

ATTENTION AND PERFORMANCE

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**From hand actions to speech: evidence and speculations**

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## *Abstract*

This paper reviews experimental evidence and presents new data supporting the idea that human language may have evolved from hand/mouth action representation. In favor of this hypothesis are both anatomical and physiological supports. Among the anatomical ones, is the fact that the monkey homologue of human Broca's area is a sector of ventral premotor cortex where goals are stored at representational level. In this region neurons have been found that respond to action-related visual stimuli such as graspable objects (canonical neurons) or actions of other individuals (mirror neurons). Among the physiological ones, are some recent findings by our group showing that (i) during speech listening the listener's motor system becomes active as if she were pronouncing the listened words; (ii) the TMS-induced temporary inactivation of Broca's region has no effects neither on phonological discrimination nor on phonological priming tasks; (iii) hand gestures where the hand is not explicitly visible (i.e. animal hand shadows) activate the hand-related mirror neuron system, including Broca's region; (iv) frontal aphasic patients are affected in their capability to correctly represent observed actions. On the basis of these data we strengthen the hypothesis that human language may have evolved from hand action representation. Finally, we conclude by speculating that an increased complexity of actions chain leading to the fabrication and use of tools, may have provided recursion to actions, a property considered peculiar of human language.

## 1. *Introduction*

“Organs develop to serve one purpose, and when they have reached a certain form in the evolutionary process, they became available for different purposes, at which point the processes of natural selection may refine them further for these purposes”. This sentence comes from Noam Chomsky and it is taken from a letter in the New York Review of Books (Chomsky, 1996, p. 41) in which he wants to stress that he does believe ‘language is part of shared biological endowment’ and can be studied in the manner of other biological systems ‘as a product of natural selection’. He claims, however, that ‘evolutionary theory has little to say, as of now, about such matters as language’.

In the present paper we will assume an evolutionary perspective in order to try to identify that possible initial purpose at the basis of language evolution, and the organ which served to that purpose.

Already the school of phrenology tried to make an attempt in individuating the seat of the faculty of language, by placing it in the anterior part of the brain, bilaterally (Gall, 1822). This opinion would no doubt have disappeared with the rest of the system if it was not modified and surrounded by a cortege of proofs demonstrating that certain brain lesions abolish the ability of speech (aphasia), without destroying intelligence, and that these lesions are always located in the anterior lobes of the brain. It was Marc Dax who, during the first years of 1800, collected observations on aphasic patients and concluded that loss of language was preferentially associated with damage to the left half of the brain (see McManus, 2002). But it was Paul Broca who in 1861 began the study of the relationship of aphasia to the brain, by being the first to prove that aphasia was linked to specific lesions. The autopsy of his famous patient “Tan” showed that in his brain was present ‘a cavity with a capacity for holding a chicken’s egg, located at the level of the fissure of Sylvius’ (Broca, 1861). This area, a region that comprises the whole back part of the third frontal convolution, was later named Broca’s area. Broca made a very interesting consideration regarding the deficits present in aphasics: “... which has perished in them, is therefore not the faculty of language, it is not the memory of words, it is not the actions of the nerves, ... it is the faculty of coordinated movements,

responsible for spoken language". Thus, he stressed the importance on the process at the basis of the capacity to coordinate meaningless articulatory movements in order to finally obtain a meaningful word. A few years after Broca's first studies, Wernicke proposed the first theory of language, which postulated an anterior, motor speech center (Broca's region); a posterior, semantic language center (Wernicke's region); and a fiber tract, the arcuate fascicle, connecting the two regions (Wernicke, 1874).

The neurosurgeon Wilder Penfield was the first who experimentally demonstrated the involvement of Broca's region in speech production by electrically stimulating the frontal lobe in awake patients undergoing brain surgery for intractable epilepsy. This method has been set up to help delimiting, during the course of the surgical procedure, regions whose excision would lead to severe language impairment, while their sparing would allow the saving of language functions. Penfield collected dozens of cases and firstly reported that the stimulation of the inferior frontal gyrus evoked the arrest of ongoing speech, although with some individual variability. The coincidence between the focus of the Penfield effect and the location of the Broca's area was a strongly convincing argument in favour of the motor role of this region (Penfield and Roberts, 1959).

However, cortical stimulation gave also a different version of Broca's area role in language processing. A series of experiments demonstrated that both Broca's and Wernicke's areas are implicated in both the comprehension and production aspects of language (Schaffler et al., 1993; Ojemann et al., 1982, 1989; Burnstine et al., 1990; Luders et al., 1991). In particular, Schaffler and colleagues (1993) reported on three patients with intractable focal seizures arising from the language-dominant left hemisphere. Arrays of subdural electrodes were placed over the left temporal lobe and adjacent supra-Sylvian region. Electrical stimulation of Broca's area produced marked interference with language output functions including speech arrest, slowing of oral reading, paraphasia and anomia. However, the authors reported that at some sites in this region cortical stimulation also produced language comprehension deficits, particularly in response to more complex auditory verbal instructions and visual semantic material.

Already Luria (1966) noted that Broca's area patients made comprehension errors in syntactically complex sentences such as passive constructions, but only when function words or knowledge of the syntactic structure were essential for comprehension. For instance, they had difficulty with the question "A lion was fatally attacked by a tiger. Which animal died?". Thus, again, the description of deficits caused by an interruption, either acute or chronic, of the activity in Broca's underlines its involvement particularly when there is the necessity to combine single elements in order to extract a particular meaning.

In a recent experiment Wilson et al. (Wilson, Saygin, Sereno, & Iacoboni, 2004) carried out an fMRI study in which subjects listened passively to monosyllables and produced the same speech sounds. Results showed a substantial overlap between regions activated by listening to and producing the syllables, and the activated regions were located primarily in the superior part of ventral premotor cortex, in both hemispheres. The task did not require any sophisticated meaning extraction and thus Broca's area was only occasionally involved. These results are in line with brain imaging studies indicating that in language comprehension Broca's area is mainly activated during processing of syntactic aspects when higher levels of linguistic processing are required (see Bookheimer, 2002 for a review). For example, Stromswold (1994) compared right-branching sentences (e.g., The child spilled the juice that stained the rug) to the more difficult center-embedded structures (The juice that the child spilled stained the rug), finding increased activity in Brodmann's area 44 (BA 44) for the more complex constructions. Subsequently, Caplan et al. (1998) used the same stimuli as Stromswold (1994) and they again found that the focus of activity was in Broca. In a second experiment, they varied the number of propositions in sentences ("The magician performed the student that included the joke" vs. "The magician performed the stunt and the joke"). In this experiment, differences were found only in temporal lobe regions, not in Broca's. Caplan et al. (1998) argue that in the latter experiment, the increased memory load is associated with the products of sentence comprehension, whereas in the former experiment, the load is with the "determination

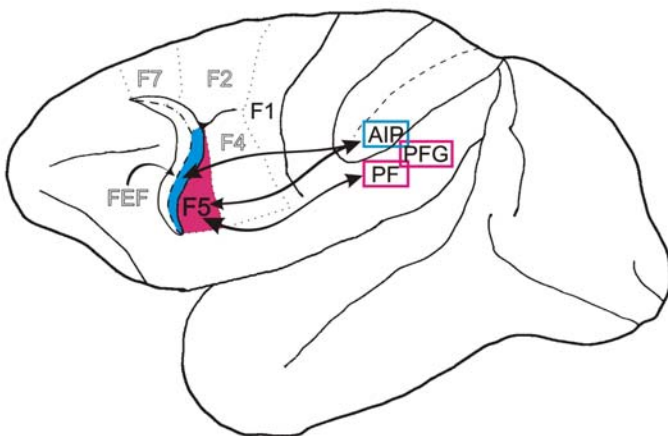
of the sentence's meaning", by stressing again the peculiar role of Broca's region in combining elements to obtain a final result.

The perceptual involvement of Broca's area seems not restricted to speech perception. Since early '70s several groups have shown a strict correlation between frontal aphasia and impairment in gestures/pantomimes recognition (Gainotti and Lemmo, 1976; Duffy and Duffy, 1975; Daniloff et al., 1982; Glosser et al., 1986; Duffy and Duffy, 1981; Bell, 1994). It is often unclear, however, whether this relationship between aphasia and gestures recognition deficits is due to Broca's area lesion only or if it depends on the involvement of other, possibly parietal, areas. In fact, it is a common observation that aphasic patients are sometimes affected by ideomotor apraxia too (see Goldenberg, 1996).

However, the story becomes more and more complicated if we review all the recent brain imaging studies which report, among others, the activation of area 44/45 (see Fadiga et al., 2006). One example is given by those studies that repeatedly observed activations of Broca's area (Mecklinger et al., 2002; Ranganath et al., 2003) while aiming at identifying the neuronal substrate of the working memory. A series of papers by Ricarda Schubotz and Yves von Cramon investigated non-motor and non-language functions of the premotor cortex (for review see Schubotz and von Cramon, 2003) and showed that premotor cortex is also involved in prospective attention to sensory events and in processing serial prediction tasks. Gruber et al (2001) compared a simple calculation task to a compound one and once again observed an activation of Broca's area. In an elegant study, Maess and colleagues (2001) have further investigated the possibility that area 44 is involved in playing with rules by studying musical syntax. By inserting unexpected harmonics Maess and co-workers (2001) created a sort of musical syntactic violation. Using magnetoencephalography (MEG) they studied the neuronal counterpart of hearing harmonic incongruity and they found an early right anterior negativity, a parameter that has already been associated with harmonics violation (Koelsch et al, 2000). The source of the activity pointed out BA 44, bilaterally.

## 2. The monkey homologue of human Broca's area

Thus, far from being exclusively involved in language related processes, Broca's area seems to be involved in multiple tasks. At the same time it emerges from neuroanatomical studies that Broca's area, and in particular its *pars opercularis*, pertains to premotor cortices. So, what is the common functional aspect of its activation? Our approach to unravel the question of the role of Broca's area will be an evolutionary one: we will stepping down the evolutionary scale in order to examine the functional properties of the homologue of BA 44 in our "progenitors". From a cytoarchitectonical point of view (Petrides and Pandya, 1997), the monkey's frontal area which closely resembles human Broca's region is an agranular/dysgranular premotor area (area F5 as defined by Matelli et al. 1985) (see Rizzolatti et al., 2002), see Figure 1. More recently, Nelissen et al. (2005) and Petrides (2006), have focused their attention on the parcelization of monkey area F5. Although with some differences, both studies agree on the fact that the caudal bank and the fundus of the arcuate sulcus differ one from each other as far as cytoarchitectonics is concerned. While the bank is mainly agranular, the fundus is dysgranular. Moreover, this last sector of area F5 remains clearly distinct from the contiguous anterior bank region that both studies consider as pertaining to prefrontal cortex. We will therefore now examine the functional properties of this area by reporting the results of experiments aiming at finding the behavioral correlate of single neurons response.



**Figure 1.** Lateral view of monkey left hemisphere. Area F5 is buried inside the arcuate sulcus (posterior bank, here in light blue) and emerges on the convexity immediately posterior to it (purple). Area F5 is bidirectionally connected with the inferior parietal lobule (areas AIP - anterior intra-parietal, PF and PFG). Within the frontal lobe, area F5 is connected with hand/mouth representations of primary motor cortex (area F1), with sectors of area F2, with the mesial area F6 (not shown) and with prefrontal area 46.

Microstimulation (Hepp-Reymond et al., 1994) and single neuron studies (see Rizzolatti et al. 1988) showed that in area F5 are represented hand and mouth movements. Most of the hand neurons discharge in association with goal-directed actions such as grasping, manipulating, tearing, holding, while they do not discharge during similar movements when made with other purposes (e.g., scratching, pushing away). Furthermore, many F5 neurons become active during movements that have an identical goal regardless of the effectors used for attaining it, suggesting that those neurons are capable to generalize the goal, independently from the acting effector.

Using the action effective in triggering neuron's discharge as classification criterion, F5 neurons can be subdivided into several classes: "grasping", "holding", "tearing", and "manipulating" neurons. Grasping neurons form the most represented class in area F5. Many of them are selective for a particular type of prehension such as precision grip, finger prehension, or whole hand prehension. By considering all the functional properties of neurons in this region, it appears that in area F5 there is a storage—a "vocabulary"—of motor actions related to the hand use. The "words" of the vocabulary are represented by populations of neurons. Each indicates a particular motor action or an aspect of it. Some indicate a complete action in general terms (e.g., take, hold, and tear). Others specify how objects must be grasped, held or torn (e.g., precision grip, finger prehension, and whole hand prehension). Finally, some subdivide the action into smaller segments (e.g., fingers flexion or extension).

All F5 neurons share similar motor properties. In addition to their motor discharge, however, several F5 neurons discharge also to the presentation of visual stimuli (visuomotor neurons). Two radically different categories of visuomotor neurons are present in area F5: Neurons of the first category discharge when the monkey observes graspable objects ("canonical" neurons, Rizzolatti et al., 1988; Rizzolatti and Fadiga, 1998). Neurons of the second category discharge when the monkey observes another individual making an action in front of it ("mirror" neurons di Pellegrino et al.,

1992, Gallese et al., 1996; Rizzolatti et al., 1996a). The two categories of F5 neurons are located in two different sub-regions of area F5: canonical neurons are mainly found in that sector of area F5 buried inside the arcuate sulcus, whereas mirror neurons are almost exclusively located in the cortical convexity of F5.

When comparing visual and motor properties of canonical neurons it becomes clear that there is a strict congruence between the two types of responses. Neurons becoming active when the monkey observes small size objects, discharge also during precision grip. On the contrary, neurons selectively active when the monkey looks at a large object discharge also during actions directed towards large objects (e.g., whole hand prehension) (Murata et al., 1997). The most likely interpretation for visual discharge in these visuomotor neurons is that, at least in adult individuals, there is a close link between the most common 3D stimuli and the actions necessary to interact with them. Thus, every time a graspable object is visually presented, the related F5 neurons are addressed and the action is "automatically" evoked. Under certain circumstances, it guides the execution of the movement, under others, it remains an unexecuted representation of it, that might be used also for semantic knowledge.

Mirror neurons, that become active when the monkey acts on an object and when it observes another monkey or the experimenter making a similar goal-directed action, appear to be identical to canonical neurons in terms of motor properties, but they radically differ from them as far as visual properties are concerned (Rizzolatti and Fadiga, 1998). In order to be triggered by visual stimuli, mirror neurons require an interaction between a biological effector (hand or mouth) and an object. The sights of an object alone, of an agent mimicking an action, or of an individual making intransitive (non-object directed) gestures are all ineffective. The object significance for the monkey has no obvious influence on mirror neuron response. Grasping a piece of food or a geometric solid produces responses of the same intensity. Typically, mirror neurons show congruence between the observed and executed action. This congruence can be extremely strict, that is the effective motor action (e.g., precision grip) coincides with the action that, when seen, triggers the neurons (e.g., precision grip). For other neurons the

congruence is broader. For them the motor requirements (e.g., precision grip) are usually stricter than the visual ones (any type of hand grasping) (Gallese et al. 1996).

It seems plausible that the visual response of both canonical and mirror neurons address the same motor vocabulary, the words of which constitute the monkey motor repertoire. What is different is the way in which “motor words” are selected: in the case of canonical neurons they are selected by object observation, in the case of mirror neurons by the sight of an action. Thus, in the case of canonical neurons, vision of graspable objects activates the motor representations more appropriate to interact with those objects. In the case of mirror neurons, objects alone are no more sufficient to evoke a premotor discharge: what is necessary is a visual stimulus describing a goal-directed hand action in which both, an acting hand and a target must be present.

Summarizing the evidence presented above, the behavioral conditions triggering the response of neurons recorded in the monkey area which is more closely related to human Broca’s (ventral premotor area F5) are: 1) Grasping with the hand and grasping with the mouth actions. 2) Observation of graspable objects. 3) Observation of hand/mouth actions performed by other individuals. Moreover, the experimental evidence suggests that, in order to activate F5 neurons, executed/observed actions must be all goal directed. Does the cytoarchitectonical homology, linking monkey area F5 with Broca’s area, correspond to some functional homology? Does human Broca’s area discharge during hand/mouth action execution/observation too? Does make difference, in terms of Broca’s activation, if observed actions are meaningful (goal-directed) or meaningless? A positive answer to these questions may come from a series of brain imaging experiments.

### ***3. The human mirror-neuron system: brain imaging.***

Direct evidence of an activation of premotor areas during observation of graspable objects was provided by a PET experiment (Grafton, Fadiga, Arbib, & Rizzolatti, 1997). Normal right-handed subjects were scanned during observation of bidimensional colored pictures (meaningless fractals), during observation of 3D objects

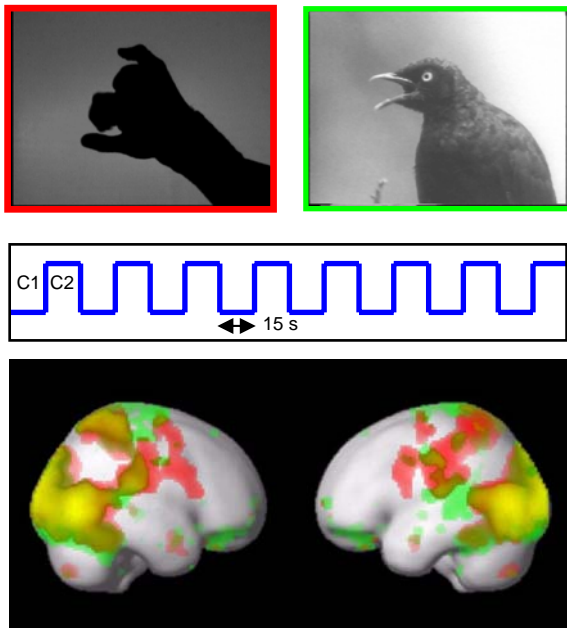
(real tools attached to a panel), and during silent naming of the presented tools and of their use. The most important result was that the premotor cortex became active during the simple observation of the tools. This premotor activation was further augmented when the subjects named the tool use. This result shows that, as in the case of canonical F5 monkey neurons, also in the absence of any overt motor response or instruction to use the observed stimuli, the presentation of graspable objects increases automatically the activity of premotor areas. A very recent PET study made by Grezes and Decety (2002) indicated that the perception of objects, irrespective of the task required to the subject (judgement of the vertical orientation, motor imagery, and silent generation of the noun or of the corresponding action verb), versus perception of non-objects, was associated with activation of a common set of cortical regions. The occipito-temporal junction, the inferior parietal lobule, the SMA-proper, the *pars triangularis* in the inferior frontal gyrus (Broca's area), the dorsal and ventral precentral gyrus, were engaged in the left hemisphere. The ipsilateral cerebellum was also involved. These activations are congruent with the idea of an involvement of motor representation already during the perception of objects, providing evidence that the perception of objects automatically affords actions that can be made toward them.

PET and fMRI experiments, carried out by various groups, demonstrated that when the participants observed actions made by human arms or hands, activations were present in the ventral premotor/inferior frontal cortex (Rizzolatti et al. 1996b; Grafton et al. 1996; Decety et al. 1997; Grèzes et al. 1998; Iacoboni et al. 1999, Decety and Chaminade; 2003; Grèzes et al. 2003). Grèzes et al. (1998) investigated whether the same areas became active during observation of both transitive (goal directed) and intransitive meaningless gestures. Normal human volunteers were instructed to observe meaningful or meaningless actions. The results confirmed that the observation of meaningful hand actions activates the left inferior frontal gyrus (Broca's region), the left inferior parietal lobule plus various occipital and inferotemporal areas. An activation of the left precentral gyrus was also found. During meaningless gesture observation there was no Broca's region activation. Furthermore, in comparison with meaningful action

observations, an increase was found in activation of the right posterior parietal lobule. More recently, two further studies have shown that a meaningful hand-object interaction more than pure movement observation, is effective in triggering Broca's area activation (Hamzei et al, 2003; Johnson-Frey et al, 2003). Similar conclusions have been reached also for mouth movement observation (Campbell et al, 2001).

Very recently (Fadiga *et al*, in press), we investigated the possibility that Broca's area become specifically active during the observation of a particular category of hand gestures: hand shadows representing animals opening their mouths. Hand shadows only implicitly 'contain' the hand creating them. Thus they are interesting stimuli that might be used to answer the question of how detailed a hand gesture must be in order to activate the mirror-neuron system. The results support the idea that Broca's area is specifically involved during meaningful action observation and that this activation is independent of any internal verbal description of the seen scene. Moreover, they demonstrate that the mirror-neuron system becomes active even if the pictorial details of the moving hand are not explicitly visible: In the case of our stimuli, the brain 'sees' the performing hand also behind the appearance. More in details, during the fMRI scanning, healthy volunteers (n=10) observed videos representing (i) the shadows of human hands depicting animals opening and closing their mouths, (ii) human hands executing sequences of meaningless finger movements, or (iii) real animals opening their mouths. Each condition was contrasted with a 'static' condition, in which the same stimuli presented in the movie were shown as static pictures (e.g. stills of animals presented for the same time as the corresponding videos). In addition, to emphasize the action component of the gesture, brain activations were further compared between pairs of conditions in a block design. Figure 2 shows, superimposed, the results of the moving vs. static contrasts for animal hand shadows and real animals conditions (red and green spots, respectively). In addition to largely overlapping occipito-parietal activations, a specific differential activation emerged in the anterior part of the brain. Animal hand shadows strongly activated left parietal cortex, pre- and post-central gyri (bilaterally), and bilateral inferior frontal gyrus (BA 44 and 45). Conversely, the only

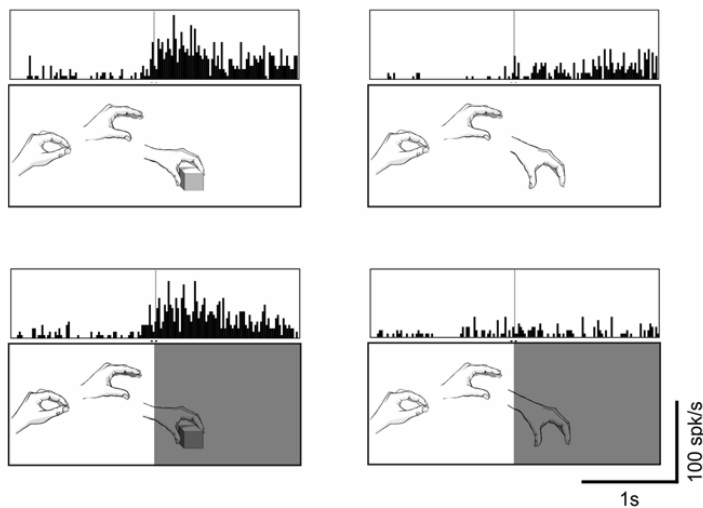
frontal activation reaching significance in the moving vs. static contrast for real animals was located in bilateral BA 6, close to the premotor activation shown in an fMRI experiment by Buccino et al. (2004) when subjects observed mouth actions performed by monkeys and dogs. This location may therefore correspond to a premotor region where a mirror-neuron system for mouth actions is present in humans.



**Figure 2.** Cortical activation pattern during observation of animal hand shadows and real animals. Significantly activated voxels ( $P < 0.001$ , fixed effects analysis) in the moving animal shadows and moving real animals conditions after subtraction of the static controls. Activity related to animal shadows (red clusters) is superimposed on that from real animals (green clusters). Those brain regions activated during both tasks are depicted in yellow. In the middle part of the figure, the experimental time-course for each contrast is shown (i.e. C1, moving; C2, static). Note the almost complete absence of frontal activation for real animals in comparison to animal shadows, which bilaterally activate the inferior frontal gyrus (arrows).

The results shown in Figure 2 indicate that the shadows of animals opening their mouths, although clearly depicting animals and not hands, convey implicit information about the human being moving her hand in creating them. Indeed, they evoke an activation pattern super-imposable on that evoked by hand action observation (Grafton et al 1996, Buccino et al 2001, Grèzes et al 2003). Consequently, the human mirror system (or at least part of it) can be seen more as an active interpreter than as a passive perceiver. Data from a recent monkey study (Umiltà et al 2002), in which the amount of visual information in observed actions was experimentally manipulated, lead to similar conclusions. In this experiment, the experimental paradigm consisted of two basic conditions. In one, the monkey was shown a fully visible action directed toward an object (“full vision” condition). In the other, the monkey saw the same action but with

its final critical part hidden (“hidden” condition). Before each trial the experimenter placed a piece of food behind the screen so that the monkey knew that there was an object behind it. The main result of the experiment was that more than half of the tested neurons discharged in hidden condition (see Figure 3).



**Figure 3.** F5 neuron responding to grasping observation in full vision and in hidden condition (leftmost two panels) but not in mimed conditions (rightmost two panels). The lower part of each panel illustrates schematically the experimenter’s action. The gray square inside the panel represents the opaque screen that prevented the monkey from seeing the action that the experimenter performed behind it. There were two basic conditions: full vision condition, and hidden condition. Grasping

actions were either really performed or mimed (without object). In each panel, histograms of neuron discharge (10 consecutive trials) are shown.

#### 4. From hand actions to ‘speech actions’

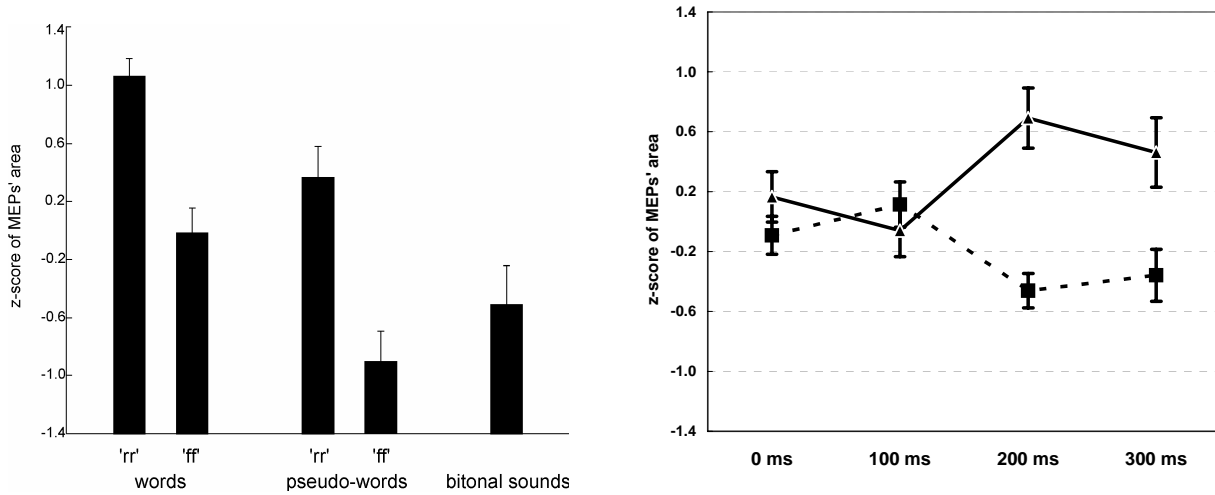
Others’ actions do not generate only visually perceivable signals. Action-generated sounds and noises are also very common in nature. One could expect, therefore, that also this sensory information, related to a particular action, could determine a motor activation specific for that same action. A very recent neurophysiological experiment addressed this point. Kohler and colleagues (2002) investigated whether there are neurons in area F5 that discharge when the monkey makes a specific hand action and also when it *hears* the corresponding action-related sounds. The experimental hypothesis started from the remark that a large number of object-related actions (e.g. breaking a peanut) can be recognized by a particular sound. The authors found that 13% of the investigated neurons discharge both when the monkey performed a hand action and when it heard the action-related sound.

Moreover, most of these neurons discharge also when the monkey observed the same action demonstrating that these ‘audio-visual mirror neurons’ represent actions independently of whether they are *performed, heard* or *seen*.

Most recently, a brain imaging study has revealed that perception of bilabial consonant (that recruited actively the lips to be pronounced) versus alveolar consonant (that, in contrast, recruited more actively the tongue) give rise to a somatotopic activation of the precentral gyrus (Puelvermueller et al, 2006). Previously, Fadiga and coworkers (2002), by using transcranial magnetic stimulation, had shed light on the motor resonance occurring while listening to words. They revealed that the passive listening to words that would involve tongue mobilization (when pronounced) induces an automatic facilitation of the listener’s motor cortex. Indeed, the tongue motor evoked potentials, evoked by TMS of left tongue motor representation, reached higher amplitudes when Italian subjects were listening to Italian words that recruited important tongue movements (/birra/) when compared to words recruiting less important tongue movements (/buffo/). Furthermore, the effect was stronger in the case of words than in the case of pseudo-words (Fig. 4, left).

These findings strengthen the idea that language and fine motor skills may share a common origin, and further suggest that recognizing a verbal stimulus to be a word or not might differentially influence the motor cortex excitability. In a more recent study (Roy et al., in preparation), we specifically addressed the hypothesis that the lexical status of a passively heard verbal item can selectively affect the excitability of the primary motor cortex of the tongue. Specifically, we aimed at answering two questions that were left unanswered by the previous study. On the one hand, the word vs. orthographically regular pseudo-word difference could be due to a familiarity effect, real words being more frequent than any pseudo-word. On the other hand, one cannot exclude that, as words, pseudo-words could yield to an effect analogous in amplitude, but delayed in time, on cortico-bulbar excitability. To shed further light onto these issues, we first sought to confirm and extend the phonological effect and then to disambiguate between the role of familiarity vs. lexical status. To this aim, we recorded

tongue motor evoked potentials evoked by TMS on left tongue motor representation, while subjects were passively listening to verbal stimuli (embedded with a double alveolar consonant i.e. /ll/) pertaining to three different classes: frequent words, rare words and pseudo-words. During listening, we examined the time course of motor cortex excitability by delivering single TMS pulses at four different time-intervals after the beginning of the double consonant (0, 100, 200, 300 ms) in correspondence of tongue representation. EMG potentials evoked by TMS were recorded as in Fadiga et al. (2002). During the experimental session, subjects were required to listen carefully to the presented stimuli and, to favor their attention, to perform a lexical decision on the last heard stimulus (word or pseudo-word?) at the occurrence of an instructional signal randomly presented. Three main results were obtained. First, by stimulating the tongue motor area at 120% of the motor threshold, we further substantiated the phonological effect previously reported by Fadiga and colleagues (2002), as listening to verbal stimuli embedded with consonant recruiting significant tongue movements induced higher motor evoked potentials (MEPs z-score for /ll/= 0.187; for non /ll/= -0.302;  $p < .05$ ). Second, we found that, with respect to uncommon words, frequent words yield to the smallest tongue motor evoked potentials. Third, this pattern varied according to the timing of the magnetic pulse: when the TMS pulse was applied at the very beginning of the consonant or 100 ms afterwards, the evoked muscle activity did not differ across stimulus class. From 100ms to 200ms, the MEPs area obtained for the rare words increased drastically (from -0.059 to 0.691). Then at 200 ms frequent words evoked the weakest tongue MEP while at 300ms the difference between frequent and rare words was still present (Fig. 4, right). Thus, the lexical status influenced the excitability of the primary motor cortex 200 ms after the beginning of the double consonant as rare words gave rise to the highest response.



**Figure 4.** Left, Average value (+ SEM) of intrasubject normalized MEPs total areas for each condition (modified from Fadiga et al 2002). Data from all subjects; 'rr' and 'ff' refer to verbal stimuli containing a double lingua-palatal fricative consonant /r/, and containing a double labio-dental fricative consonant /f/, respectively. Right, time course of normalized MEPs total area (+ SEM), as evoked by TMS on tongue motor representation at different timings during listening of frequent (dotted line) and rare (continuous line) words (Roy et al, in preparation).

Summarizing, these results indicate that the motor system is activated during speech listening. It is however unclear if this activation could be interpreted in terms of an involvement of motor representations in speech processing and, perhaps, perception. This last possibility is in agreement with the idea originally proposed by Liberman (Liberman et al., 1967; Liberman & Mattingly, 1985; Liberman & Wahlen, 2000) starting from the perspective that sounds at the basis of verbal communication could be a vehicle of motor representations (articulatory gestures) shared by both the speaker and the listener, on which speech perception could be based upon. In other terms, the listener understands the speaker when his/her articulatory gestures representations are activated by verbal sounds (motor theory of speech perception). In the next section, we will discuss this issue and we will present the results of some new experiments performed both on normal subjects and patients, that may help to clarify the role of frontal motor cortices in speech processing.

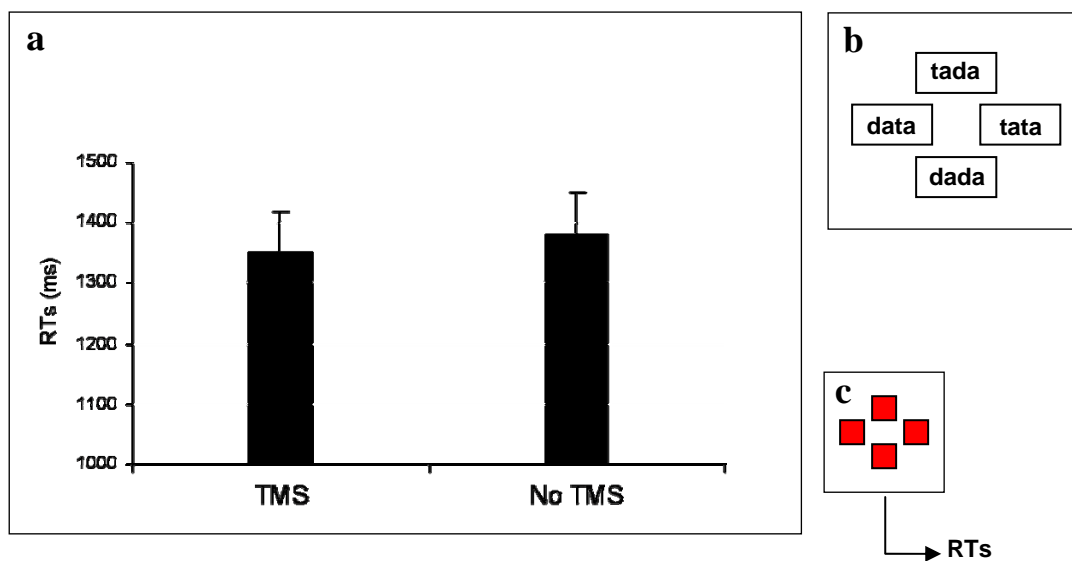
## 5. *Is Broca's region involved in speech perception?*

Studies of cortical stimulation during neurosurgical operations and clinical data from frontal aphasics suggest that this is the case (see above). However, all these studies report that comprehension deficits become evident only in the case of complex sentences processing or complex commands accomplishment. Single words (particularly if nouns) are almost always correctly understood. To verify this observation, we applied repetitive TMS (rTMS, that functionally blocks for hundreds of milliseconds the stimulated area) on speech related premotor centers during single word listening (see Fadiga et al., 2006). Data analysis showed, indeed, that rTMS was ineffective in perturbing subject's performance. A possible objection could be, however, that words, because of their lexical content, activate a complex network of areas, and thus the interruption of activity only in Broca's area is not sufficient to impair comprehension.

### 5.1 *Does TMS perturb phonological discrimination?*

On the basis of the previous results, we decided to use an experimental paradigm not involving words but meaningless pseudo-words. Subjects were instructed to categorize a sequence of acoustically presented pseudo-words according to their phonological characteristics, by pressing one among four different switches (Craighero, Fadiga and Haggard, unpublished data). Stimuli were subdivided into four different categories, according to the phonetic sequence of the middle part of the stimulus (/dada/, /data/, /tada/ or /tata/). Participants' left hemisphere was magnetically stimulated in three different regions by using rTMS: a) the focus of the tongue motor representation, b) a region 2 centimeters more anterior (ventral premotor/inferior frontal cortex), c) a region 2 centimeters more posterior (somatosensory cortex). During the task, subjects had to listen to the presented stimulus and to press on a 4-buttons keyboard (Fig. 5, c) the button identifying the middle part of the stimulus (e.g. /dada/). The correspondence between button and phonetic sequence was given by a four-picture display presented on a computer screen (Fig. 5, b) that was kept fixed for each subject but was counterbalanced across subjects. Repetitive transcranial magnetic stimulation

(120% of individual motor threshold) was delivered at a frequency of 20 Hz in correspondence of the 2nd critical formant (200 ms), in correspondence of the 1st and of the 2nd critical formants (200+200 ms), and also during the whole critical portion of the presented word (600 ms). Results (Fig. 5, a) showed no difference between the performances obtained during the different experimental conditions and for each stimulated site, neither in terms of errors nor for reaction times, demonstrating that rTMS was completely ineffective in perturbing phonological discrimination.



**Figure 5.** Panel a, Average value (+ SEM) of subjects' reaction times (RTs) during the phonological discrimination task described above in the text. Note the absence of RTs modulation depending on the administration of TMS on a point roughly corresponding to BA 44 (two centimeters in front of tongue primary motor representation). Panels b and c represent schematically the computer screen displayed to subjects and the keyboard for the response, respectively.

### 5.1 Does TMS perturb the phonological priming effect?

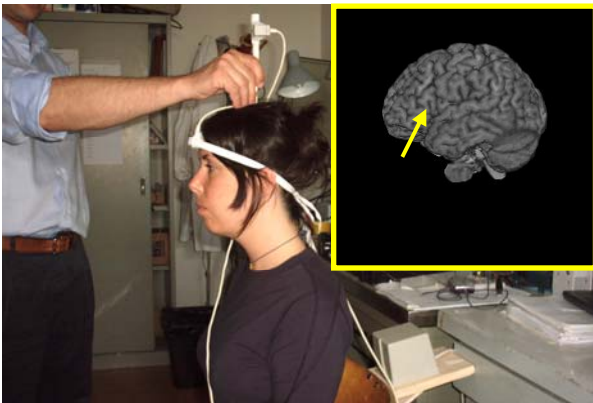
A possible interpretation of the absence of any effect of interference on phonologic discrimination might be that the discrimination task we used, either was too simple or did not require a real phonologic processing because it might be accomplished by a simple acoustic discrimination of the serial order of two different (not necessarily phonological) elements. For these reasons, we thus decided to use a “phonological priming” task, a well known experimental paradigm based on the

observation that a target verbal stimulus is recognized faster when it is preceded by a prime sharing with the target its last syllable (rhyming effect, Emmorey, 1989). In a single pulse TMS experiment we therefore stimulated participants' inferior frontal gyrus (BA 44) while they were performing a phonological priming task. TMS was administered between the prime and the target. By this way, the noise produced by the TMS was not interfering with stimuli presentation. During the task, subjects were instructed to carefully listen to a sequence of acoustically presented pairs of verbal stimuli (disyllabic 'cvcv' or 'cvccv' words and pseudo-words) in which final phonological overlap was present (rhyme prime) or, conversely, not present. The pairs of presented stimuli pertained to four categories which differed for presence of lexical content in the prime and in the target:

<b>PRIME-TARGET</b>	<b>Word-Word</b>	<b>Word-Pseudoword</b>	<b>Pseudoword-Word</b>	<b>Pseudoword-Pseudoword</b>
<b>RHYMING</b>	Tocca – Bocca Pera – Cera Tango – Fango Bolla – Folla Vita – Gita Fato – Lato Duna – Luna Fare – Mare Zucca – Mucca Fido – Nido	Corta – Zorta Freno – Preno Tasca – Masca Tizio – Cizio Rana – Mana Caso – Zaso Magno – Pagno Vecchio – Lecchio Colpe – Molpe Toro – Soro	Losse – Tosse Vanza – Stanza Comba - Bomba Muga – Ruga Ciaggia – Spiaggia Reta – Meta Paso – Vaso Rento - Lento Vugno – Pugno Vesta - Testa	Cata –Zata Buota – Suota Cobia – Robia Nago – Sago Tasna – Masna Ciato – Viato Stoca – Ruoca Dano – Viano Tecra – Gecra Polta – Solta
<b>NON RHYMING</b>	Bomba – Zebra Cesto – Sugo Fiume – Scuola Gara – Ritmo Lago – Guancia Mano – Granchio Noia – Cielo Panno – Capra Specchio – Stalla Topo – Patto	Grugno – Buota Tana – Nago Media – Tasna Strada – Terto Vela – Marto Moro – Troli Freno – Tile Terme – Caglia Truppa – Giarti Ragno – Ligri	Lufo – Lesta Stali – Letto Raga – Dopo Troli – Moro Neca – Tetro Porpo - Tino Gondo – Prato Revia – Piena Marto – Vela Zangra - Sedia	Zangra – Gispia Fazo – Rasuo Diase – Noste Copo – Lafria Zasta – Guotra Piusca – Rieta Brona – Dasta Zugra – Friepa Vutra – Ligri Tausa - Mifro

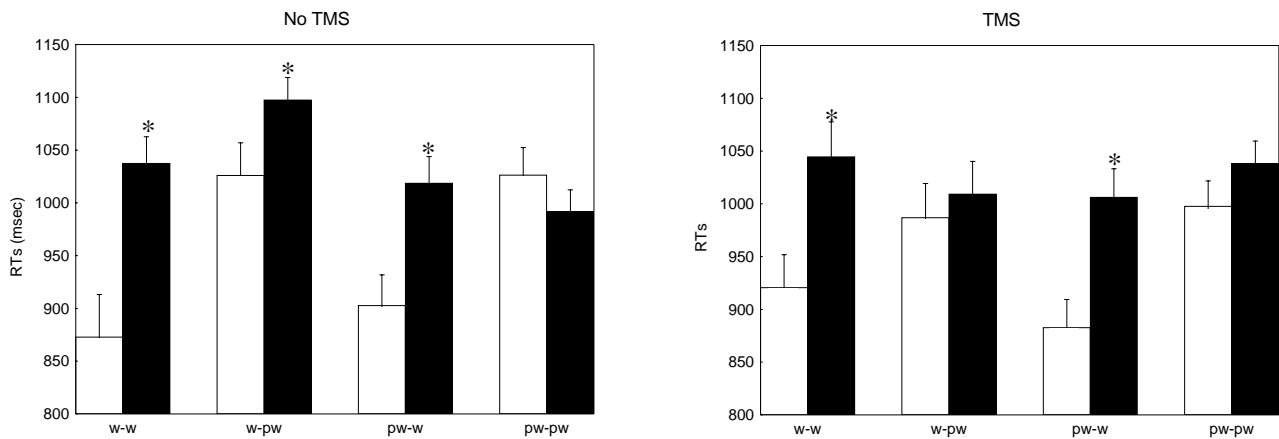
Subjects (n=8) were requested to make a lexical decision on the target by pressing one of two buttons (word/pseudo-word) with their index or middle finger. The association between fingers and lexical property was counterbalanced across subjects. Each category contained both rhyming and non-rhyming pairs. In some randomly selected trials, we administered single pulse TMS in correspondence of left BA 44 (Broca's region) during the interval (20 ms) between prime and target stimuli. To avoid mislocalization of the target brain region, each subject underwent magnetic resonance imaging (MRI) scanning, and the position of subject's scalp covering the *pars opercularis*

of the inferior frontal gyrus (BA 44) was assessed by using a neuronavigation software developed in our laboratory (see Fig. 6). In brief, a 6-DOF electromagnetic tracker (Flock of Birds, Ascension Technology) was attached to subject's forehead by an elastic band to compensate for head movements, and three *repere* points (bilateral *tragus* and *nasion*) were located by pointing on them by a stylus equipped with a second tracker. Then, the same *repere* locations were identified on the subject's MRI and the two coordinate systems, that of subject's head and that of MRI were put in register. Finally, for each point identified by the stylus on subject's scalp, the software gave in real time the corresponding three MRI section passing from it (coronal, horizontal and sagittal).



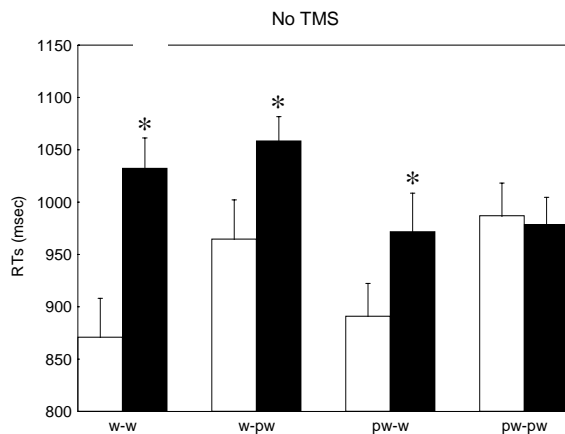
**Figure 6.** The procedure used in the phonological priming experiment to map individual Broca's areas. On the left, the electromagnetic tracking procedure is shown. For each subject, the center of pars opercularis of the inferior frontal gyrus was identified (yellow arrow). The panel on the right, shows the 3D reconstructed brain of nine subjects with superimposed a red circle indicating the location selected for administering TMS during the experimental paradigm.

In trials without TMS, three are the main results: (i) strong and statistically significant facilitation (phonological priming effect) when W-W, W-PW, PW-W pairs are presented; (ii) no phonological priming effect when the PW-PW pair is presented; (iii) faster responses when the target is a word rather than a pseudo-word (both in W-W and PW-W). An interesting finding emerges from the analysis of these results: the presence or absence of lexical content modulates the presence of the phonological priming effect. When neither the target nor the prime has the access to the lexicon (PW-PW pair), the presence of the rhyme does not facilitate the recognition of the target. In other words, in order to have a phonological effect it is necessary to have the access to the lexicon.



**Figure 7.** Reaction times (RTs  $\pm$  SEM in milliseconds) during the phonological priming task for the lexical decision, without (left panel) and with (right panel) TMS administration. White bars: presence of rhyme between prime and target. Black bars: absence of rhyme. Asterisk on the black bar indicate the presence ( $p > 0.05$ , Newman-Keuls test) of a phonological priming effect (response to rhyming target faster than response to not-rhyming target) in the relative condition. TMS administration did not influence the accuracy of the participants, that was almost always close to 100%. W-W, prime word/target-word; W-PW, prime-word/target-pseudo-word; PW-W, prime-pseudo-word/target-word; PW-PW, prime-pseudo-word/target-pseudo-word.

In trials during which TMS was delivered, only W-PW pairs were affected by brain stimulation: the W-PW pair behaving exactly as the PW-PW one. This finding suggests that the stimulation of the Broca's region might have affected the lexical property of the prime. As consequence, the impossibility to have access to the lexicon determines the absence of the phonological effect. According to our interpretation, the TMS-related effect is absent in the W-W and PW-W pairs because of the presence of a meaningful (W) target. Being aware that a possible criticism to our result is that the task was implying a lexical decision, we replicated the experiment by asking 6 new subjects to detect if the final vowel of the target stimulus was /a/ or /o/. Despite the absence of any lexicon-directed attention, the results were exactly the same as in the case of the lexical decision paradigm, demonstrating that the absence of phonological priming in the pseudo-word/pseudo-word pairs was independent from subject's task.



**Figure 8.** Reaction times (RTs $\pm$ SEM in milliseconds) during the phonological priming task for the vowel discrimination task (no TMS). Convention as in Figure 7.

Independently from the main aim of the present study, that of interfering on perception by administering TMS, the unexpected finding that in the pseudo-word/pseudo-word pair the phonological priming effect is abolished, provokes at least two necessary considerations. First, the classical view stating that before attributing a lexical content, the brain decodes the phonology (two-steps processing), seems not substantiated by our data. Second, the phonological priming effect appears to be not purely ‘phonological’ because it disappears if at least one of the two members of the pair is not characterized by a meaningful lexical content.

Our interpretation of these results is that it is impossible to dissociate phonology from lexicon, and particularly at Broca’s level because there “exist” only words. In other terms, phonologically relevant stimuli are matched on a repertoire of words and not on individually meaningless, “phonemes assembly”. The original role played by the inferior frontal gyrus in generating/extracting action meanings might have been generalized during evolution giving to this area the basics to build a new capability: a supramodal “syntax” endowed with the ability to organize and comprehend hierarchical and sequential elements in meaningful structures. The motor resonance of tongue representation revealed by TMS during speech listening (RR/FF) is probably a mixed phenomenon. Cortical regions others than area BA 44 (area 6?) might be involved in the “acoustically evoked mirror effect” (Fadiga et al., 2002) which is quite

independent from the meaning of the presented stimuli. In this direction points the recent fMRI experiment by Wilson and colleagues (2004) showing that the only cortical region constantly activated during both listening and production of meaningless syllables, was bilaterally located in the superior part of ventral premotor cortex, dorsal to BA 44. However, it remains the fact that the lexical content of the listened words exerts a significant facilitation on primary motor cortex (M1) excitability (see Fig. 4). It is likely that two distinct processes act on M1 at the same time: a meaning independent one, which could be considered as the effect of a low-level motor resonance, and a lexical one, whose origin remains to be clarified by further experiments.

### *5.2 Does frontal aphasics show deficits in motor syntax?*

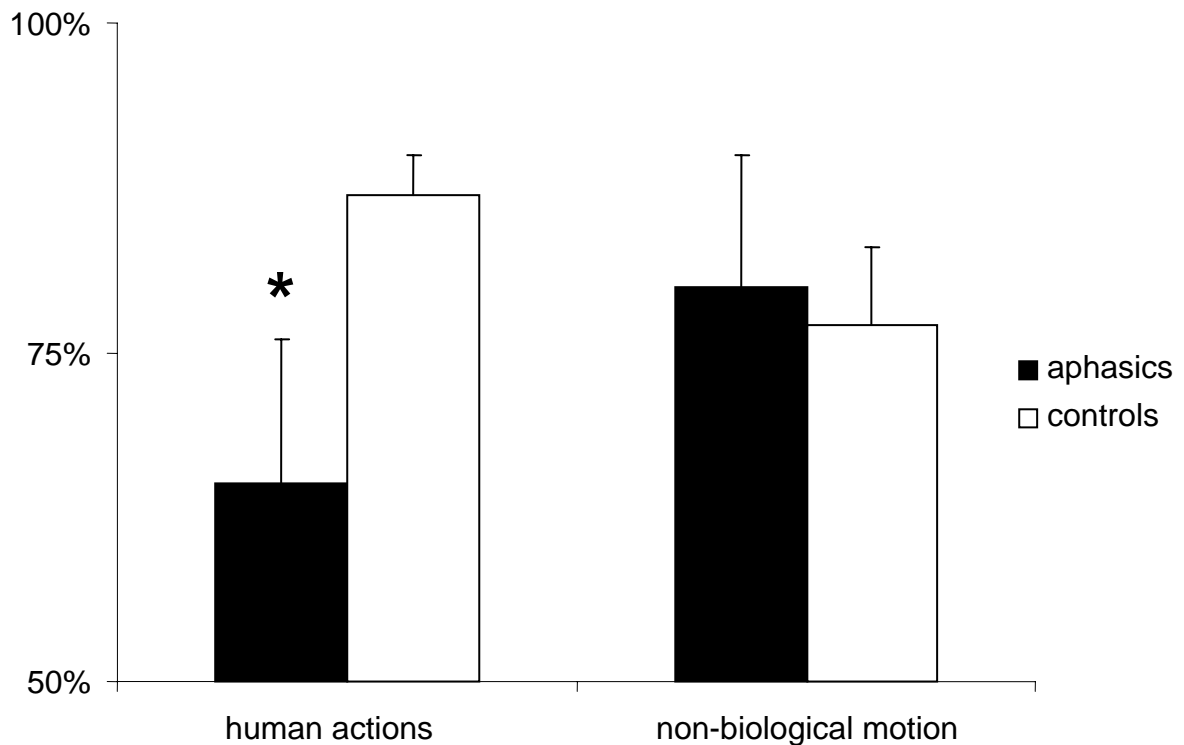
What, in conclusion emerges from Broca's area temporary inactivation is that this area is not involved with purely phonological properties of the heard stimuli. The hypothesis we suggested in the previous section is that this area, because of its premotor nature, could be involved in supramodal syntactic processing. If our hypothesis were true, we should expect that frontal aphasic patients, suffering from lesion of Broca's region, in addition to their classical symptoms in speech production and agrammatism, should also show additional deficits in a more broad 'motor' domain. In other words, people suffering from an incapability of processing syntax in the linguistic domain following frontal brain damage, should be also impaired in another, motor, field, as long as supramodal syntactic skills are required. In particular, we hypothesized the correlated defective domain would concern action. In this line are the results by Tranel et al. (2003) demonstrating that left frontal brain damaged patients have difficulties in understanding action details when shown with cards depicting various action phases. However, in their study, the authors asked patients to answer verbally to verbally posed questions. It remained thus opened the possibility that patients may have had more problems in understanding the intimate content of the action-related questions than in representing actions themselves.

To better verify the hypothesis that non fluent aphasia may be accompanied by deficits in action understanding, we designed an experiment in which Broca's aphasic

patients were presented with a simple scrambled "motor sentence" they had to reorganize (Fazio *et al*, in preparation). Patients were included in the study if they presented vascular lesions in the territory of the left middle cerebral artery, including the frontal inferior gyrus, and were diagnosed by a neuropsychologist as Broca's aphasics. Eleven patients met these initial enrollment criteria. All presented disorders of language production with agrammatic speech, while oral comprehension was largely preserved. Despite speech therapy, verbal fluency remained impaired at the time of the experimental investigation. Additionally, all 11 patients were screened to assess linguistic, praxic and general cognitive faculties and 5 patients suffering from apraxia have been successively excluded from the experimental testing. The experiment consisted in the presentation to each patient of 20 video clips, subdivided in two different classes: simple biological action (e.g., a hand grasping a bottle) and sequence of non biological moving object (e.g., a bicycle falling on the floor). Then, after each video, patients were shown with four snapshots taken from the video clip, randomly presented on a computer touch-screen; patients were then required to organize the frames such as to provide a meaningful order by touching the screen and by exchanging the position of the snapshot forming the sequence. As soon as they accomplished each trial, they had to press a validation button. We recorded and analyzed the accuracy and performance of the patients group and a healthy control group, matching for age and instruction level.

Result were as follows: Reaction time and sequencing time were about three times higher in patients than in normal subjects, although without significant differences between human actions and non-biological movements. On the contrary, while we observed no difference between human actions and non-biological sequences in the accuracy of healthy subject, Broca's aphasic patients performed significantly worse than normals when they had to organize frames describing human actions with respect to non-biological motion. Patients' accuracy in sequencing non-biological motion was  $80\pm 10\%$ , whereas during sequencing human actions their accuracy dropped to  $65.2\pm 11\%$ . Figure 9 shows the results of the experiment as far as accuracy in

reconstructing the correct sequence order for both human actions and non-biological motion is concerned.



**Figure 9.** Percentage of correct trials (mean  $\pm$  SEM) in frontal aphasic patients and in normal subjects matched for age, scholarity and gender, during the sequencing task. The asterisk indicates the presence of a statistically significant difference in the performance of patients with respect to controls in the human actions sequencing task.

This difference was statistically significant (two-tailed T-test,  $p < 0.05$ ) and was specific for videos representing human actions (all patients were able to order other kind of sequences, e.g. numbers). Conversely, control subjects correctly sequenced both the biological ( $87 \pm 3\%$ ) and the non-biological ( $77 \pm 6\%$ ) sequences without significant difference ( $p = 0.4162$ ). The difference in performance of patients between the two tasks is hardly compatible with a higher difficulty level of sequences representing human actions. Indeed, it took on average the same time to patients to perform the human and the non-biological trials while, for healthy control subjects if a tendency is present it shows exactly the opposite (more errors with non-biological motion). Furthermore, the

distribution of non-biological motion trials in terms of sequencing time (i.e. difficulty) was coincident with that of human action trials.

Finally, as an additional control for the presence of syntactic deficits in a similar task but in the language domain, the patients were required to reorganize 4 token, each containing word pieces of a phrase, to compound a meaningful sentence (e.g., I turn – the key – and open – the door). They only reached 58% of accuracy in the latter task, thus confirming their profound agrammatism.

Although preliminary, these results are promising as they indicate a common impairment in syntactically organizing linguistic and motor material that, in the motor domain, is specific for biological motion, as a much better performance was observed with a sequential, non biological material. One could argue that this difference might depend on the biological versus non biological nature of the material. In this respect, brain imaging studies have demonstrated that the observation of biological motion activates the premotor cortex, damaged in the tested population of patients, whereas non biological movement depends upon more posterior region (Grezes et al, 2001; Saygin et al, 2004). However, the patients were presented with still frames that suggested, but never showed, real motion or movement. Moreover, our results are in accordance with previous studies showing that patients with lesions of Broca's area are impaired in learning the hierarchical, but not the temporal structure of sequential tasks (Dominey et al., 2003). In the same vein, a study using event-related fMRI recently succeeded at disentangling hierarchical processes from temporal nested elements (Koechlin et Jubault, 2006). The authors reported that Broca's area and its right homologue control the selection and nesting of action segments integrated in hierarchical behavioral plans, regardless of their temporal structure. Going back to language, Broca's area is believed to processes syntax, which is not a temporal sequence of words, but precisely a hierarchical structure defining the links between words. Therefore, our results add to the growing literature on the role of Broca's region by strongly supporting its role in processing a supramodal syntax deriving from a very similarly organized structure: that at the basis of action representation embedded in the

motor system. It is important to stress here that we are not dealing neither with the evocative capability of the human language nor with its powerful competence in generating/evoking abstract concepts. What we are interested in is the way by which the verbal message is transmitted between the speaker and the listener, and syntax (at least in its canonical form) represents the set of rules allowing this transmission with efficacy.

## **6. Conclusions**

At the beginning of this chapter we formulated the hypothesis that, in agreement with experimental findings on monkeys and humans, there should have been a common evolutionary pathway linking hand/mouth action representation and verbal communication. In general terms, this hypothesis is not new. Since many years, several authors (Rizzolatti & Arbib 1998, Corballis 2003) have proposed that human language may have been evolved from hand actions/gestures more than from the vocal calls system, already present in inferior primates. Here, we believe, we give a contribution in substantiating this set of theories by providing, on one side, direct evidence in favor of an involvement of the motor system in speech processing, on the other side, by discussing, and sometimes re-interpreting, a series of experimental evidence that we may resume as follow:

- 1) Broca's area, the frontal region for speech production, is a premotor area, evolutionary linked to a sector of monkey ventral premotor cortex (area F5a) where hand/mouth actions are represented. What characterizes these representations in the monkey cortex is (i) the presence of a goal, (ii) their organization in terms of vocabulary of actions, very often effector independent (e.g. grasping a small object with the right hand, with the left hand and with the mouth), (iii) their involvement in perception of similar actions performed by others, thanks to widely diffused visuomotor properties.

- 2) Broca's area is involved in speech processing, not only during production but also during perception. This involvement is mainly at the sentence level (not at the

word level) and it is positively correlated to the complexity of the to-be-processed sentences.

3) Broca's area becomes active in several non-speech tasks having in common a syntactically organized structure (rhythms, music, mathematics, complex sequences of actions). These domains share with speech the presence of rules that govern them in non-ambiguous ways. In other terms, they all deal with sequences organized according to a precise hierarchical structure.

This last point peculiarly emphasizes, in our view, the parallelism between speech and action representations. Indeed, both processes are organized in hierarchical structures hosting, when necessary, nested subroutines. Motor and speech sequences become significant because of the presence of the goal. Otherwise they remain meaningless assemblies of movements – in the case of actions, of words – in the case of sentences, or even of phonemes, in the case of single words. The glue linking in a meaningful way the individual parts of the sequence is given by the presence of a goal.

In this light, the capability of Broca's area to deal with sequences, not strictly speech-related, has been proposed by several investigators on the basis of the evidence that this region is constantly involved in processing rhythms, music, complex actions (see the paradigmatic experiment by Gelfand and Bookheimer, 2003). In addition, the ventral part of BA 6 (vBA 6 or PMv, ventral premotor), bordering with Broca's region, is highly specialized in motor/abstract sequences processing, as shown by the seminal work by Schubotz and colleagues (Schubotz & von Cramon 2003, Schubotz & von Cramon 2004, Wolfensteller et al. 2004). Very recently, Fiebach and Schubotz (2006) have proposed a unifying theory, considering together experimental evidence on ventral premotor cortex with that arising from the study of Broca's area. Their belief is that the ensemble vBA 6-BA 44 may be considered "a highly flexible sequence processor, with the PMv mapping sequential events onto stored structural templates and Broca's area involved in more complex, hierarchical or hyper-sequential processing". To similar conclusions is recently approaching Friederici. According to her very recent paper on this topic (Frederici 2006):

“While BA 44/45 is seen to be increasingly activated whenever the internal re-construction of a hierarchical structure from a sequential input is necessary, BA 6 is involved in the processing of local structural dependencies”. Finally, in a very recent paper, Grewe and colleagues (Grewe et al 2006) add new evidence to the hypothesis that linguistic functions of Broca’s region, and more specifically of the *pars opercularis*, may depend on a "supra-syntactic" role, as suggested by the fMRI evidence that the violation of a linearization principle that is purely semantic in nature (animate arguments should precede inanimate arguments) increases the activation of *pars opercularis*.

What we add to this theoretical framework here is the idea that speech is represented in Broca’s region not because this part of the brain has developed for this specific purpose but because, in our progenitors, it was already the part of the brain where goals, and hierarchically organized motor chains planned to achieve those goals, are represented (see Fogassi et al 2005). Therefore, the involvement of Broca’s region in verbal communication could be provocatively considered an occasional ‘epiphenomenon’, motivated by its premotor origins. Consequently, forms of communication others than the verbal one, expressions of ancient mechanisms, involve Broca’s area because of its twofold involvement with motor goals: during execution of own actions and during perception of others’ ones.

Several steps concerning this (putative) evolutionary pathway linking actions representation (and mainly hand actions) to linguistic syntax, still remain to be clarified. For example, how object manipulation, introspectively driven, might had been transformed into communicative gestures. This passage has been considered a necessary prerequisite by several authors. It is possible, in our view, that the activity of the mirror neurons in the observer’s brain, while looking at actions performed by another individual, may have contributed to the self-other distinction necessary to communicate. Moreover, as soon as our progenitors realized that their own actions were sometimes determining others’ actions, the ‘spark’ may have appeared in their mind: the first nucleus of the dyadic, explicit communication.

Another issue, deserving particular consideration, is that raised by Fitch Chomsky and Hauser (2005) in a recent paper on the origin of language. One of the points they make is that human language is exquisitely human because animal communication lacks the property of recursion, i.e. the capability to combine discrete elements (words) in an infinite variety of possible expressions. If one follows this theoretical assumption, it derives that language may hardly have evolved from hand actions. Indeed actions are non-recursive by definition: one cannot eat a piece of apple before grasping it.

There is, however, a possibility that may help solving this intriguing puzzle that, as far as we know, has never been prompted before now. Being aware of its speculative nature, the idea we propose is that the intermediate step, linking action representation (and communication) to human language, might perhaps be found in the appearance during evolution of the capability to build and use tools. Tool design and tool use may possess a property equivalent to recursion in language: that of expanding the complexity of motor plans and to project actions in temporal dimensions other than the present. This is particularly true in the case of tools fabricated to build other, new tools. That forces the brain to postpone the ultimate goal following a complex, but quite flexible, hierarchy of subroutines/sub-goals. These increased spatial-temporal degrees of freedom might have provided the brain with the first example of recursion of actions.

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