

# Cortical Motor Organization, Mirror Neurons, and Embodied Language: An Evolutionary Perspective

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The recent conceptual achievement that the cortical motor system plays a crucial role not only in motor control but also in higher cognitive functions has given a new perspective also on the involvement of motor cortex in language perception and production. In particular, there is evidence that the matching mechanism based on mirror neurons can be involved in both phonological recognition and retrieval of meaning, especially for action word categories, thus suggesting a contribution of an action–perception mechanism to the automatic comprehension of semantics. Furthermore, a comparison of the anatomo-functional properties of the frontal motor cortex among different primates and their communicative modalities indicates that the combination of the voluntary control of the gestural communication systems and of the vocal apparatus has been the critical factor in the transition from a gestural-based communication into a predominantly speech-based system. Finally, considering that the monkey and human premotor-parietal motor system, plus the prefrontal cortex, are involved in the sequential motor organization of actions and in the hierarchical combination of motor elements, we propose that elements of such motor organization have been exploited in other domains, including some aspects of the syntactic structure of language.

*Keywords:* action; Broca's area; gestures; matching mechanism; monkey

## 1. Introduction

The aim of this article is to show the strong link existing between the motor system and language, with a particular emphasis on the relationship between the mirror neuron mechanism, thought to be involved in action understanding, and the mechanism underlying language comprehension. In order to address these issues, we have organized the current review as follows. First, we will describe the organization of the cortical motor system and how cognitive functions, and

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more specifically, action understanding, derive from this organization. Second, we will review the evidence suggesting that the mirror matching mechanism can apply to phonological matching. Third, we will briefly describe vocal and gestural communication systems in non-human primates, suggesting that their combination at voluntary level can have played an important role in language evolution. Fourth, we will present the anatomical and neurophysiological evidence that suggests a homology between higher order monkey motor areas and frontal regions involved in language processing. We will conclude suggesting the possible link between sequential motor behavior and syntactic structure. Although several issues of the debate concerning the role of the motor system in speech perception and language require a deeper elaboration of the different perspectives, we deliberately focus on the motor system and the action–perception mechanisms to emphasize their central contribution in different aspects of perception processes occurring in language and to challenge a theoretical position in linguistics and cognitive sciences that considers sensory and motor information processes as separate domains.

## **2. The Organization of the Motor System and the Emergence of Motor Cognitive Functions**

In the traditional way of conceiving brain processes, perception was considered the result of a higher order elaboration of sensory information, occurring in the posterior half of the brain. In this view, when we need to act on the external world, the outcome of this elaboration is fed to the anterior part of the cortex, the prefrontal and motor cortex, in order to plan actions and execute them. Thus, the posterior part of the cortex would have a main role in functions such as space perception and object perception, plus other cognitive functions, also considered as higher order elaboration of sensory functions, such as language comprehension, music, reasoning, memory, while the anterior part would simply guide our Behaviour. Although philosophers, psychologists, and neurophysiologists (Piaget 1951; Merleau-Ponty 1962; Jeannerod 1988) pointed to the motor system as to a fundamental tool for our knowledge of the world, for many years, this system was mainly considered in its executive aspects, such as, for example, movement parameters (Evarts 1968; Georgopoulos *et al.* 1982), or, at most, motor preparation (Weinrich *et al.* 1984). Interestingly, however, some researchers demonstrated that the motor cortex activates during motor imagery, which can be considered a mental function (Roland *et al.* 1980; Jeannerod 1994). Despite this evidence, the serial flow of information, i.e. from the so called associative areas of the temporal and parietal cortex to frontal areas, was not disputed, and also many computational models were organized according to this view (Poggio & Edelman 1990; Giese & Poggio 2003). In the last two decades the conceptualization about action, perception and cognitive functions radically changed. The two most important new concepts that emerged are the assignment to the motor system of a crucial role in cognitive functions and, linked with it, the recognition of its strong importance in perception. These conceptual changes have been possible due to the neurophysiological, neuroanatomical and psychological

findings achieved in the last two decades. Neurophysiological experiments in the monkey showed that the motor cortex code the goal of motor acts and contain a storage of high level motor representations. Neuroanatomical studies showed that parietal and frontal cortices are linked by reciprocal connections (Rizzolatti & Luppino 2001), thus indicating that these cortical regions have both motor and sensory properties and that motor and perceptual aspects are strictly integrated and influence each other. Finally, psychophysics studies in humans strengthen this suggestion, showing that not only higher order sensory elaboration influences the parameters of motor reactions, but, most importantly, motor representations influence perceptual processes (Craighero *et al.* 1999; Loula *et al.* 2005; Casile & Giese 2006). The next section will concentrate on neurophysiological findings.

Single neuron recording studies allow to correlate the neuronal activity with the presentation of sensory stimuli or with specific behavioural events. Using this technique, it has been demonstrated that neurons of premotor cortex (Brodmann's area 6) activate during goal-related motor acts, such as reaching, pushing, grasping, manipulating, breaking, etc., rather than during simple movements, such as, for example, arm extension or fingers flexion. In particular, single neurons of ventral premotor area F5 code various levels of abstraction of motor acts. Some activate when a monkey executes motor acts such as grasping, manipulating, holding, tearing objects (Rizzolatti *et al.* 1988). Within the category of grasping neurons, some discharge when the monkey grasps food with the hand or the mouth, or when the same goal is achieved not only with the biological effector but also with a tool, after a period of motor training to use it (Umiltà *et al.* 2008). All these studies strongly demonstrate that the main role of the motor cortex is that of coding goals. The neurons coding these goals form, together, a 'storage' of motor representations, a kind of 'internal motor knowledge' of the individual. Coming back to the motor imagery function (see above), whenever an individual imagines to perform a motor act, the activation of the motor cortex reflects the activation of specific motor representations. Notably, for the occurrence of this function a previous activity of posterior, sensory or associative cortices, is not required.

Usually, our behavior occurs in response to sensory stimuli. Therefore, based on the above described motor organization, in order to transform a sensory input into a motor output, the former must be associated to the appropriate motor representation. This is possible through the anatomical connections between parietal and motor cortex. Note that this link ensures two functions: (i) the transformation of an external input (e.g., an object) into a motor format (e.g., grasping) and (ii) a sensorimotor matching mechanism, providing an automatic attribution of motor meaning to the sensory input addressing a specific motor representation. Neurophysiological studies demonstrated that this double function is present in several circuits (Rizzolatti & Luppino 2001). For example, a circuit linking an area of intraparietal cortex (anterior intraparietal area, AIP) with an area of ventral premotor cortex (area F5) is involved in transforming the physical object properties in grasping motor acts. At the same time, the visual response of F5 neurons to object presentation appears to derive from a mechanism matching the object visual characteristics with the corresponding

motor representations (the grip used to grasp that object). Thus, this neuronal visual response represents a pragmatic description of the object because the object is described in motor terms. Another example of a sensorimotor matching process that allows individuals to achieve a specific understanding of the external world is the mirror matching mechanism. The system based on this mechanism in monkeys and humans will be described in the next section.

In conclusion, the existence of a variety of sensorimotor matching mechanisms suggest that these systems have been selected in the phylogenesis because of their pragmatic role and their capacity to perform two functions: sensorimotor integration and achievement of a motor knowledge of the external world.

### 2.1. *Mirror Neurons in the Monkey*

Mirror neurons were first discovered in area F5 (see Fig.1A) of the monkey ventral premotor cortex (Di Pellegrino *et al.* 1992; Gallese *et al.* 1996; Ferrari *et al.* 2003) and then in area PFG in the rostral part of the inferior parietal lobule (Gallese *et al.* 2002; Fogassi *et al.* 2005; Rozzi *et al.* 2008). Since the properties of mirror neurons of F5 and PFG are similar, we will describe them together. These neurons discharge when the monkey *performs* a hand or mouth goal-directed motor act (e.g., grasping, biting, tearing or manipulating an object), and when it *observes* the same, or a similar, act performed by the experimenter or by another monkey. They do not respond to the simple object presentation (differently from the neurons of the AIP-F5 circuit) and to the vision of the hand mimicking the motor act without the target. Notably, the motor acts effective in eliciting the mirror neurons response are the same as those coded by purely motor neurons, that is they correspond to the different goal types stored in ventral premotor and inferior parietal cortex.

The finding that mirror neurons respond visually to the presentation of a hand (or mouth) — object interaction strongly suggest that these neurons code the goal of the observed motor acts. This suggestion is corroborated by the results of two investigations. In the first it has been shown that mirror neurons discharged both when the monkey could fully observe a grasping act and when it could see only part of it because the hand-target interaction was hidden behind a screen (Umiltà *et al.* 2001). The access to memory of the object, combined with the vision of the reaching component of the act, allows the retrieval of the motor representation of the partially observed motor act and of its consequences. Thus, it has been concluded that the neuronal discharge obtained in the partially occluded condition codes the goal of the act, even though its target is not visible.

In the second study, monkey had to both observe motor acts (breaking, manipulating, dropping) and listen to the sound of these noisy acts, while the response of mirror neurons was recorded (Kohler *et al.* 2002) The results showed that a sub-category of them discharged not only during motor act observation but also during pure listening to the sound produced by that act ('audio-visual mirror neurons'). This indicates that the content (the goal) of the motor act can be accessed, and therefore coded, through different sensory modalities. Although the response of most mirror neurons is independent of many details of the

observed act, such as space, type of object or hand, recently two studies have demonstrated that part of mirror neurons can provide also information on the visual details.

In the first study (Caggiano *et al.* 2009) the visual response of mirror neurons have been analyzed during observation of an experimenter grasping a piece of food within the monkey reaching space (peripersonal space), or far from the monkey (extrapersonal space). The study showed that half of the tested mirror neurons responded better in one of the two conditions, the two sub-categories (peri- and extrapersonal neurons) being equally represented. This finding suggests that mirror neurons can code others' actions within different spaces, possibly in relation to the possibility to socially interact with others by performing different types of behavioural responses.

In a second study (Caggiano *et al.* 2011), the responses of F5 mirror neurons were investigated during observation of movies showing grasping motor acts seen from different perspectives (frontal, lateral, egocentric). The first interesting result of this study was that mirror neurons respond also to acts presented in movies, although the same motor acts, presented naturalistically, evoked a higher visual response. The second result was that while one quarter of the recorded mirror neurons responded to the visual presentation of motor acts in movies, independent of the visual perspective from which they were presented, the other three-quarters of neurons were tuned to specific visual perspectives.

Altogether, the two studies indicate that there are mirror neurons whose function is only that of encoding the goal of a motor act, while others, beyond this property, can also contribute to provide the observer with the details of the observed act, probably through feedback connections between motor cortex and posterior, higher order, visual areas. This mechanism, which is supported by the presence of reciprocal connections between anterior and posterior cortical areas, would explain a way in which motor representations and the corresponding sensory representations mutually interact.

The encoding property of a neuron can be read only from its output, i.e. from its discharge. A neuron has only a single output, meaning that it produces only one code. Since, however, its output depends on the integration of several inputs, it is important to know which of these inputs can drive a certain output and which cannot. In the case of mirror neurons, this input-output comparison becomes an analysis of the congruence between the observed and the executed motor act. This analysis leads to conclude that ninety percent of mirror neurons are congruent in terms of goal (Gallese *et al.* 1996; Rozzi *et al.* 2008). However, this congruence may be strict or broad. In 'strictly congruent' mirror neurons the observed and executed motor acts correspond both in the goal and the details of the act. In 'broadly congruent' mirror neurons there is also congruence of the goal but, for example, the range of observed motor acts effective in eliciting the visual response can be broader with respect to that of motor acts effective during execution. The congruence property of mirror neurons is very important for several reasons. The first is that the congruence manifests the occurrence of an efficient matching mechanism, which is the basis for understanding others' actions. In other words, the observation of a specific motor act performed by another individual elicits the activation of the corresponding motor represen-

tation in the motor system of the observer, as if he was executing the same act. Note that, during observation, an inhibitory mechanism must come into play, blocking the automatic execution of the observed act (see Kraskov *et al.* 2009). Second, a strict congruence can be very important if these neurons must be used in imitative processes (see below). Third, a broad congruence can be very helpful for the generalization of the meaning of the observed motor act. This aspect was confirmed by two studies showing that some mirror neurons can begin to respond also during observation of motor acts performed with tools, provided a long visual exposure to these acts (Ferrari *et al.* 2005) or after training to use these tools (Umiltà *et al.* 2008). Fourth, observation/execution matching can be very useful during social learning processes such as those occurring during language development.

Which is the source of visual information that contributes to the formation of the mirror matching mechanism? It is known that in the anterior part of the monkey superior temporal sulcus (STSa) there are neurons that fire during observation of biological movements, among which also hand motor acts (Perrett *et al.* 1989). These high order visual neurons are considered the source of visual input for parietal mirror neurons and, as a consequence, for ventral premotor mirror neurons. Note that both STSa and PFG, on one side, and PFG and F5, on the other, are reciprocally connected (Rozzi *et al.* 2006; Bonini *et al.* 2010), while there is no direct connection between STSa and F5. Thus, it is not known where is the first place where matching may occur.

## 2.2. *The Mirror System in Humans*

After the discovery of mirror neurons in the monkey, the presence of a mirror system (MS) in humans has been demonstrated with electrophysiological and neuroimaging techniques. For example, the transcranial magnetic stimulation (TMS) technique, that allows either to excite or to inactivate limited cortical regions, enabled several researchers to demonstrate the existence of a mirror matching system at the level of the motor cortex. In fact, if a TMS pulse at threshold intensity is given to the motor cortex of subjects observing motor acts performed by another individual, it is possible to enhance the electromyographic activation of the same muscles that would be active if the subjects themselves would perform the observed motor act (Fadiga *et al.* 1995, Gangitano *et al.* 2004). This enhancement is justified only if the stimulated region is pre-activated by observation.

While TMS provided indication of the occurrence of a matching mechanism, positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) techniques allowed to identify the anatomical location of areas active during observation of motor acts. Since up to now several brain imaging studies have been carried out on this topic, we will limit to sum up all these results. The main areas activated during observation are: A region around the superior temporal sulcus (STS), one in the supramarginal gyrus (part of the inferior parietal lobule, IPL), and a third in the ventral premotor cortex plus the posterior sector of the inferior frontal gyrus (IFG), namely areas area 44 and 45 that, in the left hemisphere, correspond to Broca's area (the 'speech' area) (see for

review Rizzolatti & Sinigaglia 2009; Caspers *et al.* 2010). In many of these studies it has been underlined that the areas activated in IFG and IPL correspond anatomically to the areas where mirror neurons have been found in monkeys (F5 and PFG, respectively). In addition, the STS region corresponds to the monkey area described by Perrett *et al.* (1989), which is active only during observation of a motor act, but not during its execution. Among activated areas can also be included the anterior intraparietal area (AIP) — corresponding to the monkey area having approximately the same location — that is mainly activated by observation of hand motor acts (Shmuelof & Zohari 2008), and, in some studies, regions of the dorsal premotor cortex and superior parietal lobule, that can become active during observation of reaching motor acts (Filimon *et al.* 2007).

Finally, electroencephalographic (EEG) and magnetoencephalographic (MEG) studies were very useful not only to confirm the activation of the frontal cortex during action observation (Cochin *et al.* 1999; Nishitani & Hari 2000), but also to show the time course of activation. In fact, it has been shown that, after activation of the occipital lobe, the activation of IFG precedes that of precentral cortex.

In monkeys, MNs respond exclusively or stronger to goal-directed acts than to intransitive movements, the only exception being communicative MNs (see below). Differently from monkey studies, in humans also the observation of meaningless movements can elicit an activation of areas belonging to the motor system. For example, TMS studies showed that observation of meaningless movements determine a resonance in the motor cortex (Fadiga *et al.* 1995). Some neuroimaging studies showed that observation of meaningless movements activate a dorsal premotor-parietal circuit (Grèzes *et al.* 1998), others show that observation of mimed motor acts activate the same premotor, IFG and parietal regions activated by the goal-directed ones (Grèzes *et al.* 1998; Buccino *et al.* 2001). Interestingly, observation of symbolic gestures appear to activate both ventral premotor and inferior parietal cortex, but this latter activation involves more posterior sectors than those activated by observation of goal-directed motor acts (Lui *et al.* 2008). Thus, observation of non goal-directed movements may activate areas belonging to the MS, and these areas may be different depending on whether the observed movements are meaningful or meaningless.

Interestingly, it has been claimed that intransitive gestures (pantomimes) play a very important role in language evolution, because they facilitated the transition from object-related actions to intentional movements to “protosign, a manual-based communication system that broke through the fixed repertoire of primate vocalizations to yield an open repertoire of communicative gestures” (Arbib 2005: 107).

### 2.3. *The Involvement of the Mirror System in Imitation*

A very interesting issue, strictly related to the properties of mirror neurons and very important for human learning and evolution of language, is that of imitation. In adult monkeys there are no clear reports of this behavior, in particular of imitation learning (Visalberghi & Fragaszy 2002). Thus, in these species, the mirror neuron system, besides providing individuals with the capacity of

understanding actions, can be perhaps exploited for imitative processes such as neonatal imitation and action facilitation (Ferrari *et al.* 2009, 2012). In humans, however, the imitative function, and specifically imitation learning, is very well developed and is critical particularly during language acquisition in children. Many brain imaging studies carried out in the last decade, showed that the parieto-premotor mirror system is activated when subjects are required to observe and imitate simple finger movements, goal-related motor acts and complex action sequences (Buccino *et al.* 2004; see for review Iacoboni 2009). Thus, observation and imitation share the same neural circuits. In fact, during imitation learning, a crucial step is represented by the recognition of the motor acts belonging to the action to be imitated. This step is very likely accomplished by mirror neurons. A second step concerns the internal reconstruction of the sequence of motor acts to be reproduced. Is this a property of mirror neurons or is performed by other cortical regions? An fMRI experiment in which subjects were required to observe novel guitar chords performed by an expert player and then to imitate them (Buccino *et al.* 2004), show, beyond that of the parieto-frontal mirror neuron system, a strong activation of the middle frontal cortex (area 46) during the phase interleaved between observation and imitation. In this phase the subject has to decompose the action into its basic motor elements and then subsequently recombining them into a new action matching the observed one. This is probably the role of prefrontal cortex, known to be crucial in action planning, attention and working memory.

### 3. Matching Sounds with Actions

The acoustic signal generated by a biological event is the result of a motor act. This motor act corresponds to a specific motor representation stored in the cortical motor system. When this signal, either a phoneme, a word or a sentence, is listened by another individual, a series of neuronal processes are taking place in the brain, starting from the auditory pathway but not ending into the primary auditory cortex and higher order acoustic areas. In fact, many neurophysiological investigations clearly show that part of this information reaches premotor cortex and connects with a specific motor representation (for a review, see Pulvermüller & Fadiga 2010). The activation of this motor representation, in turn, is crucial for the production of the same acoustic signal.

The described process can be considered similar to that occurring in a linguistic interaction between a sender and a receiver. Although the linguistic signal has a specific pattern and characteristics that distinguish it from an action sound or a physical sound, nevertheless also in this domain the matching mechanism can operate similarly to that occurring during listening to an action sound. As a matching mechanism allows the understanding of an action meaning, the same mechanism allows the understanding of a phoneme. Thus, a syllable is not understood simply because of the perception of its acoustic features, but because these features retrieve an invariant motor representation. Interestingly, during the first year of life, infants demonstrate an increased sensitivity to phonological properties and during the babbling phase it is likely

that the articulation of sounds and the first produced phonemes play an important part not only in sensorimotor association but also in strengthening and mapping neuroanatomical connections between acoustic areas and cortical motor representations involved in sounds production (Pulvermüller & Fadiga 2010).

This proposal of a 'pragmatic' and embodied understanding of spoken words resembles very much the motor theory of speech perception (Liberman & Mattingly 1985), postulating that "the objects of speech perception are the intended phonetic gestures of the speaker, represented in the brain as invariant motor commands" (p. 2). From these considerations two important implications follow: (i) Speech (and maybe language) understanding can be rooted on a motor ground and (ii) the mechanism matching the auditory and motor representation of an utterance can subserve both phonological matching and the retrieval of the associated meaning. This would constitute a motor-based mechanism for automatic comprehension of semantics.

A series of behavioral and neuroscientific studies support these two claims. One of the first demonstrations of a phonological motor-based matching system is that of Fadiga *et al.* (2002), who recorded motor evoked potentials (MEPs) from the tongue muscles by stimulating with TMS the left motor cortex of normal volunteers instructed to listen to acoustically presented words and pseudo-words, containing either a double 'f' or a double 'r', that require a different tongue muscles involvement to be pronounced (stronger during words containing double 'r'). The TMS pulse was given at the time in which the double consonant was produced by the speaker. The results showed that listening to words and pseudo-words containing the double 'r' determined a significant increase of the amplitude of MEPs recorded from the tongue muscles with respect to listening to words and pseudo-words containing the double 'f' and bitonal sounds. Furthermore, the tongue muscle activation during word listening was higher than that during listening to pseudo-words. These data strongly suggest that phonology and perhaps, partly, semantics, are processed within the motor system. In a related TMS experiments, Watkins *et al.* (2003) stimulated the face motor field of subjects listening to speech or viewing speech-related lip movements, as compared to listening to non-verbal sounds and viewing eyes and brow movements. The results show that, compared to control conditions, listening to and viewing speech enhanced the size of MEPs.

In a more recent experiment (D'Ausilio *et al.* 2009) TMS pulses were given to the lip and tongue cortical motor fields while subjects listened to phonemes produced with the lips (b and p) and the tongue (d and t) and performed a phoneme discrimination task. The TMS pulses were applied just before stimulus presentation to selectively prime the cortical activity specifically in the lip or tongue representations, with the hypothesis to obtain a bias in perception. Results showed that indeed the stimulation of a given motor representation led to a better performance in recognizing speech sounds produced with the concordant effector compared with discordant sounds produced with a different effector.

These and other studies clearly support the view that the motor system contributes to the identification and discrimination of speech sounds. However, the investigations reviewed so far have described the involvement of the motor

system at the phonological level. Is there any evidence that during listening to a word the premotor and primary motor cortex are involved, thus contributing to the comprehension of the meaning?

There is some evidence suggesting that the meaning of a word can be indeed processed in these areas. Functional MRI studies demonstrated that pure listening to action verbs or action-related sentences produces an effector specific, somatotopic, activation of the motor cortex (Hauk *et al.* 2004; Tettamanti *et al.* 2005), similar to that found by Buccino *et al.* (2001) during observation of motor acts performed with the mouth, the hand or the foot. In all these cases, as in the above reported TMS studies, listening to action-related verbal material produced an enhancement of motor cortical activation. On the contrary, Buccino *et al.* (2005), using TMS, found a suppression of motor activity while stimulating either the hand or the foot/leg motor area of the left hemisphere, while participants were listening to sentences expressing hand and foot actions. They found a decrease of MEPs amplitude when the stimulated field corresponded to the effector involved in the listened action. A complementary reaction time study, in which subjects had to respond with the hand or the foot to the same sentences, confirmed this suppression effect. If, on one side, these data demonstrate an effector specific modulation of the motor system during listening to action-related material, on the other side, this modulation is consistent with an inhibition effect. Following one of the authors' interpretations, it is plausible that the motor representation elicited by listening to the sentence interfered with the motor program activated in order to respond with the required same effector.

Interestingly, although it has been suggested that the activation of the inferior frontal areas during action-verb listening is not related to a process of meaning comprehension (Hickok 2009), other studies contradict this view. In fact patients with motor neuron disease or lesions in the left inferior frontal cortex have deficits in action-verb understanding and in semantic understanding of pictures depicting actions (Bak *et al.* 2001, 2006).

It must be noted however, that several words are not related to verbs and describe, for example, categories of objects or abstract concepts that are unrelated to actions. In these cases, brain imaging studies have shown activations in areas of the temporal lobe, thus suggesting that the motor links in the semantic processing is limited to words related to actions (see Pulvermüller & Fadiga 2010).

Altogether, these and other findings support the idea of a strong embodiment of speech during acoustic processing, both at phonological and semantic level. However, other theoretical approaches contrast with this view (see, for example, Hickok 2009; Lotto *et al.* 2009). Their arguments are against a main role of the motor system in general and of the mirror system in particular, in speech perception. They report, for example, that infants could discriminate speech sounds that they could not yet produce (Eimas *et al.* 1971). Furthermore, Broca's aphasia does not seem to prevent normal receptive speech ability (Damasio 1992; Goodglass 1993). Furthermore, there are data of double dissociation in Broca's aphasics showing that there are patients impaired in syllables discrimination but as good as normal in word comprehension and other patients that, although impaired in speech discrimination, can be good in repeating heard speech (see Hickok & Poeppel 2007 and Lotto *et al.* 2009 for review). Note, however, that

other studies aimed at investigating how deep were the impairments in speech comprehension in these patients, found that some deficits were evident especially in single-word comprehension (Utman *et al.* 2001; Yee *et al.* 2008; see Pulvermüller & Fadiga 2010).

About the role of the motor system in the comprehension of semantics, the critics of the 'motor' approach, although recognizing that its involvement has been shown by several works, maintain that, instead of being central to language understanding, it could play a post-recognition epiphenomenal role (see Hickok 2009).

Altogether, these data suggest that the proposal concerning the involvement of the motor system in speech perception warrants more attention concerning how central is its role and clearly this requires further investigations to better understand the underlying neural mechanisms.

#### 4. Vocal and Gestural Communication

It is broadly accepted that several aspects of human language rely on basic elements that are shared with other animals. However, it is still a matter of debate which feature belongs exclusively to language (Hauser *et al.* 2002). Vocal communication in nonhuman primates has been often compared to human language in an effort to understand possible commonalities and the basic components from which human language might have emerged (Ghazanfar & Hauser 1999; Seyfarth & Cheney 2010). Undoubtedly, monkeys can emit utterances in different contexts to signal urgent events such as the presence of predators or food, or to threat a conspecific during a dispute. The seminal study by Cheney & Seyfarth (1982) showed that vervet monkeys are capable of referential communication, providing information through alarm calls to conspecifics about the different types of predators approaching. Recipients seem to understand the different meaning of the call or, as demonstrated in other studies, are able to take into account the possible causes of the alarm calls (Zuberbühler 2000).

The signs of flexibility in the vocalization systems of many nonhuman primate species is supported by their capacity to modify their utterances based on their assessment of the possible consequence they produce on other individuals. This phenomenon, named the audience effect, demonstrates the capacity of monkeys and apes to modify their vocalizations depending on the social context (Caine *et al.* 1995; Tomasello & Zuberbühler 2002). More recently, it has been demonstrated that wild chimpanzees emit alarm calls with low or high frequency based on the state of knowledge of the group member about a danger (Crockford *et al.* 2012). These data suggest that in some nonhuman primates it has been developed a capacity to control vocalization to inform group members depending on the information available to them about environmental dangers.

In terms of learning, nonhuman primates vocalization shows a certain degree of flexibility. For example some species display population-specific vocal signals and in the course of ontogeny there are modifications in the structure of their vocalization and in their capacity to use it in the appropriate context (Tomasello & Zuberbühler 2002; Egnor & Hauser 2006). However, cross-fostering

studies demonstrate that the capacity to learn new vocalizations is very limited (Owren *et al.* 1993). Furthermore, this limitation has also been supported by several experimental studies showing that monkeys and apes cannot learn completely new vocal patterns (see Yamaguchi & Izumi 2008). This is illustrated, for example, by the failure in teaching human spoken language to apes, even though some of the basic cognitive components that are found in language (e.g., use of signs or symbols for communication) are present, as it has been clearly demonstrated by the old experiments involving symbolic communication teaching by means of keyboards (Gardner & Gardner 1969; Patterson 1978; Savage-Rumbaugh *et al.* 1986).

One of the main reasons of the limited flexibility in the vocal patterns may stem from a limited capacity in voluntarily controlling the vocal apparatus. Although behavioral studies have demonstrated that macaque monkeys can achieve a significant level of voluntary vocal control when submitted to operant conditioning tasks (Sutton *et al.* 1973; Aitken & Wilson 1979; Hihara *et al.* 2003; Yamaguchi & Izumi 2008), the success rate of vocal training studies remains variable (Yamaguchi & Myers 1972; Pierce 1985). In a recent experiment we demonstrated that when macaques are subjected to an intensive training aimed at emitting coo calls, they are capable to reach a significant level of success (Coudè *et al.* 2011). However, it also emerged that often the monkeys were able to modify correctly the mouth configuration but showed difficulties in sound emission, thus suggesting that in macaque monkeys there is only a partial voluntary control and coordination of the mouth together with the larynx muscles.

#### 4.1. *Gestures in Monkeys and Apes*

In one of our previous review we proposed the terms gesture to describe both goal-related actions (e.g., grasping an object with the hand) and communicative oro-facial and brachio-manual movements devoid of an explicit target (Fogassi & Ferrari 2007). Some scholars make different distinctions about what is gesture, emphasizing the motor ineffectiveness, the persistence and the role of gaze etc. (Call & Tomasello 2007). We are not going to cover all the theoretical accounts that define a gesture but instead we would like to make an attempt in understanding the possible link at the neurological level between the control of a movement directed to a target (i.e. a motor act) and the intentional movement that is directed toward another individual which has a communicative meaning. There are several converging evidence from neuroscience, ethology, and developmental psychology that many of the gestures displayed by nonhuman primates began their existence as actions devoid of a communicative function, but over time they became co-opted and transformed into communicative devices that accomplished similar functions (Fogassi & Ferrari 2007; Liebal & Call 2012). Probably, only at a later stage in primate and hominin evolution the vocalization system has been integrated in such gestural system, and in our species we can testify the presence of such ancestral linkage (Corballis 2003).

It's outside the scope of our review to provide a full account of gestural communication in nonhuman primates as it has been already extensively covered elsewhere (Liebal *et al.* 2004; Liebal & Call 2012). However, what is relevant for

the current work is to describe some aspects of this type of communication in relation to neurological mechanisms and language evolution. Gestures can involve the oro-facial and/or the brachio-manual system in conjunction with body postures. Although some of the facial gestures are elicited by less urgent contingent situation, they often involve face-to-face exchanges, involuntary acts and autonomic responses. Some of these gestures have been extensively studied by comparative investigations that could reconstruct, with reliable approximation, their possible relatedness and origin among the different species (van Hooff 1962, 1967). Some of these, we believe, might be particularly relevant for the current topic. For example, lipsmacking has been described in several Old World primate species. It is characterized by regular cycles of vertical jaw movement, often involving a parting of the lips, but sometimes occurring with closed, puckered lips and sometimes alternated with tongue protrusions. Importantly, as a communication signal, the lipsmack is always directed at another individual to signal affiliative and benevolent intentions and it is displayed during face-to-face interactions in which both individuals might lipsmack at each other (Maestripietri 1996; Ferrari *et al.* 2009; Morrill *et al.* 2012). Interestingly, this behavior is one of the first to emerge in the course of ontogeny and undergoes into changes both in the pattern and in the frequency with which it is emitted (Ferrari *et al.* 2009). We have recently found that in rhesus macaques, infants produce lipsmacking at a slower frequency than adults and that these cyclic movements become faster and less variable with age (Morrill *et al.* 2012). We also found that other cyclic movements like chewing do not follow similar developmental patterns. We proposed that the development of lipsmacking follows a trajectory that resembles that of babbling in humans.

From an evolutionary perspective it has been proposed that some communicative gestures such as lips-smacking and pucker face very likely evolved from movements aimed to remove and eat particles, such as skin parasites, from the fur of group mates during grooming sessions. This suggestion is corroborated by the observation that the beginning of a grooming session can be preceded or accompanied by a lips-smacking action without ingestion (see Van Hooff 1962, 1967; Maestripietri 1996). Through a process of ritualization, an ingestive action could have lost its behavioral meaning related to feeding and achieved an affiliative meaning. Together, these evolutionary and ontogenetic accounts seem to be in agreement with the proposal by MacNeilage (1998) that the rhythmic cyclic mandibular open-close alternation produced during infant babbling might have evolved from rhythmic mouth movement of our ancestral primates.

Concerning brachio-manual gestural communication, apes use them in a richer and more elaborated way than monkeys (Call & Tomasello 2007). In the last few years there has been an increasing body of research, in part stimulated by the idea that brachio-manual gestures have probably played a role in language evolution (Liebal & Call 2012). Apes, for example, are capable to use several types of gestures, often in combination, to request for food (Leavens *et al.* 2004, 2005; Gomez 2007). In captivity, chimpanzees and also some monkeys point to request food or objects and, in the case of chimpanzees, they are sensitive to the attentional state of the human experimenter when they point. Although they do not gesture to share information or to inform others, it has been pointed out

that they might use brachio-manual gestures in many flexible ways. Under human rearing conditions some apes have been reported to use declarative gestures, thus showing the potential to expand their cognitive and contextual use of the communicative gestures (Lyn *et al.* 2011).

Another important aspect of gestural communication is the possibility to perform sequences and to combine them with other communicative signals such as face gestures and vocalization. The issue of sequencing has been investigated in a few studies on apes (Liebal *et al.* 2004; Pollick & de Waal 2007). Chimpanzees can use hands gesture sequences producing signals in one or more modalities (visual, auditory, or tactile) (Liebal *et al.* 2004). Although the sequences could involve the repetition of the same gesture, it has been noted that several were composed by three or more different gestures. Most of them were used in a play context but other sequences were often used in more diverse situations. Sometimes the use of the sequence was the result of the failure to gather the recipient attention (Liebal *et al.* 2004). Other studies demonstrate that chimpanzees can often display attention-gather hand gestures in combination with sound production (Leavens *et al.* 2004). More recently, the use of these combinations has been extensively studied in chimpanzees and bonobos (Pollick & de Waal 2007). The results showed that brachio-manual gestures were more flexible across contexts than the facial/vocal communicative ones. The former appear to be less tied to incipient events that may induce high emotional responses than facial gestures and vocalization. These authors conclude that very likely the flexibility of brachio-manual gestures might have played a central role as a prerequisite model for language evolution. This would be also supported by other data showing that apes can imitate brachio-manual gestures and by the report of population-specificity of some of these gestures. However, one of the limitations in these studies is that they have been carried out on animals living in captivity where both the exposure to humans and the weak ecological value in displaying the full-range of communicative behaviors could limit our knowledge on the natural combinatorial use of different gestures and vocalization in the perspective of language evolution.

## **5. Anatomical-Functional Homologies between Monkey Premotor Cortex and Human Broca's Area**

The relation between the mirror neuron system and language is corroborated by comparative data. We will briefly summarize the main evidence of such homology. First, cytoarchitectonic data suggest that dysgranular area 44 (the posterior part of Broca's area) and monkey area F5 share similar features (Petrides & Pandya 1994; Rizzolatti & Arbib 1998) (see Fig. 1 below). Although some authors have emphasized the anatomical characteristics of monkey area 44 (located, according to Petrides *et al.* (2005), in the fundus of the inferior limb of arcuate sulcus) as a possible precursor of human 44, neurophysiological recordings provided evidence that the whole rostral part of ventral premotor cortex in monkeys has typical features (see below) that are shared with those recently described for Broca's area.

Second, area F5 contains motor neurons related to the execution of both hand and/or mouth actions. Similarly, brain imaging experiments in humans demonstrated that Broca's area, traditionally considered as a 'speech' area, is also involved in hand movement tasks such as complex finger movements, mental imagery of grasping actions, and hand imitation tasks (see Rizzolatti *et al.* 2009).

Third, a recent neurophysiological study showed that in the lateral part of area F5 there are neurons specifically activated during conditioned vocalization (Coudé *et al.* 2011, see below), suggesting its possible role in the evolution of voluntary controlled phonation. These findings are relatively surprising because it is known that ventral premotor cortex contains a representation of the larynx (Hast *et al.* 1974; Simonyan & Jurgens 2003).

Fourth, both areas are considered to be the rostral pole of the mirror neuron system. In fact, the evidence reviewed above demonstrates that Broca's area, as F5 mirror neurons, is activated when subjects observe goal-related hand and mouth motor acts done by another individual (see Rizzolatti *et al.* 2009). Furthermore, in accord with the presence of F5 mirror neurons responding to the sound of motor acts (Kohler *et al.* 2002), also the human left motor cortex is activated when subjects listen to sounds associated with motor acts (Aziz-Zadeh *et al.* 2004; Gazzola *et al.* 2006; Ricciardi *et al.* 2009).

Fifth, in agreement with the presence of oro-facial communicative mirror neurons in F5, Broca's area activates when subjects observe silent speech (Buccino *et al.* 2004b).

Summing up, in monkey premotor cortex there are several features that can pre-adapt this cortical sector for the evolution of a sophisticated communicative system. The core of these features consists in encoding the production and perception of both oro-facial and forelimb gestures in the same cortical area. This double control, once integrated with that of vocalization, would have constituted the basis for a communicative system with an increased complexity and efficiency, and a higher level of flexibility in transferring information to conspecifics.

### 5.1. *Toward the Integration of Vocalization with Gestures*

Nonhuman primate vocal behavior was traditionally assumed to be predominantly emotional (Seyfart & Cheney 1997; Fitch 2000; Premack 2004) and mainly consisting of involuntary or reflexive responses. However, several investigations partly contrast this view showing that monkeys can achieve a significant level of voluntary vocal control when submitted to operant conditioning tasks (Sutton *et al.* 1973; Aitken & Wilson 1979; Hihara *et al.* 2003).

From a neurophysiological perspective vocal production in nonhuman primates is considered to be controlled by the brainstem and by mesial cortical areas which, besides other functions, are also involved in emotional behavior (West & Larson 1995; Izumi *et al.* 2001; Jurgens 2002). We have recently challenged this view with a study (Coudé *et al.* 2011) in which we recorded from ventral premotor cortex of macaques trained to control simple calls (i.e. coo-calls). The results showed that the rostro-lateral part of PMv (mostly area F5) contains neurons that fire during conditioned but not during spontaneous vocalization. Interestingly, in the majority of these neurons the discharge begun before sound

onset, thus suggesting their causal relation with vocal production. Furthermore, these neurons have been found intermingled with other neurons controlling mouth and hand motor acts, and with mirror neurons. The link of these neurons with the motor control of vocalization has been also supported by the electrical microstimulation of this sector, which in some cases elicited larynx contraction.

Interestingly, although it is known that acoustic input related to motor acts reaches area F5, we did not find neurons that, beyond their responses during vocalization, responded also during listening to the same or a similar call. This could be due to the fact that while in monkeys during face-to-face gestural communication there is a frequent exposure to oro-facial gestures of their conspecifics with reciprocal exchanges, the same was not true, in this study, for vocal calls. In other words, these monkeys had a feedback from their own voluntary controlled call production, but they were never exposed, except during specific testing, to voluntary calls produced by others and to their associated facial expressions. Another possible explanation for the absence of mirror neurons for vocal calls is that they exist only for emotional vocalizations, in other brain areas. On the other hand, other studies clearly showed that in the superior temporal and prefrontal cortices of the macaque there are neurons coding listened species-specific vocalizations (Rauschecker *et al.* 1995; Ghazanfar *et al.* 2005; Romanski *et al.* 2005), apparently in absence of vocal production-related discharge. Although these perceptual responses could be simply the result of a high order sensory elaboration, it is also possible that in monkeys the acoustic input reaching frontal areas is not coupled yet with the motor representation of vocalizations, at difference with what occurs in other species, such as humans and songbirds (Pulvermüller *et al.* 2006; Prather *et al.* 2008).

These findings suggest that in monkey may exist, in the lateral part of the cortex, a primitive system for the voluntary control of phonation, anatomically embedded in that controlling hand and mouth goal-directed motor acts. Thus, it is plausible to propose that in a further evolutionary step, these two systems could have been integrated. This is, indeed, what has been found, at a behavioral level, in chimpanzees, in which communicative brachio-manual gestures are often accompanied by vocalization (see previous section). At the neurological level, the investigations on chimpanzees or other apes is by far more complex. However, in the last decades structural and functional neuroimaging studies in apes have provided relevant information concerning the neural control of vocalization and communicative gestures in relation to the possible homology with Broca's area. First, it has been shown that in apes there is an asymmetry of the inferior frontal gyrus (Cantalupo *et al.* 2001, 2009; Keller *et al.* 2009) even though it remains to be clarified whether this effect is due to the contribution of gray and/or white matter (see Schenker *et al.* 2010). Second, it has been shown in chimpanzees that right-lateralized skillful hand behaviors correlate with left asymmetry of the hand field of precentral gyrus (Hopkins *et al.* 2010). Third, a PET study in chimpanzees demonstrated the activation of the homolog of Broca's area during the production of communicative vocal and hand gestures (Tagliatella *et al.* 2008). This latter finding is important, because it suggests that, with respect to monkeys, the lateral frontal cortex (area 44 and 45) of chimpanzees (Fig. 1) can control brachio-manual communicative gestures, possibly in conjunc-

tion with vocal production, and that this function is lateralized. Fourth, although indirectly related to communication, a recent PET study reported that a parieto-frontal system is activated in chimpanzees during execution (performed without seeing its own hand) and observation of grasping actions (Hecht *et al.* 2011), giving support to the evolutionary continuity between monkey and human mirror system. Whether the chimpanzee's mirror system is involved in communication still needs to be investigated.

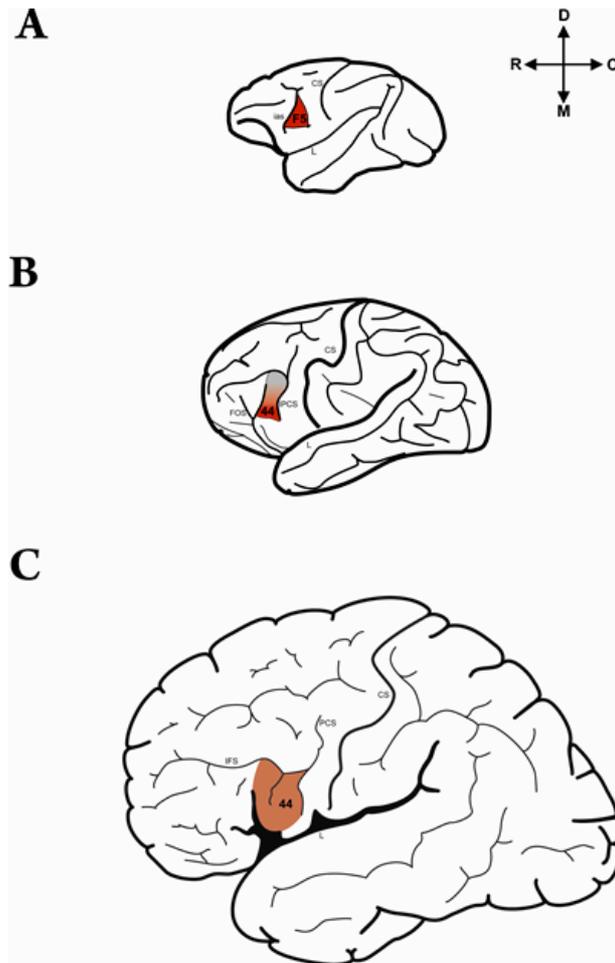


Figure 1: Location (in red color) of area F5 in the macaque monkey (A) and the proposed homologue areas in chimpanzee (B) and man (C). In the chimpanzee brain area 44 has been reconstructed based on the anatomical description of the sulci and contours made by several authors (Bailey *et al.* 1950; Keller *et al.* 2009; Schenker *et al.* 2010; Keller *et al.* 2011). Area 44 in the human brain has been defined according to Brodmann (1909). CS: central sulcus; IAS: inferior arcuate sulcus; FOS: fronto-orbicular sulcus; IFS: inferior frontal sulcus; IPCS: inferior precentral sulcus; L: lateral sulcus; PCS: precentral sulcus.

## 5.2. Hypothetical Transitions from Gestures to Language

The achieved integration, at the apes phylogenetic level, between communicative brachio-manual gestures and vocalization, very likely has been preserved in the next evolutionary steps, even in the presence of a clear predominance of the pho-

natory system. Although it is speculative to mark when the phonatory system reached an autonomous function, in modern humans, the tight observed connection between spoken language and gestures (McNeill 1992; Goldin-Meadow 1999) seems to testify an old common origin. This link is not just an evolutionary relic without a meaningful function, but enables individuals to possess an enriched multimodal communicative system. Although in some situations only vocal communication can be used, it is also true that under specific acoustic impairment conditions (i.e. in deaf people), gestures can assume the main role in communication (Capirci & Volterra 2008). A support to this role is given also by brain imaging studies showing an activation of the inferior frontal cortex in deaf people during production of meaningful signs (Petitto *et al.* 2000).

Interestingly, a wealth of work by Gentilucci and colleagues provided strong evidence for a reciprocal influence between hand actions/gestures and verbal production (Gentilucci & Corballis 2006). For example, they demonstrated that execution or observation of two different types of grasping (precision grip or whole hand prehension) while subjects were pronouncing syllables affected both lips kinematics and voice formants (Gentilucci *et al.* 2004). In another study they showed that in the contemporaneous production or observation of a hand symbolic gesture and a word, the kinematic parameters of the former were inhibited by the latter, while voice spectra were enhanced by the gesture (Bernardis & Gentilucci 2006). From the findings of this latter study they conclude that spoken word and symbolic gesture can be coded as a single signal by a unique communication system and that this signal may represent the intention to engage a closer interaction with a hypothetical interlocutor.

Summing up, there is much evidence that language and gestures share a common motor code, thus supporting several theories proposing that at cortical level some of the properties and organization of the motor system have been exploited within the vocal domain (Rizzolatti & Arbib 1998; Arbib 2005; Fogassi & Ferrari 2007). In line with this, several brain imaging studies show a great degree of overlap of these two systems, in particular in the frontal lobe. The spatial resolution limitation of these techniques does not allow, at present, to assess whether these two functions activate different anatomical subsectors within the frontal lobe. Even neurologically it is well known that higher order praxic and linguistic deficits can appear associated, but this is not consistent among patients, thus suggesting a partial independence of the two functions (De Renzi 1989).

Once a primitive communicative system based on an association between gestures and vocalization took place, a further step in both the motor and sensory development of this system probably occurred through the acquisition of a more sophisticated phonatory mechanism, which allowed the association of a gesture with a specific sound. At this stage of language evolution the possibility of creating a theoretically infinite set of combinations rendered the phonatory system alone more efficient than the previous vocal-gestural system. This stage was crucial for the development of a speech-based communicative system.

### 5.3. *Action Sequences and Syntax*

The idea of a possible similarity between the organization of actions and

syntactic structure is worth to investigate, in particular under the evolutionary perspective discussed in the previous sections. According to some linguists, syntax function can be defined as a regulator of language (Pinker & Jackendoff 2005). One of the mechanisms belonging to this function is that of combining elements, i.e. words, hierarchically, into meaningful phrases. Similarly to syntactic structure, as shown by classical behavioral and psychophysical studies (Jeannerod 1988; Bernstein 1996; Rosenbaum *et al.* 2007), the 'action' is considered as the top level of the motor organization, and is formed by a sequence of motor acts. Motor acts are the basic constituents of the motor system endowed with a meaning (the motor goal), playing a role similar to that of words within a phrase. The hierarchical sequencing of motor acts into a specific action (for example, (a) grasping a piece of food, (b) bringing it to the mouth, and (c) biting it) aims to a superordinate behavioral goal (eating the food). If the order of the motor act is changed (e.g., biting the food with the mouth, bringing the hand to the mouth, and grasping the food with the hand: c–b–a) the action goal can change (take the food out of the mouth). Similarly, the meaning of a phrase is given by the sequential organization of words. By changing the position of the words in a sentence, its meaning changes or is lost.

With respect to the hierarchical organization of motor sequences, two main series of studies attempted to address this issue at the single neuron level. The first series assessed the responses of neurons in mesial cortices (pre-supplementary motor area, pre-SMA/F6 and supplementary motor area, SMA proper/F3) and prefrontal cortex while monkeys executed sequences of movements (Tanji 2001; Tanji & Hoshi 2008), such as turning, pulling and pushing, or specific sequences of reaching movements, or a series of movements in a maze. These studies showed that the recorded neurons could code either the sequence, the order of a movement inside a sequence or the final location of a trajectory. Another series of studies, carried out in our laboratory (Fogassi *et al.* 2005; Bonini *et al.* 2011), assessed the responses of parietal and premotor neurons during execution and observation of natural action sequences. The results showed that grasping neurons of areas PFG or F5 can discharge differently depending on the specific action sequence in which the grasping is embedded (see Fig. 2 below). Notably, this differential response is shown also by mirror neurons during observation of grasping embedded in different action sequences performed by another individual. This latter series of data suggests that motor neurons of parietal and ventral premotor cortex are organized in motor chains, each coding a specific action goal. Within this organization, a neuron coding a given motor act can discharge differently according to the action sequence to which this act belongs.

Summing up, both the order of a motor series and the organization of a natural action sequence can be coded by cortical single neurons. The premotor-parietal motor system plus the prefrontal cortex can provide a substrate for sequential organization and hierarchical combination of motor elements. We posit that such an organization has been exploited in other domains including some aspects of the syntactic structure of language (see also Fogassi & Ferrari 2007).

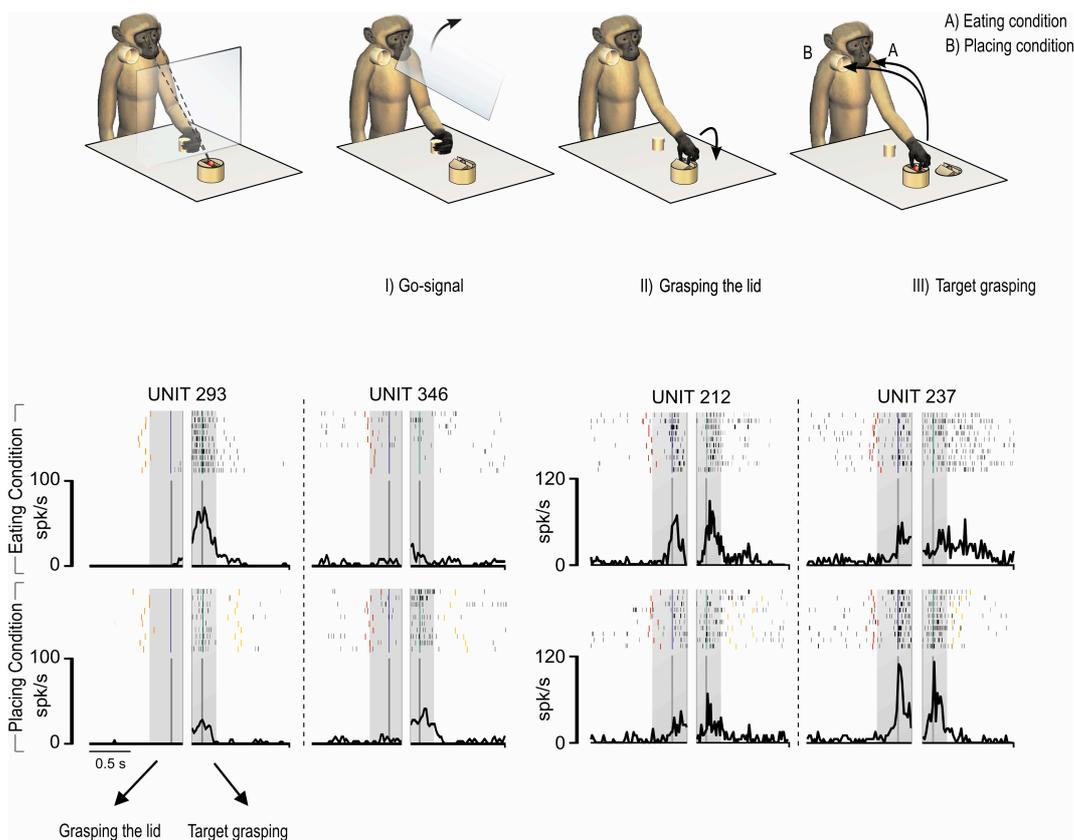


Figure 2: Top. Action sequence tasks. A transparent screen allowed the monkey to establish from the beginning which of the two action goals (eating or placing) had to be performed. Once the screen was removed (I) the monkey had to grasp a lid that covered a container (II), and then, after the removal of the lid, grasped an object inside the container in order to eating it (A) or placing it into another container (B) located near the mouth. Bottom. Activity of four neurons recorded from parietal area PFG during the task. Rasters and histograms representing neuronal activity is aligned on the first (left) and second (right) grasping act performed by the monkey. Ordinate represents neuronal discharge in spikes/sec. Abscissae indicate time course. Modified from Bonini *et al.* (2011).

In humans it is more difficult to directly demonstrate the existence of a mechanism involved in organizing action sequences, although a few investigations attempted to explore this issue. In an fMRI study (Frey & Gerry 2006) subjects had to just observe or to observe with the purpose to reproduce the constructions, by another individual, of multiparts objects, that required structured motor sequences. During the task the activated regions were inferior frontal and parietal cortices (part of the mirror system), dorsal premotor cortex and pre-SMA, plus subcortical motor structures. In the observation/imitation study by Buccino *et al.* (2004a), described in a previous section, in which subjects had to observe, in order to imitate, sequences of guitar chords performed by a model, the activation involved the parieto-frontal mirror system, the SMA and prefrontal cortex. Altogether, these areas seem to play a role in encoding the meaning of motor acts, in parsing the action sequence into its discrete motor elements and, vice versa, in constructing new actions starting from single motor acts.

Since the first reports of Broca's patients, the IFG region has been repetitively considered as having a crucial role in syntactic processing. However, although not denying this role, other studies provided information that make this picture more complex. In fact there are other areas such as, for example, superior temporal cortex, that are activated during syntactic processing. Moreover, the activation of IFG by syntactic construction involves also concurrent semantic coding. Lastly, this region appears to be more activated when the level of complexity of syntactic comprehension of the sentence is higher (see Gernsbacher & Kaschak 2003; Grodzinsky & Friederici 2006). In addition, as it is clear also from the extension of the lesion in Broca's aphasics, an important role is also played by nearby regions, such as, for example, the middle prefrontal cortex, located just medially to IFG, that probably provides this latter region with the working memory mechanism necessary for building and understanding long and complex sentences. Altogether, these reports indicate that within the IFG region, areas contribute to processing linguistic information beyond syntactic structure. This would be in agreement with the proposal that in the IFG region (BA 44, 45 and 47) there are subsectors involved in phonology, syntax and semantics, that appear to be roughly organized along a caudal-to-rostral anatomical sequence, with a certain overlap between them (Bookheimer 2002; Hagoort 2005).

This type of organization of IFG region does not contradict its possible derivation from a system responsible for action organization. Indeed this latter requires, for its optimal functioning, a hierarchical structure, a precise order that makes the action sequence meaningful, and a coded semantics, that is observed both at the level of whole action and of the motor acts composing it, similarly to what it occurs for the meaning of a sentence and a word, respectively. In agreement with this, neuroimaging studies showed that IFG activation is higher when the meaning of a sentence depends not only from word meanings but also from the syntactic structure in which the words are ordered (Dapretto & Bookheimer 1999). On the other hand, other studies suggest that Broca's area is involved in processing hierarchical structures in multiple domains of human cognition (Thompson-Schill *et al.* 2005; Koechlin & Jubault 2006). Thus, although the transition from action to language could have been long and may have required a complex adjustment of the mechanisms involved in sequence organization, nonetheless the existence of a motor substrate endowed with a motor meaning, organized in chunks and accessible by visual and acoustic higher order input, seems an important prerequisite for both language construction and its comprehension.

## References

- Aitken, P. G. & W. A. Wilson Jr. 1979. Discriminative vocal conditioning in rhesus monkeys: Evidence for volitional control? *Brain Language* 8, 227–240.
- Arbib, M. 2005. From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. *Behavioral Brain Sciences* 28, 105–167.

- Aziz-Zadeh, L., M. Iacoboni, E. Zeidel, S. Wilson & J. Mazziotta. 2004. Left hemisphere action facilitation in response to manual action sounds. *European Journal of Neuroscience* 19, 2609–2612.
- Bailey, P., G. von Bonin & W. S. McCulloch. 1950. *The Isocortex of the Chimpanzee*. Urbana, IL: University of Illinois Press.
- Bak, T. H., D. G. O'Donovan, J. H. Xuereb, S. Boniface & J. R. Hodges. 2001. Selective impairment of verb processing associated with pathological changes in Brodmann areas 44 and 45 in the motor neurone disease–dementia–aphasia syndrome. *Brain* 124, 103–120.
- Bak, T. H., D. Yancopoulou, P. J. Nestor, J. H. Xuereb, M. G. Spillantini, F. Pulvermüller & J. R. Hodges. 2006. Clinical, imaging and pathological correlates of a hereditary deficit in verb and action processing. *Brain* 129, 321–332.
- Bernardis, P. & M. Gentilucci. 2006. Speech and gesture share the same communication system. *Neuropsychologia* 44, 178–190.
- Bernstein, N. A. 1996. On dexterity and its development. In M. L. Latash & M. T Turvey (eds.), *Dexterity and its Development*. Mahwah, NJ: Lawrence Erlbaum.
- Bonini L., S. Rozzi, F. U. Serventi, L. Simone, P. F. Ferrari & L. Fogassi. 2010. Ventral premotor and inferior parietal cortices make distinct contribution to action organization and intention understanding. *Journal of Neuroscience* 20, 1372–1385.
- Bonini, L., F. U. Serventi, L. Simone, S. Rozzi, P. F. Ferrari & L. Fogassi. 2011. Grasping neurons of monkey parietal and premotor cortices encode action goals at distinct levels of abstraction during complex action sequences. *Journal of Neuroscience* 31, 5876–5886.
- Bookheimer, S. 2002. Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience* 25, 151–188.
- Brodmann, K. 1909. *Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien Dargestellt auf Grund des Zellenbaues*. Leipzig: Barth.
- Buccino, G., F. Binkofski, G. R. Fink, L. Fadiga, L. Fogassi, V. Gallese, R. J. Seitz, K. Zilles, G. Rizzolatti & H. J. Freund. 2001. Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience* 13, 400–404.
- Buccino, G., S. Vogt, A. Ritzl, G. R. Fink, K. Zilles, H.-J. Freund & G. Rizzolatti. 2004a. Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. *Neuron* 42, 323–334.
- Buccino, G., F. Lui, N. Canessa, I. Patteri, G. Lagravinese, F. Benuzzi, C. A. Porro & G. Rizzolatti. 2004b. Neural circuits involved in the recognition of actions performed by non-conspecifics: An fMRI study. *Journal of Cognitive Neuroscience* 16, 114–126.
- Buccino, G., L. Riggio, G. Melli, F. Binkofski, V. Gallese & G. Rizzolatti. 2005. Listening to action-related sentences modulates the activity of the motor system: A combined TMS and behavioral study. *Cognitive Brain Research* 24, 355–363.
- Caggiano, V., L. Fogassi, G. Rizzolatti, P. Thier & A. Casile. 2009. Mirror neurons

- differentially encode the peripersonal and extrapersonal space of monkeys. *Science* 324, 403–406.
- Caggiano, V., L. Fogassi, G. Rizzolatti, J. K. Pomper, P. Thier, M. A. Giese & A. Casile. 2011. View-based encoding of actions in mirror neurons of area f5 in macaque premotor cortex. *Current Biology* 21, 144–148.
- Caine, N. G., R. L. Addington & T. L. Windfelder. 1995. Factors affecting the rates of food calls given by red-bellied tamarins. *Animal Behaviour* 50, 53–60.
- Call, J. & M. Tomasello 2007. The gestural communication of apes and monkeys. Mahwah, NJ: Lawrence Erlbaum.
- Cantalupo, C. & W. D. Hopkins. 2001. Asymmetric Broca's area in great apes. *Nature* 414, 505.
- Cantalupo, C., J. Oliver, J. Smith, T. Nir, J. P. Tagliabattola & W. D. Hopkins. 2009. The chimpanzee brain shows human-like perisylvian asymmetries in white matter. *European Journal of Neuroscience* 30, 431–4318.
- Capirci O. & V. Volterra. 2008. Gesture and speech. The emergence and development of a strong changing partnership. *Gesture* 8, 22–44.
- Casile, A. & M. A. Giese. 2006. Nonvisual motor training influences biological motion perception. *Current Biology* 16, 69–74.
- Caspers, S., K. Zilles, A. R. Laird & S. B. Eickhoff. 2010. ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage* 50, 1148–1167.
- Cheney D. L. & R. M. Seyfarth. 1982. How vervet monkeys perceive their grunts. *Animal Behaviour* 30, 739–751.
- Cochin, S., C. Barthelemy, S. Roux & J. Martineau. 1999. Observation and execution of movement: Similarities demonstrated by quantified electroencephalography. *European Journal of Neuroscience* 11, 1839–1842.
- Corballis, M. C. 2003. From mouth to hand: Gesture, speech, and the evolution of right-handedness. *Behavioral and Brain Sciences* 26, 199–260.
- Coudè, G., P. F. Ferrari, F. Rodà, M. Maranesi, E. Borelli, V. Veroni, F. Monti, S. Rozzi & L. Fogassi. 2011. Neurons controlling voluntary vocalization in the macaque ventral premotor cortex. *PLoS One* 6(11), e26822.
- Craighero, L., L. Fadiga, G. Rizzolatti & C. Umiltà. 1999. Action for perception: A motor-visual attentional effect. *Journal of Experimental Psychology Human Perception Performance* 25, 1673–1692.
- Crockford, C., R. M. Wittig, R. Mundry & K. Zuberbühler. 2012. Wild chimpanzees inform ignorant group members of danger. *Current Biology* 22, 142–146.
- Damasio, A. R. 1992. Aphasia. *The New England Journal of Medicine* 326, 531–539.
- D'Ausilio, A., F. Pulvermüller, P. Salmas, I. Bufalari, C. Begliomini & L. Fadiga. 2009. The motor somatotopy of speech perception. *Current Biology* 19, 381–385.
- Dapretto, M. & S. Y. Bookheimer. 1999. Form and content: Dissociating syntax and semantics in sentence comprehension. *Neuron* 24, 427–432.
- De Renzi, E. 1989. Apraxia. In: F. Boller & J. Grafman (eds.), *Handbook of Neuropsychology*, vol. 2, 245–263. Amsterdam: Elsevier.
- Di Pellegrino, G., L. Fadiga, L. Fogassi, V. Gallese & G. Rizzolatti. 1992. Understanding motor events: A neurophysiological study. *Experimental Brain*

- Research* 91, 176–80.
- Egnor, S. E. & M. D. Hauser. 2006. Noise-induced vocal modulation in cotton-top tamarins (*Saguinus oedipus*). *American Journal of Primatology* 68, 1183–1190.
- Eimas, P. D., E. R. Siqueland, P. Jusczyk & J. Vigorito. 1971. Speech perception in infants. *Science* 3968, 303–306.
- Evarts, E. V. 1968. Relation of pyramidal tract activity to force exerted during voluntary movement. *Journal of Neurophysiology* 31, 14–27.
- Fadiga, L., L. Fogassi, G. Pavesi & G. Rizzolatti. 1995. Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology* 73, 2608–2611.
- Fadiga, L., L. Craighero, G. Buccino & G. Rizzolatti. 2002. Speech listening specifically modulates the excitability of tongue muscles: A TMS study. *European Journal of Neuroscience* 15, 399–402.
- Ferrari, P. F., V. Gallese, G. Rizzolatti & L. Fogassi. 2003. Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *European Journal of Neuroscience* 17, 1703–1714.
- Ferrari, P. F., A. Paukner, C. Ionica & S. J. Suomi. 2009. Reciprocal face-to-face communication between rhesus macaque mother and their newborn infants. *Current Biology* 19, 1768–1772.
- Ferrari, P. F., S. Rozzi & L. Fogassi. 2005. Mirror neurons responding to observation of actions made with tools in monkey ventral premotor cortex. *Journal of Cognitive Neuroscience* 17, 212–226.
- Ferrari, P. F., R. E. Vanderwert, A. Paukner, S. Bower, S. J. Suomi & N. A. Fox. 2012. Distinct EEG amplitude suppression to facial gestures as evidence for a mirror mechanism in newborn monkeys. *Journal of Cognitive Neuroscience* 24, 1165–1172.
- Filimon, F., J. D. Nelson, D. J. Hagler & M. I. Sereno. 2007. Human cortical representations for reaching: mirror neurons for execution, observation, and imagery. *NeuroImage* 37, 1315–1328.
- Fitch W. T. 2000. The evolution of speech: A comparative review. *Trends in Cognitive Sciences* 4, 258–267.
- Fogassi, L. & P. F. Ferrari. 2007. From mirror neurons to embodied language. *Current Directions in Psychological Science* 16, 136–141.
- Fogassi, L., P. F. Ferrari, B. Gesierich, S. Rozzi, F. Chersi & G. Rizzolatti. 2005. Parietal lobe: From action organization to intention understanding. *Science* 308, 662–667.
- Frey, S. H. & V. E. Gerry. 2006. Modulation of neural activity during observational learning of actions and their sequential orders. *Journal of Neuroscience* 6, 13194–13201.
- Fuster, J. 2008. *The Prefrontal Cortex*. London: Academic Press.
- Gallese, V., L. Fadiga, L. Fogassi & G. Rizzolatti. 1996. Action recognition in the premotor cortex. *Brain* 119, 593–609.
- Gallese, V., L. Fadiga, L. Fogassi & G. Rizzolatti. 2002. Action representation and the inferior parietal lobule. In W. Prinz & B. Hommel (eds.), *Common Mechanisms in Perception and Action: Attention and Performance, Vol. XIX*, 334–355. Oxford: Oxford University Press.

- Gangitano, M., F. M. Mottaghy & A. Pascual-Leone. 2004. Modulation of premotor mirror neuron activity during observation of unpredictable grasping movements. *European Journal of Neuroscience* 20, 2193–2202.
- Gardner, R. A. & B. T. Gardner. 1969. Teaching sign language to a chimpanzee. *Science* 165, 664–672.
- Gazzola, V. L. Aziz-Zadeh & C. Keysers. 2006. Empathy and the somatotopic auditory mirror system in humans. *Current Biology* 16, 1824–1829.
- Gentilucci, M., S. Stefanini, A. C. Roy & P. Santunione. 2004. Action observation and speech production: Study on children and adults. *Neuropsychologia* 42, 1554–1567.
- Gentilucci, M. & M. C. Corballis. 2006. From manual gesture to speech: A gradual transition. *Neuroscience and Biobehavioral Reviews* 30, 949–960.
- Georgopoulos, A. P., J. F. Kalaska, R. Caminiti & J. T. Massey. 1982. On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *Journal of Neuroscience* 2, 1527–1537.
- Gernsbacher, M. A. & P. Kaschak. 2003. Neuroimaging studies of language. Production and comprehension. *Annual Review in Psychology* 54, 91–114.
- Ghazanfar, A. A. & M. D. Hauser. 1999. The neuroethology of primate vocal communication: Substrates for the evolution of speech. *Trends in Cognitive Sciences* 3, 377–384.
- Ghazanfar, A. A., J. X. Maier, K. L. Hoffman & N. K. Logothetis. 2005. Multisensory integration of dynamic faces and voices in rhesus monkey auditory cortex. *Journal of Neuroscience* 25, 5004–5012.
- Giese, M. A. & T. Poggio. 2003. Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience* 4, 179–192.
- Goldin-Meadow, S. 1999. The role of gestures in communication and thinking. *Trends in Cognitive Sciences* 3, 419–429.
- Gomez, J. C. 2007. Pointing behaviors in apes and human infants: A balanced interpretation. *Child Development* 78, 729–734.
- Goodglass, H. 1993. *Understanding Aphasia*. San Diego, CA: Academic Press.
- Gregoriou, G. G., E. Borra, M. Matelli & G. Luppino 2006. Architectonic organization of the inferior parietal convexity of the macaque monkey. *Journal of Comparative Neurology* 496, 422–451.
- Grèzes, J., N. Costes & J. Decety. 1998. Top down effect of the strategy to imitate on the brain areas engaged in perception of biological motion: A PET investigation. *Cognitive Neuropsychology* 15, 553–582.
- Grodzinsky, Y. & A. D. Friederici. 2006. Neuroimaging of syntax and syntactic processing. *Current Opinion in Neurobiology* 16, 240–246.
- Hagoort, P. 2005. On Broca, brain, and binding: A new framework. *Trends in Cognitive Sciences* 9, 416–423.
- Hast, M. H., J. M. Fischer, A. B. Wetzel & V. E. Thompson. 1974. Cortical motor representation of the laryngeal muscles in *Macaca mulatta*. *Brain Research* 73, 229–240.
- Hauk, O., I. Johnsrude & F. Pulvermüller. 2004. Somatotopic representation of action words in human motor and premotor cortex. *Neuron* 41, 301–307.
- Hauser, M. D., N. Chomsky & W. T. Fitch. 2002. The faculty of language: What is it, who has it, and how did it evolve? *Science* 298, 1569–1579.

- Hecht, E. E., L. Davis & L. A. Parr. 2011. Do chimpanzees 'mirror' others' actions? A functional neuroimaging study of action execution and observation. *Society for Neuroscience Abstracts* 932.05.
- Hickok, G. 2009. Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *Journal of Cognitive Neuroscience* 21, 1229–1243.
- Hickok, G. & D. Poeppel 2007. The cortical organization of speech processing. *Nature Reviews Neuroscience* 8, 393–402.
- Hihara, S., H. Yamada, A. Iriki & K. Okanoya. 2003. Spontaneous vocal differentiation of coo-calls for tools and food in Japanese monkeys. *Neuroscience Research* 45, 383–389.
- Hopkins, W. D., J. P. Taglialatela, J. L. Russell, T. M. Nir & J. Schaeffer. 2010. Cortical representation of lateralized grasping in chimpanzees (*Pan troglodytes*): A combined MRI and PET study. *PLoS ONE* 5(10), e13383.
- Iacoboni, M. 2009. Neurobiology of imitation. *Current Opinion in Neurobiology* 19, 661–665.
- Izumi, A., K. Kuraoka, S. Kojima & K. Nakamura. 2001. Visually guided facial actions in rhesus monkeys. *Cognitive, Affective & Behavioral Neuroscience* 1, 266–269.
- Jeannerod, M. 1988. *The Neural and Behavioural Organization of Goal-Directed Movements*. Oxford: Oxford University Press.
- Jeannerod, M. 1994. The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences* 17, 187–245.
- Jürgens, U. 2002. Neural pathways underlying vocal control. *Neuroscience and Biobehavioral Review* 26, 235–258.
- Keller, S. S., N. Roberts & W. J. Hopkins. 2009. A comparative magnetic resonance imaging study of the anatomy, variability, and asymmetry of Broca's area in the human and chimpanzee brain. *Journal of Neuroscience* 29, 14607–14616.
- Keller, S. S., M. Deppe, M. Herbin & E. Gilissen. 2011. Variability and asymmetry of the sulcal contours defining Broca's area homologue in the chimpanzee brain. *Journal of Comparative Neurology* 520(6), 1165–1180.
- Koechlin, E. & T. Jubault. 2006. Broca's area and the hierarchical organization of human behavior. *Neuron* 50, 963–974.
- Kohler, E., C. Keysers, M. A. Umiltà, L. Fogassi, V. Gallese & G. Rizzolatti. 2002. Hearing sounds, understanding actions: Action representation in mirror neurons. *Science* 297, 846–848.
- Kraskov, A., N. Dancause, M. M. Quallo, S. Shepherd & R. N. Lemon. 2009. Corticospinal neurons in macaque ventral premotor cortex with mirror properties: A potential mechanism for action suppression? *Neuron* 64, 922–930.
- Leavens, D. A., W. D. Hopkins & R. K. Thomas. 2004. Referential communication by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 118, 48–57.
- Leavens, D. A., W. D. Hopkins & K. A. Bard. 2005. Understanding the point of chimpanzee pointing. *Current Directions in Psychological Science* 14, 185–189.
- Liberman, A. M. & I. G. Mattingly. 1985. The motor theory of speech perception

- revised. *Cognition* 21, 1–36.
- Liebal, K., J. Call & M. Tomasello. 2004. Use of gestures sequences in chimpanzees (*Pan troglodytes*). *American Journal of Primatology* 64, 377–396.
- Liebal, K. & J. Call. 2012. The origins of non-human primates' gestures. *Philosophical Transactions of the Royal Society B* 367, 118–128.
- Lotto, A. J., G. S. Hickok & L. L. Holt. 2009. Reflections on mirror neurons and speech perception. *Trends in Cognitive Sciences* 13, 110–114.
- Loula, F, S. Prasad, K. Harber & M. Shiffrar. 2005. Recognizing people from their movement. *Journal of Experimental Psychology: Human Perception and Performance* 31, 210–220.
- Lui, F., G. Buccino, D. Duzzi, F. Benuzzi, G. Crisi, P. Baraldi, P. Nichelli, C. A. Porro & G. Rizzolatti. 2008. Neural substrates for observing and imagining non-object-directed actions. *Social Neuroscience* 3, 261–275.
- Lyn, H., P. M. Greenfield, S. Savage-Rumbaugh, K. Gillespie-Lynch & W. D. Hopkins. 2011. Nonhuman primates do declare! A comparison of declarative symbol and gesture use in two children, two bonobos, and a chimpanzee. *Language and Communication* 31, 63–74.
- MacNeilage, P. F. 1998. The frame/content theory of evolution of speech production. *Behavioral and Brain Sciences* 21, 499–546.
- Maestripietri, D. 1996. Gestural communication and its cognitive implications in pigtail macaques (*Macaca nemestrina*). *Behaviour* 133, 997–1022.
- McNeill, D. 1992. *Hand and Mind*. Chicago, IL: University of Chicago Press.
- Merleau-Ponty, M. 1962. *Phenomenology of Perception* (Transl. C. Smith). London: Routledge.
- Morrill, R. J., A. Paukner, P. F. Ferrari & A. A. Ghazanfar. 2012. Lip-smacking develops like speech. *Developmental Science* 15, 557–568.
- Nishitani, N. & R. Hari. 2000. Temporal dynamics of cortical representation for action. *Proceedings of the National Academy of Sciences of USA* 97, 913–918.
- Owren, M. J., J. A. Dieter, R. M. Seyfarth & D. L. Cheney. 1993. Vocalizations of rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques cross-fostered between species show evidence of only limited modification. *Developmental Psychobiology* 26, 389–406.
- Patterson, F. G. 1978. The gestures of a gorilla: Language acquisition in another pongid. *Brain and Language* 5, 72–97.
- Perrett, D. I., M. H. Harries, R. Bevan, S. Thomas, P.J. Benson, A.J. Mistlin, A. K. Chitty, J. K. Hietanen & J. E. Ortega. 1989. Frameworks of analysis for the neural representation of animate objects and actions. *Journal of Experimental Biology* 146, 87–113.
- Petitto, L. A., R. J. Zatorre, K. Gauna, E. J. Nikelski, D. Dostie & A. C. Evans. 2000. Speech-like cerebral activity in profoundly deaf people processing signed languages: Implications for the neural basis of human language. *Proceedings of the National Academy of Sciences of USA* 97, 13961–13966.
- Petrides, M. & D. N. Pandya. 1994. Comparative architectonic analysis of the human and the macaque frontal cortex. In F. Boller & J. Grafman (eds.), *Handbook of Neuropsychology*, 17–58. Amsterdam: Elsevier Science.
- Petrides, M., G. Cadoret & S. Mackey. 2005. Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature* 435, 1235–1238.

- Pierce, J. D. 1985. A review of attempts to condition operantly alloprimate vocalizations. *Primates* 26, 202–213.
- Piaget, J. 1951. *The Psychology of Intelligence*. London: Routledge/Kegan Paul.
- Pinker, S. & R. Jackendoff. 2005. The faculty of language: What's special about it? *Cognition* 95, 201–236.
- Poggio, T. & S. Edelman. 1990. A network that learns to recognize three-dimensional objects. *Nature* 343, 263–266.
- Pollick, A. S. & F. B. de Waal. 2007. Ape gestures and language evolution. *Proceedings of the National Academy of Sciences of USA* 104, 8184–8189.
- Prather, J. F., S. Peters, S. Nowicki & R. Mooney. 2008. Precise auditory-vocal mirroring in neurons for learned vocal communication. *Nature* 451, 305–310.
- Premack, D. 2004. Psychology. Is language the key to human intelligence? *Science* 303, 318–320.
- Price, C. J., R. J. Wise, E. A. Warburton, C. J. Moore, D. Howard, K. Patterson, R. S. Frackowiak & K. J. Friston. 1996. Hearing and saying. The functional neuro-anatomy of auditory word processing. *Brain* 119, 919–931.
- Pulvermüller, F. & L. Fadiga. 2010. Active perception: Sensorimotor circuits as a cortical basis for language. *Nature Reviews Neuroscience* 11, 351–360.
- Pulvermüller, F., M. Huss, F. Kherif, F. Moscoso del Prado Martin, O. Hauk & Y. Shtyrov. 2006. Motor cortex maps articulatory features of speech sounds. *Proceedings of the National Academy of Sciences of USA* 103, 7865–7870.
- Rauschecker, J. P., B. Tian & M. Hauser. 1995. Processing of complex sounds in the macaque nonprimary auditory cortex. *Science* 268, 111–114.
- Ricciardi, E., D. Bonino, L. Sani, T. Vecchi, M. Guazzelli, J. V. Haxby, L. Fadiga & P. Pietrini. 2009. Do we really need vision? How blind people 'see' the actions of others. *Journal of Neuroscience* 29, 9719–9724.
- Rizzolatti, G. & M. A. Arbib. 1998. Language within our grasp. *Trends in Neurosciences* 21, 188–194.
- Rizzolatti, G. & G. Luppino, 2001. The cortical motor system. *Neuron* 31, 889–901.
- Rizzolatti, G. & C. Sinigaglia. 2009. The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Review Neuroscience* 11, 264274.
- Rizzolatti, G., L. Fogassi & V. Gallese. 2009. The mirror neuron system: A motor-based mechanism for action and intention understanding. In M. Gazzaniga (ed.), *The Cognitive Neuroscience IV*, 625–640. Cambridge, MA: MIT Press.
- Rizzolatti, G., R. Camarda, L. Fogassi, M. Gentilucci, G. Luppino & M. Matelli. 1988. Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Experimental Brain Research* 71, 491–507.
- Roland, P. E., B. Larsen, N. A. Lassen & E. Skinhøj. 1980. Supplementary motor area and other cortical areas in organization of voluntary movements in man. *Journal of Neurophysiology* 43, 118–36.
- Romanski, L. M., B. B. Averbeck & M. Diltz. 2005. Neural representation of vocalizations in the primate ventrolateral prefrontal cortex. *Journal of Neurophysiology* 93, 734–747.
- Rosenbaum, D. A., R. G. Cohen, S. A. Jax, D. J. Weiss & R. van der Wel. 2007. The

- problem of serial order in behavior: Lashley's legacy. *Human Movement Science* 26, 525–554.
- Rozzi, S., R. Calzavara, A. Belmalih, E. Borra, G. G. Gregoriou, M. Matelli & G. Luppino. 2006. Cortical connections of the inferior parietal cortical convexity of the macaque monkey. *Journal of Neuroscience* 16, 1389–1417.
- Rozzi, S., P. F. Ferrari, L. Bonini, G. Rizzolatti & L. Fogassi. 2008. Functional organization of inferior parietal lobule convexity in the macaque monkey: Electrophysiological characterization of motor, sensory and mirror responses and their correlation with cytoarchitectonic areas. *European Journal of Neuroscience* 28, 1569–1588.
- Savage-Rumbaugh, S., K. McDonald, R. A. Sevcik, W. D. Hopkins & E. Rubert. 1986. Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *Journal of Experimental Psychology General* 115, 211–235.
- Schenker, N. M., W. D. Hopkins, M. A. Spocter, A. R. Garrison, C. D. Stimpson, J. M. Erwin, P. R. Hof & C. C. Sherwood. 2010. Broca's area homologue in chimpanzees (*Pan troglodytes*): Probabilistic mapping, asymmetry, and comparison to humans. *Cerebral Cortex* 20, 730–742.
- Seyfarth, R. M. & D. L. Cheney. 1997. Behavioral mechanisms underlying vocal communication in nonhuman primates. *Animal Learning & Behavior* 25, 249–267.
- Seyfarth, R. M. & D. L. Cheney. 2010. Primate vocal communication. In M. L. Platt & A. A. Ghazanfar (eds.), *Primate Neuroethology*, 84–97. Oxford: Oxford University Press.
- Shmuelof, L. & E. Zohary. 2008. A mirror representation of others' actions in the human anterior parietal cortex. *Nature Neuroscience* 11, 1267–1269.
- Simonyan, K. & U. Jürgens. 2003. Efferent subcortical projections of the laryngeal motorcortex in the rhesus monkey. *Brain Research* 974, 43–59.
- Sutton, D., C. Larson, E. M. Taylor & R. C. Lindeman. 1973. Vocalization in rhesus monkeys: Conditionability. *Brain Research* 52, 225–231.
- Tagliabata, J. P., J. L. Russell, J. A. Schaeffer & W. D. Hopkins. 2008. Communicative signaling activates 'Broca's' homolog in chimpanzees. *Current Biology* 18, 343–348.
- Tanji, J. 2001. Sequential organization of multiple movements: Involvement of cortical motor areas. *Annual Review of Neuroscience* 24, 631–651.
- Tanji, J. & E. Hoshi. 2008. Role of the lateral prefrontal cortex in executive behavioral control. *Physiological Reviews* 88, 37–57.
- Tettamanti, M., G. Buccino, M. C. Saccuman, V. Gallese, M. Danna, P. Scifo, F. Fazio, G. Rizzolatti, S. F. Cappa & D. Perani. 2005. Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience* 17, 273–281.
- Thompson-Schill, S. L., M. Bedny & R. F. Goldberg. 2005. The frontal lobes and the regulation of mental activity. *Current Opinion in Neurobiology* 15, 219–224.
- Tomasello, M. & K. Zuberbühler. 2002. Primate vocal and gestural communication. In A. Collin, M. Bekoff & G. Burghardt (eds.), *The Cognitive Animal*, 293–299. Cambridge, MA: MIT Press.

- Umiltà, M. A., E. Kohler, V. Gallese, L. Fogassi, L. Fadiga, C. Keyzers & G. Rizzolatti. 2001. I know what you are doing: A neurophysiological study. *Neuron* 31, 155–165.
- Umiltà, M. A., L. Escola, I. Intskirveli, F. Grammont, M. Rochat, F. Caruana, A. Jezzini, V. Gallese & G. Rizzolatti. 2008. When pliers become fingers in the monkey motor system. *Proceedings of the National Academy of Sciences of USA* 105, 2209–2213.
- Utman, J. A., S. E. Blumstein & K. Sullivan. 2001. Mapping from sound to meaning: reduced lexical activation in Broca's aphasics. *Brain and Language* 79, 444–472.
- Van Hooff, J. A. R. A. M. 1962. Facial expressions in higher primates. *Symposium of the Zoological Society of London* 8, 97–125.
- Van Hooff, J. A. R. A. M. 1967. The facial displays of the catarrhine monkeys and apes. In D. Morris (ed.), *Primate Ethology*, 7–68. London: Weidenfield & Nicolson.
- Visalberghi, E. & D. M. Fragaszy. 2002. 'Do monkeys ape?' Ten years after. In K. Dautenhahn & C. Nehaniv (eds.), *Imitation in Animals and Artifacts*. Cambridge, MA: MIT Press.
- Yamaguchi, S. I. & R. E. Myers. 1972. Failure of discriminative vocal conditioning in Rhesus monkey. *Brain Research* 37, 109–111.
- Yamaguchi, C. & A. Izumi. 2008. Vocal learning in nonhuman primates: Importance of vocal contexts. In N. Masataka (ed.), *The Origins of Language: Unraveling Evolutionary Forces*. Tokyo: Springer Verlag Japan.
- Yee, E., S. E. Blumstein & J. C. Sedivy. 2008. Lexical semantic activation in Broca's and Wernicke's aphasia: Evidence from eye movements. *Journal of Cognitive Neuroscience* 20, 592–612.
- Watkins, K. E., A. P. Strafella & T. Paus. 2003. Seeing and hearing speech excites the motor system involved in speech production. *Neuropsychologia* 41, 989–994.
- West, R. A. & C. R. Larson. 1995. Neurons of the anterior mesial cortex related to faciovocal activity in the awake monkey. *Journal Neurophysiology* 74, 1856–1869.
- Weinrich, M., S. P. Wise & K. H. Mauritz. 1984. A neurophysiological study of the premotor cortex in the rhesus monkey. *Brain* 107, 385–414.
- Zuberbühler, K. 2000. Causal cognition in a non-human primate: Field playback experiments with Diana monkeys. *Cognition* 76, 195–207.

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