

Mirror Neurons and the Evolution of Embodied Language

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ABSTRACT—*Mirror neurons are a class of neurons first discovered in the monkey premotor cortex that activate both when the monkey executes an action and when it observes the same action made by another individual. These neurons enable individuals to understand actions performed by others. Two subcategories of mirror neurons in monkeys activate when they listen to action sounds and when they observe communicative gestures made by others, respectively. The properties of mirror neurons could constitute a substrate from which more sophisticated forms of communication evolved; this would make sense, given the anatomical and functional homology between part of the monkey premotor cortex and Broca's area (the "speech" area of the brain) in humans. We hypothesize that several components of human language, including some aspects of phonology and syntax, could be embedded in the organizational properties of the motor system and that a deeper knowledge of this system could shed light on how language evolved.*

KEYWORDS—*vocalization; gesture; phonology; syntax; action understanding; F5; premotor cortex; Broca's area*

The scientific community is still debating whether human language evolved from nonhuman primate vocalizations or gestures or is a completely new acquisition of the human species (Hauser, Chomsky, & Fitch, 2002). Recently, the latter view has been partially modified. Hauser and colleagues (2002) proposed that only the abstract linguistic computational system, whose key property is recursion (producing many propositions within a single sentence), is uniquely human and was shaped by natural selection from preexisting structures that had evolved for reasons other than communication. Other authors (Pinker & Jackendoff, 2005) have suggested that several aspects of human

language besides recursion—such as phonology (articulate speech sounds), morphology (rules for combining words and affixes into larger words), and many properties of speech perception—are specific to humans. With few exceptions (Arbib, 2005), these proposals do not specifically address the issue of a plausible route whereby, starting from nonhuman primates' sensorimotor and cognitive processes, basic language components could have evolved.

COMMUNICATION IN NONHUMAN PRIMATES: EMOTIONAL OR VOLUNTARY?

A basic approach to investigating the evolutionary origin of language is looking at our closest relatives' capacity to use vocalizations for communication. Although anatomical constraints limit the variety of utterances nonhuman primates can produce, ethological studies have shown the capacity for referential communication (i.e., using calls or gestures for referring to specific categories of animate or inanimate objects) to be present in some primate species (Ghazanfar & Hauser, 1999). It is unlikely, however, that this capacity played an important role in the evolution of language (Hauser, Chomsky, & Fitch, 2002). In fact, important characteristics differentiate nonhuman primate vocal calls from human speech. First, the call repertoires of nonhuman primates are relatively small and highly stereotyped and show little combinatorial power. Second, call production in nonhuman primates is correlated with intense emotional states, with the main function being to signal urgent or imminent events. Altogether, these aspects limit the communicative power of vocal calls and do not allow their flexible use in communication between two individuals (Corballis, 2003).

Another common form of communication in primates, especially in apes, consists of body postures and gestures of the forelimb and face (see Parr & Maestripieri, 2003). Gestural communication not related to aggression or sex, such as lip-smacking (an affiliative gesture consisting of rhythmically opening and closing the mouth) in macaques or hand begging in chimpanzees, is often devoid of strong emotional content.

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Scientists have not found consistent homologies between the brain mechanisms responsible for the control of vocalization in nonhuman primates and those in humans. In fact, anatomical and neuroethological studies have shown that monkey vocal calls are under the neural control of the primitive limbic circuit, which is known to be involved in emotional behavior and the initiation and control of stereotyped utterances. In contrast, a sophisticated voluntary control of forelimb and facial movements, supported by the lateral motor cortex, gives the potential to voluntarily generate a higher number of gestures related to communication and to use them in a more flexible way and in support of utterances (Parr & Maestripietri, 2003).

In the following section, we will illustrate how, in our view, (a) the capacity of the motor system to voluntarily control goal-directed actions and (b) links between the motor system and the perception of others' actions and gestures have played a primary role in the emergence of complex sensorimotor and cognitive capacities related to communication and, more specifically, to linguistic faculties.

THE MIRROR-NEURON SYSTEM IN MONKEYS: FROM ACTION UNDERSTANDING TO COMMUNICATION

Interindividual communication involves at least two individuals, a sender and a receiver. Crucially, both sender and receiver must share similar motor programs necessary to produce a message and similar pathways for accessing these programs. We hypothesize that at the core of this executive/perceptual capacity there is a neural mechanism for matching executed actions with observed actions—namely, the mirror-neuron system (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti & Craighero, 2004). Mirror neurons were originally discovered in the premotor cortex of monkeys (see Fig. 1A). In order to better understand their properties, it is necessary to describe the basic organization of this cortical region.

Basic Organization of the Motor Cortex

Motor neurons of the premotor cortex activate during goal-directed motor acts such as grasping, manipulating, or reaching for an object (Rizzolatti & Craighero, 2004) and constitute a kind of internal storage of motor knowledge. Sensory information can access this internal motor knowledge, allowing the translation of sensory information into action. For example, when an object is seen, its visual features activate the motor knowledge necessary to interact with it. In some cases, activation of motor knowledge leads not to an action but to a mental representation of that action, constituting the basis for the emergence of cognitive properties. Mirror neurons of the monkey premotor area F5 (Fig. 1A) are a good example of these motor cognitive properties. These neurons discharge both when the monkey performs hand or mouth motor acts and when it observes another individual

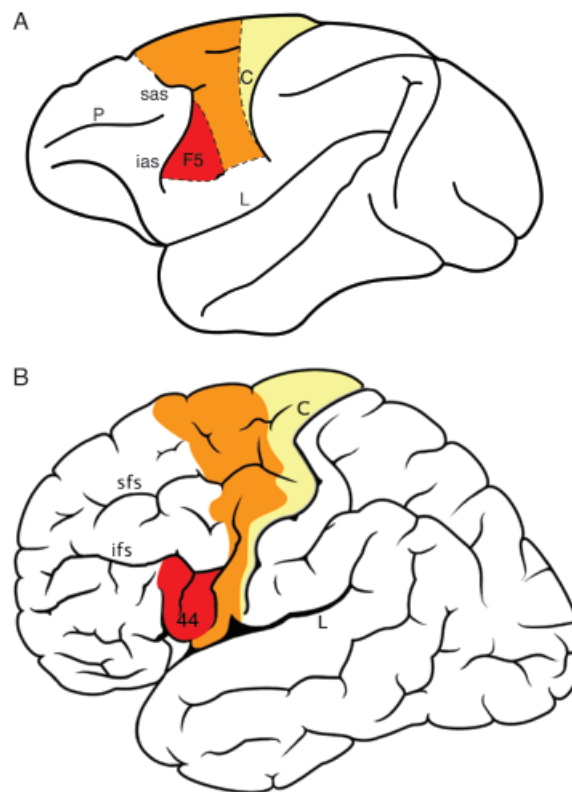


Fig. 1. Lateral view of the macaque (A) and human (B) cerebral cortex showing homologue cortical regions (colored areas). The regions shown in yellow and orange, in both the monkey and human brain, indicate the primary motor and the premotor cortex, respectively. The red colored region indicates the hypothesized homologue cortical motor areas related to communication and language (monkey area F5 and human area 44, or Broca's area). (C: central sulcus; ias: inferior arcuate sulcus; ifs: inferior frontal sulcus; L: lateral sulcus; P: principal sulcus; sas: superior arcuate sulcus; sfs: superior frontal sulcus.)

performing similar acts (Gallese et al., 1996; Rizzolatti & Craighero, 2004).

In most mirror neurons, there is a very good congruence between the effective observed and executed motor acts. This observation–execution matching mechanism is at the basis of the capacity to understand the actions made by others: Observation of a motor act retrieves in the observer the internal motor circuit representing that act and, as a consequence, the knowledge of the goal associated with it. This system may underlie some aspects of communication: A communicative gesture made by an actor (the sender) retrieves in the observer (the receiver) the neural circuit encoding the motor representation of the same gesture—that is, its goal/meaning—thus enabling the receiver to understand the gesture or message of the sender (Rizzolatti & Arbib, 1998). If this account is accepted, it is possible to trace an evolutionary pathway that, starting from some elements of the mirror-neuron system in the monkey, may have led to the emergence of human speech.

These elements have been found in specific categories of mirror neurons. Mirror neurons of one category (“audio-visual” mirror neurons) respond not only when a monkey observes

a motor act performed by another individual but also when the monkey only hears the sound of this act (Kohler et al., 2002; Fig. 2, left). These neurons have acoustic responses specific for only one sound—for example, peanut breaking—and, consequently, respond also when the monkey performs the act that produces that sound. Thus, the acoustic input becomes meaningful when

matched with the motor knowledge coded by the neurons of the premotor cortex.

Another category of mirror neurons called “communicative mouth mirror neurons” (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Fig. 2, right) are specifically activated by the observation of mouth-communicative gestures belonging to the monkey

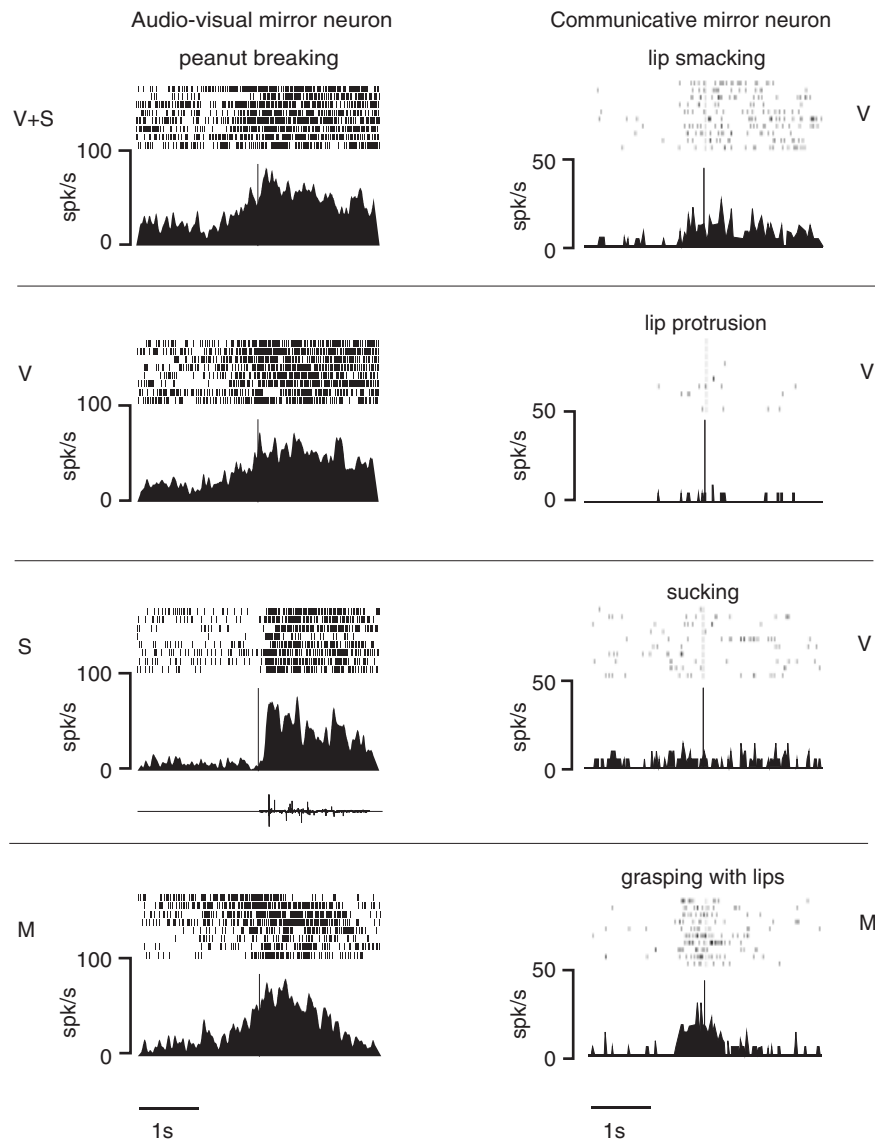


Fig. 2. Rastergrams (recorded neuron activity in a series of trials) and spike activity (averaged across the trials) showing the responses of an audio-visual mirror neuron to the sound of a motor act (left) and of a communicative mirror neuron to a communicative gesture (right). The left column shows responses when a monkey observes (V) or hears (S) the experimenter breaking a peanut, or both (V+S), or when the monkey performs an act similar to the one seen/heard (M); vertical lines indicate the time when the sound occurs or (in M) when the monkey touches the object. (Traces under the spike density functions in S condition represent recordings of the frequency and amplitude of the sounds used to test the neurons; modified from Kohler et al., 2002). The right column shows mirror-neuron responses when the monkey sees the experimenter making a lip-smacking gesture, protruding his lips, and sucking juice from a syringe, and lastly when the monkey protrudes its own lips and takes food offered by the experimenter (M condition, bottom). Rastergrams and spike density function are aligned (in V conditions) with the moment the experimenter fully expresses the communicative gesture or touches a syringe filled with juice, or (in M) with the moment the monkey touches the food.

repertoire, such as lip-smacking, lip protrusion, or tongue protrusion. Interestingly enough, all acts found to be effective in triggering the visual response of these neurons are affiliative acts—that is, friendly gestures with low emotional content—and not threatening or aggressive gestures. These neurons respond during communicative gestures produced by the monkey in response to an experimenter's gesture, but they also respond when the monkey makes motor actions associated with eating. The visuomotor response of these neurons seems to reveal the phylogenetic transition from the voluntary control of actions involved in ingestive behavior to that of facial gestures with communicative value (Ferrari et al., 2003). Ethological studies show that this transition from ingestive to communicative gestures—namely, from tasting food to lip-smacking—occurred in monkeys: Lip-smacking has a motor pattern that resembles that of an ingestive action, but its meaning shifted, in the course of evolution, to a communicative domain (ritualization process).

Summing up, in the monkey premotor cortex we observe an integration of several features that can preadapt this area for the evolution of a sophisticated communicative system. The main feature is the encoding of the production and perception of both facial and forelimb actions in the same cortical area. This double control might have been a key function for the subsequent evolution of a coupling between gestures and calls that provided the communicative system with an improved efficiency and a higher level of flexibility in transferring information to other members of the same species. The presence of this coupling is evident in humans and is already visible in apes, as revealed by several observations: (a) The gestural repertoire of chimpanzees is often used in association with vocal calls (Corballis, 2003, and commentaries to it in the same issue); (b) gestures usually accompany language production; (c) sign languages have the same essential properties as spoken language; and (d) the execution or observation of hand actions affects both lip opening and sound emission during syllable production of the executing or observing agent, respectively (Gentilucci & Corballis, 2006).

COMPARING THE MONKEY PREMOTOR CORTEX AND THE HUMAN BROCA'S AREA: WHAT IS SIMILAR? WHAT IS NEW?

The relation between the mirror-neuron system and language is corroborated by comparative anatomy between monkeys and humans. Cytoarchitectonic studies (i.e., studies of anatomical organization based on cell morphology and distribution) suggest a homology between area 44 (part of Broca's area) in the human brain and area F5 of the monkey brain (Fig. 1; Rizzolatti & Arbib, 1998). This homology is further supported by functional data.

First, area F5 contains motor neurons related to the execution of both hand and mouth actions. Similarly, brain-imaging ex-

periments in humans demonstrated that Broca's area, traditionally considered a "speech" area, is also involved in hand-movement tasks such as complex finger movements, mental imagery of grasping actions, and hand-imitation tasks (Rizzolatti & Craighero, 2004). Second, both areas are endowed with a mirror-neuron system. In fact, experiments in humans demonstrated that, like the F5 mirror neurons, Broca's area is activated when subjects observe goal-related hand and mouth motor acts performed by other individuals (Rizzolatti & Craighero, 2004). Third, in accord with the presence of audio-visual mirror neurons in F5, Broca's area and the premotor cortex are activated while listening to sounds associated with actions. Fourth, consistent with the presence of communicative mirror neurons in F5, Broca's area activates when subjects observe another individual speaking without hearing the sound (Rizzolatti & Craighero, 2004). A difference between monkeys and humans is that, in humans, the mirror-neuron system can be activated also by action-related linguistic material. In fact, reading or listening to action-related words and sentences (for example, "He grasps the glass") activate the premotor cortex and Broca's area (Tettamanti et al., 2005). Thus, it appears that some semantic aspects of language can be processed through the sensorimotor systems.

Although brain-imaging data establish a clear link between language and the motor system, they do not directly show an involvement of the mirror-neuron mechanism. More direct evidence of such a link was provided by a transcranial magnetic stimulation (TMS) study by Fadiga and colleagues (Rizzolatti & Craighero, 2004). They found an enhancement of tongue-muscle activity during TMS in subjects listening to words containing syllables that, when produced, require a strong activation of those muscles. The enhanced excitability of the motor cortex was very likely due to the preactivation of Broca's area while listening to words. This experiment is very interesting, as it indicates the existence of a matching mechanism that determines a phonological resonance¹ between heard phonemes and their motor representations. Furthermore, the same study showed stronger tongue-muscle activation for words compared to non-words, suggesting that this phonological resonance also involves understanding of words' meaning. This mechanism fits with the motor theory of speech perception (Liberman & Mattingly, 1985), according to which "the objects of speech perception are represented by the intended phonetic gestures of the speaker, represented in the brain as invariant motor commands" (p. 2).

Do these activations reflect the existence of a dedicated mirror-neuron system for speech? The actual findings do not make it possible to disentangle a multipurpose mirror-neuron system from a specific one exploited only in humans for linguistic purposes.

¹The term "resonance" is a metaphor to express the idea that an observed or heard biologically meaningful stimulus directly activates the corresponding motor representation in the brain without eliciting an overt execution of it.

The evidence we have discussed so far suggests that some aspects of language, such as part of semantics and phonology, can be embodied in the sensorimotor system represented by mirror neurons. Interestingly, brain-imaging data and studies on neurological patients identify Broca's area in syntactic processing involving reconstruction and interpretation of structured sequences of sentences (Grodzinsky & Friederici, 2006). If we broadly define syntax as a rule-based system combining elements into a sequence that has a specific meaning, we may attempt to trace its possible link with the basic cortical organization of intentional action sequences in monkeys. Recently we found (Fogassi et al., 2005) that mirror neurons belonging to the parieto-frontal motor system² differentially code a motor act according to the final goal of the action sequence in which the act is embedded. For example, a certain mirror neuron activates when the monkey observes another individual grasping food for eating it (the action's final goal) and not when that individual grasps it for placing it into a container. Based on these findings, we postulated that the motor system is organized into neuronal chains, each coding a specific goal and combining different elements (motor acts) of the action. Further preliminary data on the monkey parietal and premotor cortex have shown that this type of organization is valid also for longer action sequences in which the same element of a chain is recursively involved in different steps of the sequence. Although this organization is certainly very basic, in terms of hierarchical arrangement, combinatorial power, achievement of meaning, and predictive value (i.e., every neuron coding a specific motor act of an action sequence facilitates predicting the outcome of that sequence) it has much in common with the syntactic structure of language. At present it is not clear how and whether this sequential motor organization could have been exploited for linguistic construction, but we can assume that, over the course of evolution, the more the motor system became capable of flexibly combining motor acts in order to generate a greater number of actions, the more it approximated a linguistic-like syntactic system. Such a capability could have extended to a motor system dedicated not only to the generation of mouth, face, and larynx movements involved in eating and breathing, but also to the combination of such movements in phono-articulatory gestures for communicative purposes.

Future Perspectives

The data discussed above leave open many issues. One of the most important concerns the role the mirror-neuron system played in the evolutionary changes that led to the emergence of vocal communication. A suggestive hypothesis would be that the ventral premotor cortex, endowed with the control of both hand

and mouth actions, could have played a pivotal role in associating gestures with vocalizations, thus producing new motor representations. At this stage, the mirror-neuron system, because of its capacity to match the seen/heard gesture or vocalization with internal motor representations, allowed the observer/listener to assign a meaning to these new vocal-gesture combinations.

A second important issue that requires further investigations is the relation between mirror neurons and imitation. It is intuitive that a mechanism linking observed action with its reproduction is very useful for learning new motor skills. In fact, in the last few years it has been demonstrated that the human mirror-neuron system becomes active during imitation tasks (Rizzolatti & Craighero, 2004). Furthermore it is known that, during child development, language acquisition profits very much from imitative processes (Arbib, 2005). However, whether the mirror-neuron system is recruited also in learning new material related to language (e.g., words, grammar, prosody) remains to be studied more in depth.

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²The parieto-frontal motor system corresponds to the premotor cortex and the part of the parietal cortex connected to it containing neurons with motor properties.

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