

CHAPTER 6

Cues on the origin of language**From electrophysiological data on mirror neurons and motor representations**

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Introduction

There are two main views on the origin of human language. The first is that it derives from animal's call, the other from gestures. In the present article we argue that the second view is much more plausible. We discuss first a neurophysiological mechanism, the mirror neuron system, which solves the problem of direct comprehension of action meaning. We discuss then how this system can be also at the basis of speech perception.

The faculty of language is a cognitive ability that only humans possess. How then, did language appear? This is a completely open question. Yet, the discovery of a new class of neurons in the monkey, the so-called *mirror neurons*, indicates a mechanism that may give some clues on the origin of speech and its continuity with non-human primate behaviour. This mechanism, in fact, is of great evolutionary importance since it is supposed to be at the basis of the way in which primates understand actions made by their conspecifics. Moreover, evidence coming from different experimental approaches has demonstrated that a mirror-neuron system is present also in humans. The most intriguing finding deriving from brain imaging studies is that one of the regions mainly involved in this system is the left inferior frontal cortex in correspondence of the Broca's region which is classically considered a language-related brain region. In the present article we will briefly describe the basic properties of mirror neurons in non-human primates and man and we will present some experimental data indicating that the mirror neuron system in humans could be at the basis of speech perception.

Mirror neurons in monkeys

Mirror neurons are a set of neurons originally discovered in the ventral premotor cortex of the macaque monkey. Their defining property is that they became active both when the monkey *does* a particular action (like grasping an object) and when it *observes* another individual making a similar action (see Rizzolatti et al. 2001). In order to be triggered by visual stimuli, mirror neurons require an interaction between a biological effector (hand or mouth) and an object. The sights of an object alone, of an agent mimicking an action, or of an individual making intransitive (non-object directed) gestures are all ineffective. The object significance for the monkey has no obvious influence on mirror neuron response. Grasping a piece of food or a geometric solid produces responses of the same intensity. Mirror neurons show a large degree of generalization. Largely different visual stimuli, but representing the same action, are equally effective. For example, the same grasping mirror neuron that responds to a human hand grasping an object, responds also when the grasping hand is that of a monkey. Similarly, the response is, typically, not affected if the action is done near or far from the monkey, in spite of the fact that the size of the observed hand is obviously different in the two conditions. It is also of little importance for neuron activation if the observed action is eventually rewarded. The discharge is of the same intensity if the experimenter grasps the food and gives it to the recorded monkey or to another monkey, introduced in the experimental room.

An important functional aspect of mirror neurons is the relation between their visual and motor properties. Virtually, all mirror neurons show congruence between the visual actions they respond to and the motor responses they code. According to the type of congruence they exhibit, mirror neurons have been subdivided into “strictly congruent” and “broadly congruent” neurons (Gallese et al. 1996). Mirror neurons in which the effective observed and effective executed actions correspond in terms of goal (e.g. grasping) and means for reaching the goal (e.g. precision grip) have been classed as “strictly congruent”. They represent about one third of F5 mirror neurons. Mirror neurons that, in order to be triggered, do not require the observation of exactly the same action that they code motorically, have been classed as “broadly congruent”. They represent about two-third of F5 mirror neurons.

Mirror-neuron system in humans

There are no studies in which single neurons were recorded from the putative mirror-neuron areas in humans. Thus, a direct evidence of the existence of mirror neurons in humans is lacking. There is, however, a rich amount of data proving,

indirectly, that a mirror-neuron system does exist also in humans. Evidence in this sense comes from neurophysiological and brain-imaging experiments (Gastaut & Bert 1954; Cochin et al. 1998, 1999; Altschuler et al. 1997, 2000; Hari et al. 1998; Salmelin & Hari 1994; Hari & Salmelin 1997). More direct evidence that the motor system in humans has mirror properties was provided by transcranial magnetic stimulation (TMS) studies. Fadiga et al. (1995) recorded motor evoked potentials (MEPs), elicited by stimulation of the left motor cortex, from the right hand and arm muscles in volunteers required to observe an experimenter grasping objects (transitive hand actions) or performing meaningless arm gestures (intransitive arm movements). Detection of the dimming of a small spot of light and presentation of 3-D objects were used as control conditions. The results showed that the observation of both transitive and intransitive actions determined an increase of the recorded MEPs with respect to the control conditions. The increase concerned selectively those muscles that the participants use for producing the observed movements.

The MEPs facilitation during movement observation may result from a facilitation of the primary motor cortex due to mirror activity of the premotor areas, to a direct facilitatory input to the spinal cord originating from the same areas, or from both. Support for the cortical hypothesis (see also below, brain imaging experiments) came from a study by Strafella and Paus (2000). By using a double-pulse TMS technique, they demonstrated that the duration of intracortical recurrent inhibition, occurring during action observation, closely corresponds to that occurring during action execution.

A large number of brain imaging studies showed that the observation of actions done by others activates in humans a complex network formed by occipital, temporal and parietal visual areas, and two cortical regions whose function is fundamentally or predominantly motor (Rizzolatti et al. 1996; Grafton et al. 1996; Grèzes et al. 1998, 2001, 2003; Jacoboni et al. 1999, 2001; Nishitani & Hari 2000, 2002; Buccino et al. 2001; Perani et al. 2001; Decety et al. 2002, Koski et al. 2002, 2003; Manthey et al. 2003). These two last regions are the rostral part of the inferior parietal lobule and the lower part of the precentral gyrus plus the posterior part of the inferior frontal gyrus (IFG). These regions form the core of the human mirror-neuron system. Hand grasping movements (Grafton et al. 1996; Rizzolatti et al. 1996) as well as more complex hand/arm movements were used as visual stimuli (Decety et al. 1997; Grèzes et al. 1998). The results of the first experiments showed that during the observation of hand grasping there was an activation of the left inferior frontal cortex, in correspondence of the Broca's region. In addition activations were found in the left superior temporal sulcus (STS), the rostral part of the left inferior parietal lobule (area 40), the left opercular parietal region and the rostral part of the supplementary motor area (SMA-proper) (Grafton et al. 1996; Rizzolatti et al. 1996). The first three regions most likely correspond to the

monkey cortical areas where there are neurons that discharge when the monkey observes biological actions, namely: area F5 (Gallese et al. 1996), the STS region (Perrett et al. 1989; Carey et al. 1997) and the rostral part of the inferior parietal lobule (Fogassi et al. 1998).

In studies carried out by the Lyon group (Decety et al. 1997; Grèzes et al. 1998) the involvement of Broca's area during observation of hand/arm actions was further confirmed. The authors instructed subjects to observe meaningful (with a goal) and meaningless movements. The main results of the condition in which subjects observed meaningless arm movements were this: an activation of the parietal lobe bilaterally, in the left precentral gyrus and the cerebellum on the right side (Grèzes et al. 1998). On the contrary, the observation of meaningful hand actions, in addition to the already mentioned frontal and parietal areas, activates the left inferior frontal gyrus (Broca's region). Note that the activation of Broca's region during observation of action, suggests for this area the putative role of human homologue of area F5. In this direction point also some comparative cytoarchitectonical data (see Petrides & Pandya 1997) which entail a morphological parallel between monkey premotor area F5 (a disgranular frontal cortex) with Broca's area (BA44 and the most posterior part of 45), and fMRI data from Binkofsky et al. (1999) demonstrating that Broca's region become active also during manipulation of complex objects. In an fMRI study (Buccino et al. 2001), it was assessed whether the observation of actions made with different effectors would activate specific parts of the premotor cortex in accord with the somatotopic organization of the region. While being scanned, normal participants were asked to carefully observe different videotaped object- and non-object-related actions, performed by another individual with different effectors (mouth, arm/hand and foot). Results showed that observation of both object- and non-object-related actions determined a somatotopically organized activation of premotor cortex. The somatotopic pattern was similar to that of the classical motor cortex homunculus. In addition, during the observation of object-related actions, an activation, also somatotopically organized, was found in the posterior parietal lobe. Thus, when individuals observe an action, an internal replica of that action is automatically generated in their premotor cortex. In the case of object-related actions, a further object-related analysis is performed in the parietal lobe, as if the subjects were indeed using those objects. These results bring the previous concept of an action observation/execution matching system (mirror system) into a broader perspective: this system is not restricted to the ventral premotor cortex, but involves several somatotopically organized motor circuits.

It is important to note that the observation of transitive actions activated both the parietal and the frontal node of the mirror-neuron system, while the intransitive actions the frontal node only. This observation is in accord with the lack of inferior parietal lobule activation found in other studies in which intransitive

actions were used (e.g. finger movements, Iacoboni et al. 1999, 2001; Koski et al. 2002, 2003). Considering that the premotor areas receive visual information from the inferior parietal lobule, it is hard to believe that inferior parietal lobule was not activated during the observation of intransitive actions. It is more likely, therefore, that when an object is present, the inferior parietal activation is stronger than when the object is lacking, and the activation, in the latter case, does not reach statistical significance.

What links hand actions with speech?

Mirror neurons represent the neural basis of a mechanism that creates a direct link between the sender of a message and its receiver. By transforming an action done by an individual into a representation of the same action in the motor cortex of the observer, this mechanism creates a direct, non-arbitrary link between two communicating individuals. Actions done by other individuals become messages that are understood by an observer without any cognitive mediation.

Others' actions, however, do not generate only visually perceivable signals. Action-generated sounds and noises are also very common in nature. One could expect, therefore, that also this sensory information, related to a particular action, could determine a motor activation specific for that same action. A recent neurophysiological experiment addressed this point. Kohler and colleagues (2002) investigated whether there are neurons in area F5 that discharge when the monkey makes a specific hand action and also when it *hears* the corresponding action-related sounds. The experimental hypothesis started from the remark that a large number of object-related actions (e.g. breaking a peanut) can be recognized by a particular sound. The authors found that 13% of the investigated 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, evokes the Liberman's hypothesis on the mechanism at the basis of speech perception (motor theory of speech perception, Liberman et al. 1967; Liberman & Mattingly 1985; Liberman & Wahlen 2000). The motor theory of speech perception maintains that the ultimate constituents of speech are not sounds, but articulatory gestures that have evolved exclusively at the service of language. A cognitive translation into phonology is not necessary because the articulatory gestures are phonologic in nature. Furthermore, speech perception and speech production processes use a common repertoire of motor

primitives that, during speech production, are at the basis of articulatory gesture generation, while during speech perception, are activated in the listener as the result of an acoustically evoked motor “resonance”. Thus, sounds conveying verbal communication are the 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.

Fadiga et al. (2002), in a TMS experiment based on the paradigm used in 1995 (Fadiga et al. 1995), tested for the presence in humans of a system that motorically “resonates” when the individuals listen to verbal stimuli. Normal subjects were requested to attend to an acoustically presented randomized sequence of disyllabic words, disyllabic pseudo-words and bitonal sounds of equivalent intensity and duration. Words and pseudo-words were selected according to a consonant-vowel-consonant-consonant-vowel (cvccv) scheme. The embedded consonants in the middle of words and of pseudo-words were either a double ‘f’ (labio-dental fricative consonant that, when pronounced, requires slight tongue tip mobilization) or a double ‘r’ (lingua-palatal fricative consonant that, when pronounced, requires strong tongue tip mobilization). Bitonal sounds, lasting about the same time as verbal stimuli and replicating their intonation pattern, were used as a control. The excitability of motor cortex in correspondence of tongue movements representation was assessed by using single pulse TMS and by recording MEPs from the anterior tongue muscles. The TMS stimuli were applied synchronously with the double consonant of presented verbal stimuli (words and pseudo-words) and in the middle of the bitonal sounds. Results (see Figure 1) showed that during speech listening there is an increase of motor evoked potentials recorded from the listeners’ tongue muscles when the listened word strongly involves tongue movements, indicating that when an individual listens to verbal stimuli his/her speech related motor centres are specifically activated. Moreover, word-related facilitation was significantly larger than in the case of pseudo-words related to.

These results indicate that the passive listening to words that would involve tongue mobilization (when pronounced) induces an automatic facilitation of the listener’s motor cortex. Furthermore, the effect is stronger in the case of words than in the case of pseudo-words suggesting a possible unspecific facilitation of the motor speech centre due to recognition that the presented material belongs to an extant word.

The presence of “audio-visual” mirror neurons in the monkey and the presence of “speech-related acoustic motor resonance” in humans, indicate that independently from the sensory nature of the perceived stimulus, the mirror-resonant system retrieves from action vocabulary (stored in the frontal cortex) the stimulus-related motor representations.

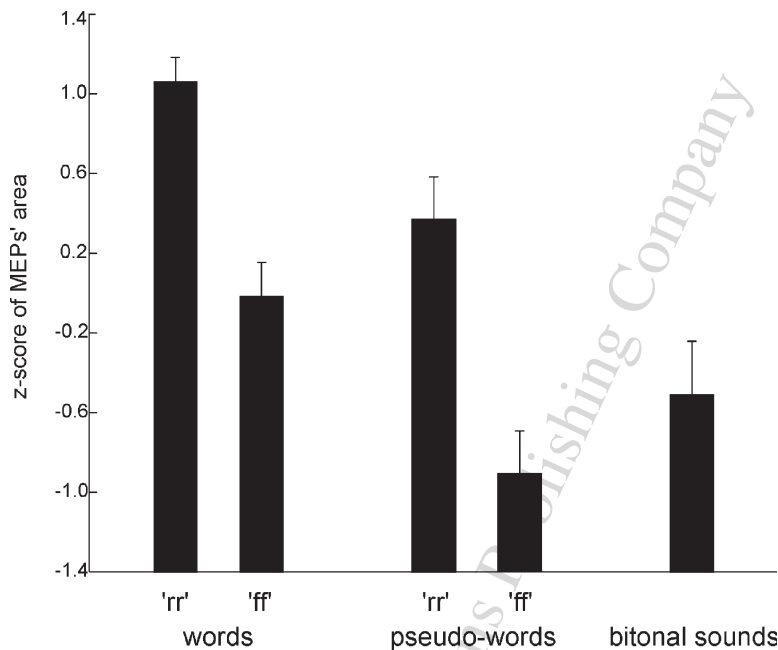


Figure 1. Average value (+ SEM) of intrasubject normalized MEPs total areas for each condition. Data from all subjects; 'rr' and 'ff' refer to verbal stimuli containing a double lingua-palatal fricative consonant 'r', and containing a double labio-dental fricative consonant 'f', respectively.

Conclusions

Mirror neurons represent the neural basis of a mechanism that creates a direct link between the sender of a message and its receiver. This mechanism, by transforming an action done by an individual into a representation of the same action in the motor cortex of the observer, creates a direct, non-arbitrary link between two communicating individuals. Actions done by other individuals become messages that are understood by an observer without any cognitive mediation. On the basis of this property, Rizzolatti and Arbib (1998) propose that the mirror-neuron system represents the neurophysiological mechanism from which language evolved. Their theoretical proposal is consistent with theories that postulate that speech evolved mostly from gestural communication and that sound was a late communicative acquisition developed on the top of it, with no link with ancient calls (see Armstrong et al. 1995; Corballis 2002). The novelty of the theory proposed by Rizzolatti and Arbib consists in their indication of a neurophysiological mechanism that creates a common (parity requirement), non-arbitrary, semantic link between communicating individuals.

An alternative view, based on the fact that humans mostly communicate by sounds, is that language evolved from the sound-based animal communication. In fact, human speech and animals' calls are widely different phenomena. First of all, the anatomical structures underlying speech and primates' calls are different. Primates' calls are mediated primarily by the cingulate cortex and by subcortical structures (see Jürgens 2002). In contrast, human speech network is located on the lateral cortical surface. Second, speech is not necessarily linked to emotions, whilst animals' calls are. Third, speech is endowed with combinatorial properties that are absent in animal communication. Finally, the anatomical heterogeneity of speech and animals' calls represents an enormous difficulty for theories that claim that speech derived from animals' calls. How could speech centres in evolution have "jumped" from one side of the brain to another?

A complete theory on the origin of speech, however, is well beyond the scope of this chapter. Our aim in writing was to suggest to the readers some stimulating starting points and to make an attempt to conciliate two streams of research, which start from very different positions: the study of speech representation in humans and the study of hand action representation in monkeys. These two approaches reach a common target: the premotor region of the inferior frontal gyrus where Paul Broca first localized its "frontal speech area".

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