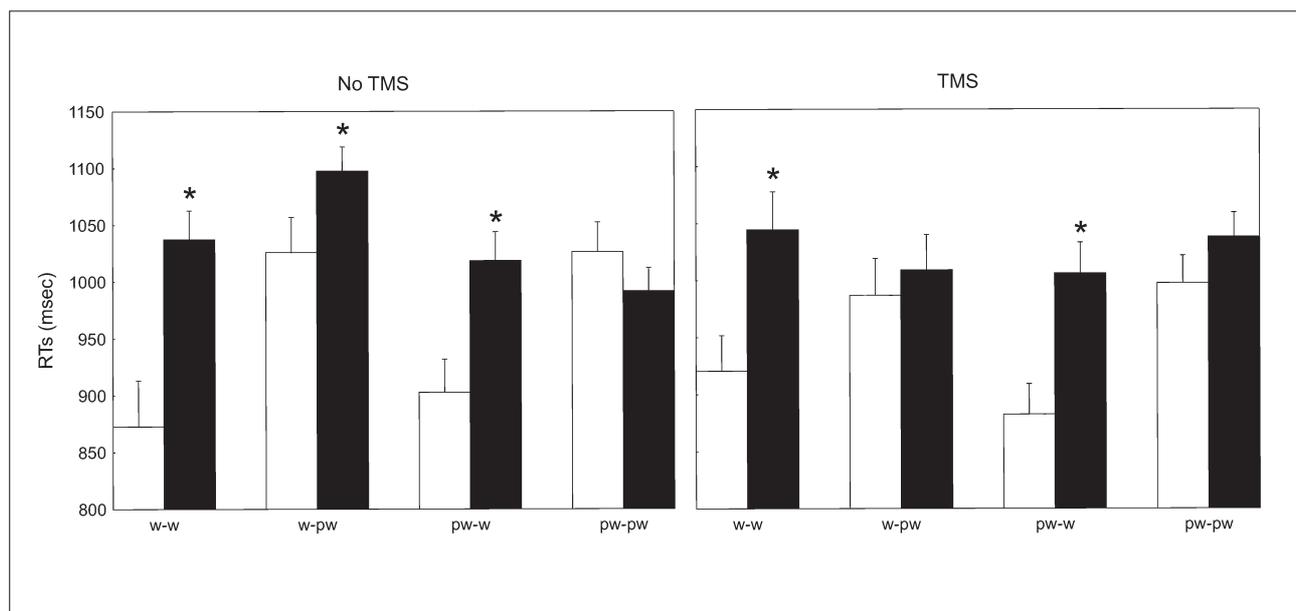


Fig. 1 – Reaction times (RTs \pm standard error of mean – SEM – in msec) for the lexical decision during the phonological priming task without (left panel) and with (right panel) transcranial magnetic stimulation (TMS) administration. White bars: conditions in which prime and target share a rhyme. Black bars: no rhyme. Asterisk on the black bar means the presence ($p > .05$, Newman-Keuls test) of a phonological priming effect (response to rhyming target faster than response to not-rhyming target) in the relative condition. TMS administration did not influence the accuracy of the participants that was always close to 100%. W-W: prime-word/target-word; W-PW: prime-word/target-pseudo-word; PW-W: prime-pseudo-word/target-word; PW-PW: prime-pseudo-word/target-pseudo-word.

interpretation are recent results from Blumstein et al. (2000) who have found that Broca's aphasics display deficits in the facilitation of lexical decision targets by prime words that rhyme with the target. In contrast, Wernicke's aphasics showed a pattern of results similar to that of normal subjects. Moreover, Milberg et al. (1988), in a phonological distortion study, showed that Broca's aphasics failed to show semantic priming when the phonological form of the prime stimulus was distorted. The authors interpreted this finding in the framework of the hypothesis that Broca's aphasics have reduced lexical activation levels (Utman et al., 2001). As a result, while in normal subjects an acoustically degraded input is able to activate the lexical representation, in aphasics it fails to reach a sufficient level of activation. However, there is evidence that Broca's aphasics have impaired lexical access even in response to intact acoustic inputs (Milberg et al., 1988).

The results of our TMS experiment on phonological priming, together with the data on patients reported above, lead to the conclusion that Broca's region is not the main responsible for the acoustic motor resonance effect shown by Fadiga et al. (2002). This effect was in fact present during listening of both words and pseudo-words and was only partially related to lexical properties of the heard stimuli. The localization of the premotor area involved in such a "low level" motor resonance will be the argument of our future experimental work.

CONCLUSIONS

In the present paper we discuss the possibility that the activation of Broca's region during speech processing, more than indicating a specific role of this area, may reflect its general involvement in meaningful action recognition. This possibility finds its basis on the observation that in addition to speech-related activation, this area is activated during observation of meaningful hand or mouth actions. Speech represents a particular case of this general framework: among meaningful actions, phonoarticulatory gestures are meaningful actions conveying words. This hypothesis is moreover supported by the observation that Broca's aphasics, in addition to speech production deficits, show an impaired access to the lexicon (although for some category of verbal stimuli). The consideration that Broca's area is the human homologue of monkey mirror neurons area, opens the possibility that human language may have evolved from an ancient ability to recognize actions performed by others, visually or acoustically perceived. The Liberman's intuition (Liberman et al., 1967; Liberman and Mattingly, 1985; Liberman and Wahlen, 2000) that the ultimate constituents of speech are not sounds but articulatory gestures that have evolved

exclusively at the service of language, seems to us a good way to consider speech processing in the more general context of action recognition.

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