

# **Understanding Others: Imitation, Language, Empathy**

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## Abstract

Brain imaging techniques allow the mapping of cognitive functions onto neural systems, but also the understanding of mechanisms of human behavior. In a series of imaging studies we have described a minimal neural architecture for imitation. This architecture comprises a brain region that codes an early visual description of the action to be imitated, a second region that codes the detailed motor specification of the action to be copied, and a third region that codes the goal of the imitated action. Neural signals predicting the sensory consequences of the planned imitative action are sent back to the brain region coding the early visual description of the imitated action, for monitoring purposes ("my planned action is like the one I have just seen"). The three brain regions forming this minimal neural architecture belong to a part of the cerebral cortex called perisylvian, a critical cortical region for language. This suggests that the neural mechanisms implementing imitation are also used for other forms of human communication, such as language. Indeed, imaging data on warping of chimpanzee brains onto human brains indicate that the largest expansion between the two species is perisylvian. Functional similarities between the structure of actions and the structure of language as it unfolds during conversation reinforce this notion.

Additional data suggest also that empathy occurs via the minimal neural architecture for imitation interacting with regions of the brain relevant to emotion. All in all, we come to understand others via imitation, and imitation shares functional mechanisms with language and empathy.

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## 1. Introduction

The study of the neural basis of imitation is at its first steps. Until few years ago, the only available information on the neural underpinnings of imitative behavior were restricted to lesion data in neurological patients. Although extremely valuable, the information obtained from neurological observations is limited, mostly because the lesions determining the imitative deficits are naturally occurring ones and do not have the precise anatomical boundaries that allow a detailed brain-behavior relationship study. Two main factors have limited the neuroscience of imitation: first, there is little consensus on a definition of imitation (Byrne and Russon, 1998; Heyes, 2002). This lack of consensus has reduced the enthusiasm of neuroscientists in investigating the neural basis of imitative behavior. Second, even though some neuroimaging techniques have been around for about a quarter of a century, brain mappers had initially the tendency to stay away from complex phenomena and imitation has been definitely perceived by them as a complex phenomenon. These two factors have led to the paradoxical situation of the late nineties, when there were tens of peer-reviewed imaging studies on, say, saccades, and not even one on imitation!

A series of reports on experiments investigating the neural basis of imitation, however, has been published recently (see for instance Decety's chapter in this volume). This trend seems determined by two main reasons. First, there is a recent tendency in the neuro-imaging world to study complex phenomena, such as theory of mind (Frith and Frith, 1999) or even 'social'-like interactions (Montague et al., 2002; Rilling et al., 2002). Second, macaque single-cell observations published in the early nineties have provided

good neuronal models of functional properties that are relevant to imitation (diPellegrino et al., 1992; Gallese et al., 1996). This is particularly important because the mainstream imaging techniques generally rely on indirect measures of neuronal activity, such as blood flow. The existence of neurophysiological data that can help constraining the interpretation of the imaging data is generally considered extremely valuable.

In this chapter I will summarize the most meaningful data obtained so far on the neural underpinnings of imitation. The plan is to relate these findings to a neural and functional model of imitation and of its relations with two other functional domains, language and empathy. The approach I am using here envisions brain mapping techniques as investigative techniques with explanatory power. Typically, brain mapping is perceived as some kind of sophisticated phrenology. Detailed aspects of cognitive functions are mapped onto precise neural structures. Obviously, the map obtained looks way more sophisticated than the phrenological maps of the nineteenth century. However, the explanatory power of this approach remains limited with regard to testing models. What I advocate here is an approach that combines imaging data with functional information obtained from single-cell observations. With this approach, it is possible to test information processing models of imitation and of its relations with other domains.

## **2. Minimal neural architecture for imitation**

### *a. Action recognition system in the macaque brain*

Two European labs, Dave Perrett's and Giacomo Rizzolatti's, have studied systematically the properties of temporal, parietal, and frontal neural systems of the macaque brain that seem relevant to action representation and potentially imitation. Following the leads resulted from the studies of Charles Gross on the complex visual properties of inferior temporal neurons, Dave Perrett and collaborators have studied neurons in the superior temporal sulcus (STS) that respond to moving biological stimuli, such as hands, faces, bodies (Perrett et al., 1989; Perrett et al., 1990; Perrett and Emery, 1994). These neurons seem to respond to moving bodies and body parts only when the body or body part is engaged in goal-oriented actions. For instance, some of these neurons respond to the sight of a hand reaching and grasping an object. The same neuron will not fire at the sight of the hand reaching toward the object but not grasping it. The modulation of activity in STS neurons is independent of low-level visual features. In fact, a point-light version of the same action, that is, a hand reaching and grasping an object, will suffice to activate a neuronal response in these STS cells (Jellema et al., 2002). In other words, what these STS neurons code is the sight of a meaningful interaction between an object and an intentional agent.

The properties of STS neurons are limited exclusively, at least so far, to the visual domain, in that no neuronal responses in STS seem associated with motor behavior. In contrast, Giacomo Rizzolatti and his collaborators have described frontal and parietal neurons with motor properties (in that they are active when the monkey performs a movement) that also have visual responses similar to the ones observed in STS by Dave Perrett (di Pellegrino et al., 1992; Gallese et al., 1996). These neurons have been described for the first time in a region of the inferior frontal cortex called area F5,

according to an anatomical nomenclature that is becoming increasingly used (Matelli et al., 1985). In area F5 there exist two types of neurons with identical motor properties and quite different visual properties. The two types of neurons are called *canonical* and *mirror*. Both types fire when the monkey executes goal-directed actions, such as grasping, holding, tearing, manipulating. Some of these neurons fire for precision grip, when the monkey grasps small objects like a raisin, and some other neurons fire for whole-hand grasp, when the monkey grasps bigger objects, such as an apple. When it comes to their visual properties, *canonical* neurons that fire when the monkey grasps a small object with a precision grip, respond also to the sight of small objects graspable with precision grip but not to the sight of bigger objects graspable with, say, a whole-hand grip. Note that these visual responses are obtained when the monkey does NOT reach and grasp the object; the simple sight of the object is sufficient to activate *canonical* neurons. In other words, *canonical* neurons seem to be coding the affordance of an object, the pragmatic aspect of how-to-grab-that-thing, rather than its semantic content.

In contrast, *mirror* neurons do not fire at the sight of an object but will fire at the sight of a whole action. So, say that there is a neuron in F5 that fires when the monkey grasps an object. That same neuron, if it is a *mirror* neuron, will fire at the sight of another individual grasping an object, but will not fire at the sight of the object alone and will not fire at the sight of a pantomime of a grasp in absence of the object. In other words, these neurons seem to be matching the execution and the observation of an action. The functional properties of these neurons suggest that they may implement a simple,

non-inferential mechanism of action recognition based on neural identity. This mechanism may be a building block for imitative behavior.

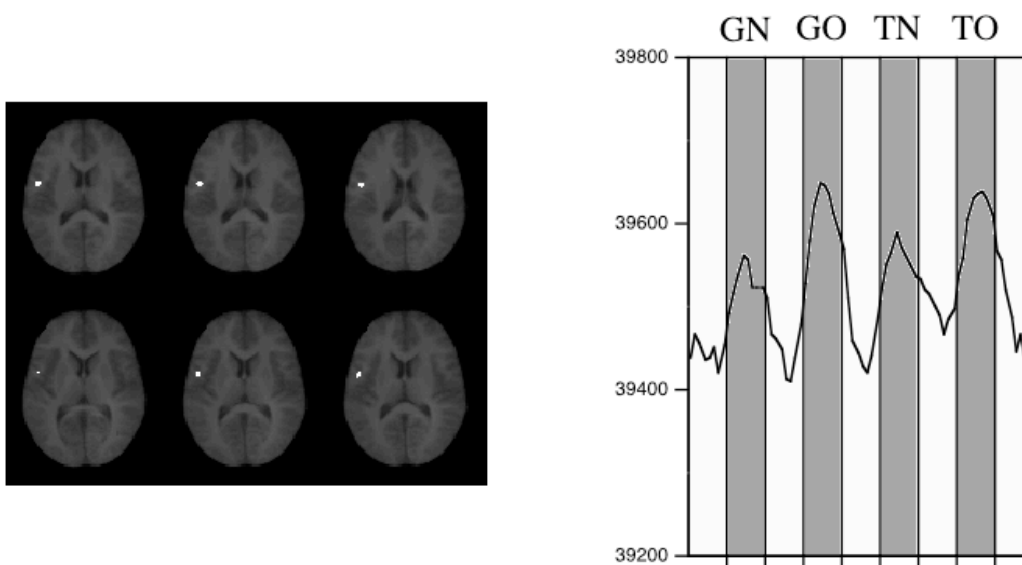
A posterior parietal area of the macaque, area PF, situated in the rostral sector of the inferior parietal lobule, contains *mirror* neurons with functional properties substantially identical to the ones described in F5 (Rizzolatti et al., 2001). Area PF and area F5 are anatomically connected with robust projections (Rizzolatti et al., 1998). This pattern of cortico-cortical connectivity leads to believe that F5 and PF belong to an integrated circuit for action recognition. Furthermore, STS, the region where Dave Perrett has discovered the neurons with the complex visual properties described above, is connected with the posterior parietal cortex (Seltzer and Pandya, 1994). Thus, these three cortical regions of the macaque brain, STS in the superior temporal cortex, area F5 in the inferior frontal cortex, and area PF in the posterior parietal cortex, seem to have functional properties and connectivity patterns that may instantiate a whole circuit for coding actions. The question that I will address in the next section is: is there a similar circuit for action recognition and possibly imitation in the human brain?

*b. Human minimal neural architecture for imitation*

The first attempts to demonstrate an action recognition system in the human brain similar to the one in the macaque brain were made using Positron Emission Tomography (PET) and, as activation tasks, grasping execution and grasping observation (Grafton et al., 1996; Rizzolatti et al., 1996). The idea behind these studies was the following: if there is a human action recognition system similar to the one described in macaques, human brain

motor areas belonging to this system should be active during both grasping execution and grasping observation. Ideally, there should also be some anatomical correspondence between the human and the macaque areas. The early PET attempts were not entirely successful, even though some aspects of the empirical findings were encouraging. The two broadly defined regions of superior temporal cortex and inferior frontal cortex were indeed activated during both observation and execution of action. The areas activated within inferior frontal and superior temporal cortex during grasping execution, however, did not spatially match the areas activated within inferior frontal and superior temporal cortex during grasping observation. Further, the posterior parietal cortex was found activated only during grasping execution (Rizzolatti et al., 1996). However, a second study comparing grasping observation with grasping imagination did report an activation of the posterior parietal cortex during grasping observation (Grafton et al., 1996). The reason why the results of these first studies were successful only in part is probably due to technical limitations of the 2D PET methodology used.

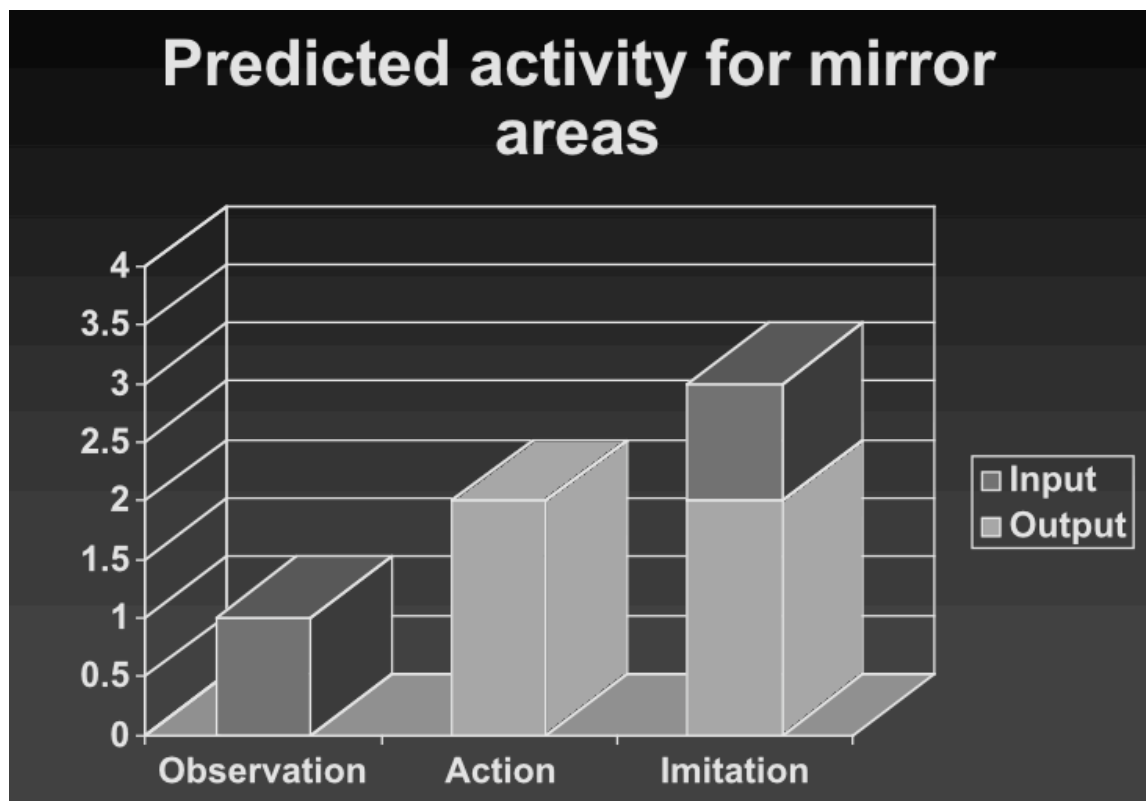
The second important feature of the action recognition system described in the macaque is that it is driven by goal-directed actions. To test whether human brain areas of the grasping circuit show a similar feature, we performed a functional magnetic resonance imaging (fMRI) experiment in which subjects either performed an object-directed action (grasping or touching an object) or simply pantomimed the action without actually interacting with the object. The prediction is that hand-object interaction should yield greater activity in regions coding goal-oriented behavior. Consistently with the macaque single-cell data, we found that the inferior frontal cortex had this pattern of activity (Figure 1).



**Figure 1.** Activity in human inferior frontal cortex (putative Brodmann area 44, in white) in object-directed and pantomimed actions. Dark grey bands correspond to task periods, whereas white bands correspond to resting periods. Greater activity is observed for grasping (GO) and touching (TO) an object, compared to pantomime of grasping (GN) and touching (TN).

The early studies on grasping, however, had a conceptual limitation. Even though continuity is important, such that it makes sense to see some features of the action recognition system of the macaque in the human brain, one must also factor in the changes that the evolutionary process might have produced. Thus, keep focusing on grasping seemed to us a mistake. Imitation seemed a much more promising paradigm to use. In fact, the action recognition system of the macaque has the property of being active when the monkey makes an action and when it observes an action. These neural properties make this system an ideal candidate for being involved in or at least facilitating imitation. It is true that the imitative abilities of monkeys are limited, but even if one wants to apply the most stringent definition of imitation and thus conclude that monkeys do not imitate at all, one can also conceivably argue that the action recognition system made monkeys 'imitation-ready'. Thus, it is plausible to predict an involvement of this

system in imitation. The way we conceptualized it is captured in Figure 2. The idea behind it is simply that during imitation there is both observation and execution of an action. Thus, one can predict that areas endowed with *mirror* properties would show an activity pattern similar to the one graphed in the figure, with activity during imitation corresponding roughly to the sum of the activity during observation and execution of action. With the use of fMRI, we found two areas with these properties (Iacoboni et al., 1999). The first area was located in pars opercularis of the inferior frontal gyrus, in inferior frontal cortex, and the second one was located rostrally in the posterior parietal cortex. Thus, there was a convincing anatomical correspondence between the areas identified in the human brain as having *mirror* properties, and the macaque *mirror* areas.



**Figure 2.** Predicted activity during imitation for mirror areas is approximately the sum of the activity observed during observation of action and execution of action.

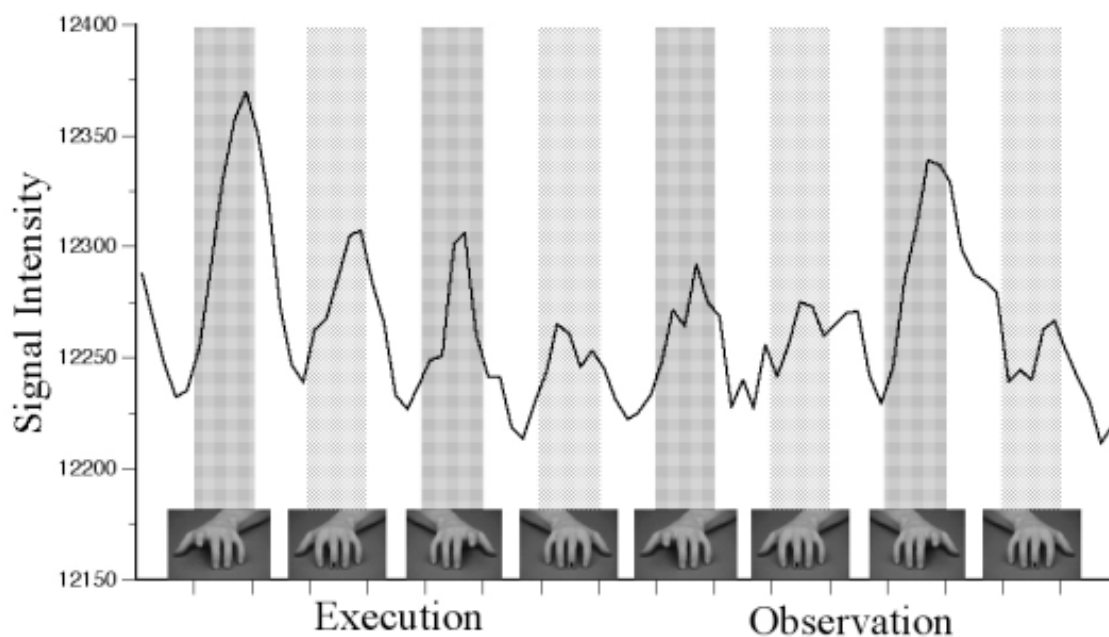
We initially proposed some sort of 'division of labor' between the frontal and the posterior parietal *mirror* areas, such that frontal *mirror* areas would code the goal of the imitated action and the posterior parietal *mirror* areas would code somatosensory information relevant to the imitated action. This division of labor was based on considerations inspired by single-cell (Sakata et al., 1973; Mountcastle et al., 1975; Kalaska et al., 1983; Lacquaniti et al., 1995) and neuroimaging data (Decety et al., 1997; Grezes et al., 1998). An empirical support to this proposed 'division of labor' has been recently provided by an imaging study of our group. The study shows a modulation of activity in inferior frontal *mirror* areas during imitation of goal-oriented action, with greater activity during goal-oriented imitation compared to non goal-oriented imitation (Koski et al., 2002).

To go back to the first experiment on imitation (Iacoboni et al., 1999), the third region identified by single-cell studies in the macaque as relevant to action recognition, STS, demonstrated a somewhat unexpected pattern of activity. As expected, there was greater activity in STS for action observation compared to control visual tasks and for imitation compared to control motor tasks. However, there was also greater activity for imitation compared to action observation in STS. This was a somewhat unexpected finding because the observed action was the same during imitation and during action observation. If STS simply encodes the visual description of actions, its activity should be the same during imitation and action observation. Two possible explanations of this finding are as follows: first, the increased activity during imitation may simply reflect increased attention to the visual stimulus, due to the fact that subjects are supposed to imitate it. Alternatively, the increased STS activity may be due to efferent copies of

motor commands originating from the fronto-parietal *mirror* areas. These efferent copies would allow a prediction of the sensory consequences of the planned imitative action that would be compared with the description of the observed action provided by STS. If a good match is obtained, then the planned imitative action can be performed.

To test these contrasting hypotheses, we performed a second fMRI study of imitation in which subjects were asked to imitate in two different configurations, *specular* (as in a mirror) and *anatomical*. During *specular* imitation subjects moved their right hand to imitate a left hand action. During *anatomical* imitation subjects moved their right hand to imitate a right hand action. It turns out that the *specular* form of imitation is the most common or spontaneous form of imitation early on in human development (Wapner and Cirillo, 1968), and that tends to yield a better performance also in adults (Ishikura and Inomata, 1995). Thus, we predicted that the *specular* form of imitation should produce greater activity in *mirror* areas, if they are critical cortical areas for imitation. In fact, in pars opercularis of the inferior frontal gyrus (the human homologue of F5) we found a reliably greater activity for *specular* imitation compared to *anatomical* imitation (Koski et al., in press). This differential activity in the inferior frontal cortex during the two forms of imitation allowed us to test the two contrasting hypotheses on STS, the *attentional* versus the *predictive* hypothesis. If the increased activity in STS during imitation is due to *attentional* factors, the two forms of imitation, *specular* and *anatomical*, should yield similarly increased STS activity compared to action observation. If any, the *anatomical* form of imitation, being less natural than the *specular* one, might yield greater activity due to increased attentional demands. In contrast, if the increased activity in STS is due to efferent copies of motor commands with *predictive*

value allowing control of the imitative output, then the STS activity should be similar to the activity in the *mirror* inferior frontal area, with greater activity for *specular* imitation than *anatomical* imitation. Also, given that efferent copies of motor commands are not produced during action observation, STS activity should NOT be greater during observation without imitation of left hand action compared to observation without imitation of right hand action. The results, shown in Figure 3, support the *predictive* hypothesis, with greater activity during *specular* imitation compared to *anatomical* imitation but not during left hand versus right hand action observation (Iacoboni et al., 2001). This suggests that the increased activity in STS during imitation is due to efferent copies of motor commands that are originating from fronto-parietal *mirror* areas and are sent back to STS for monitoring purposes.



**Figure 3.** Time-series of STS activity during imitation and observation of hand movements. The dark bands correspond to task periods and the white bands correspond to resting periods. From left to right, the first four task are motor tasks, the last four are observation only tasks. The hands with the finger lifted up represent task periods when subjects were shown finger movements. The hands with the cross on the finger represent task periods when subjects were shown a static hand with a cue on one of the fingers. Thus, the first and third task periods here correspond to *mirror* and *anatomical* imitation, respectively. There is reliable greater activity in STS for *mirror* compared to *anatomic* imitation. With regard to observation tasks, observed left hand action do not yield greater STS activity, suggesting that the effect observed during

imitation is due to efferent copies of motor commands. Reprinted from Iacoboni et al., PNAS 2001; 98: 13995-13999.

To summarize, the information flow within the three areas (superior temporal, posterior parietal, inferior frontal) that form what we call the *minimal neural architecture* for imitation would be as follows:

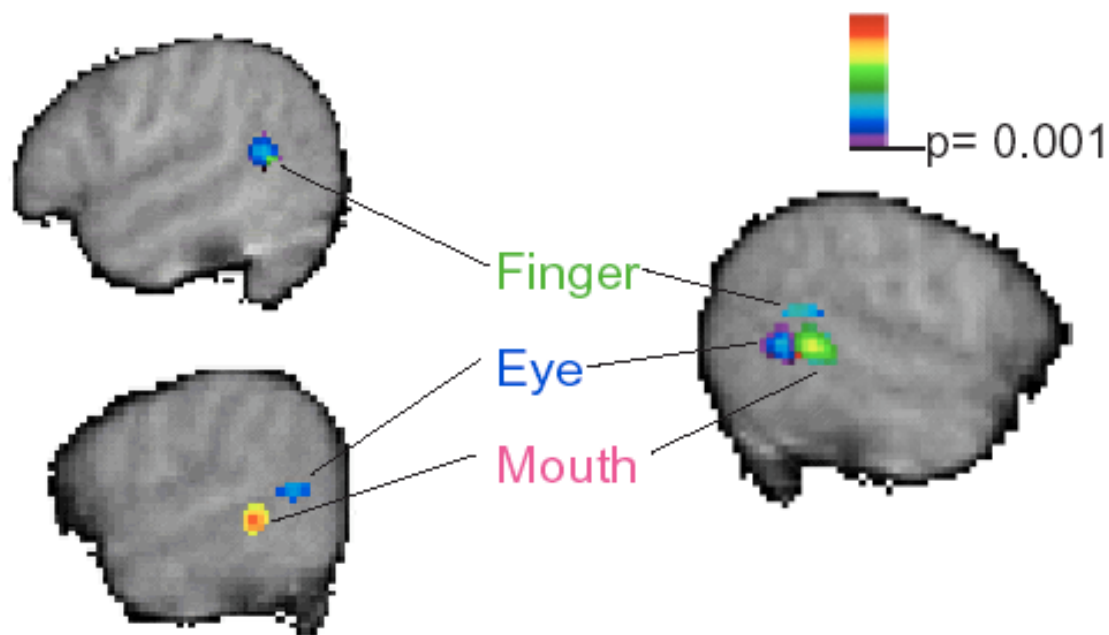
- the superior temporal cortex provides a visual description of the observed action to be imitated to posterior parietal *mirror* neurons<sup>1</sup>
- the posterior parietal *mirror* neurons provide additional somatosensory information regarding the action to be imitated and this information is sent to inferior frontal *mirror* neurons
- inferior frontal *mirror* neurons code the goal of the action to be imitated
- efferent copies of motor commands providing the predicted sensory consequences of the planned imitative actions are sent back to STS<sup>2</sup>
- in STS occurs a matching process between the visual description of the action and the predicted sensory consequences of the planned imitative actions; if there is a good match, the imitative action is initiated; if there is a large error signal, the imitative motor plan is corrected until convergence is reached between the superior temporal description of the action and the description of the sensory consequences of the planned action

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<sup>1</sup> A privileged information flow from superior temporal to posterior parietal rather than to inferior frontal is postulated on the basis of more robust projections from superior temporal cortex to posterior parietal cortex compared to inferior frontal cortex

<sup>2</sup> Elsewhere, we called these efferent copies 'reafferent' Iacoboni M, Koski LM, Brass M, Bekkering H, Woods RP, Dubeau MC, Mazziotta JC, Rizzolatti G (2001) Reafferent copies of imitated actions in the right superior temporal cortex. Proc Natl Acad Sci U S A 98:13995-13999., to emphasize the information flow going from STS to fronto-parietal mirror areas and *back* to STS

This model predicts two things: first of all, the role of STS is extremely important when the action to be imitated is a novel action not in the motor repertoire of the imitator. Second, if there is such a robust shuffling of information between STS and fronto-parietal *mirror* areas with regard to imitation, then the body maps of these cortices should have similar organizational principles. The first prediction has never been tested, as far as I know. The second prediction has been tested by us with fMRI. Given that at premotor and posterior parietal level it is possible to observe a somatotopic representation of body parts, we predicted topography of body parts in STS. Several labs had previously reported human STS responses to biological motion, but due to differences in methodology it was difficult to extrapolate a map of body parts in STS from the published data. We thus performed another fMRI experiment in which subjects observed hand actions, mouth movements, and eye movements (Dubeau et al., 2001). An orderly topography of body parts was observed in STS, as shown in Figure 4. Such topography has been subsequently confirmed by independent observations in our lab, in separate studies using faces or hands as visual stimuli.



**Figure 4.** Topography of body parts representation in human STS.

*c. Functional properties of the minimal neural architecture for imitation*

The temporo-parieto-frontal circuit we have delineated in the previous section seems to have relatively well defined functional properties. Combining information from single-unit and from brain imaging data, we have described a plausible information processing flow that goes from STS to fronto-parietal mirror areas, back to STS and then back to fronto-parietal areas for the initiation of the imitative movement. In this section, we will extend the discussion on the functional properties of this model.

The functional properties of the minimal neural architecture for imitation can be mapped onto the functional architecture of modular pairs of forward and inverse models,

a computational architecture developed in the motor control literature (Wolpert and Kawato, 1998; Kawato, 1999). Inverse models are important for motor control, whereas forward models are important for motor learning. An inverse model retrieves the motor plan necessary to reach a desired sensory state. The input of the inverse model is the desired sensory state and the output of the inverse model is the motor plan necessary to reach that desired sensory state. In our case, the imitator desires to imitate the action of the actor, and an inverse model is created by STS inputting the visual description of the observed action into fronto-parietal mirror areas that produce the output of the inverse model, the motor command necessary to imitate the actor. An efferent copy of the motor command (from fronto-parietal mirror areas) is fed into STS to create a forward model that allows predicting the sensory consequences of the planned imitative action. A forward model is a mimic (ironically so, this is imitation after all...) of the motor system and if the prediction is confirmed by re-afferent feedback, then the pair of forward and inverse model is reinforced by a 'responsibility signal' (Haruno et al., 2001) that assign high responsibility for imitating that given action to that specific forward-inverse model pair.

Several questions are left unanswered by this scenario. For instance, how does the pairing of STS input and fronto-parietal output that determines inverse modeling occur?<sup>3</sup> Remember that STS neurons are driven by hand-object interactions and show visual invariance, that is, under widely different visual circumstances the same neuron will fire

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<sup>3</sup> The same question is addressed by Cecilia Heyes in her chapter. She calls it the 'correspondence problem'. The solution that she proposes addresses a level of explanation somewhat different from the one we are addressing here. However, what she proposes is not only very plausible, but also compatible with the functional architecture presented here.

at the sight of the same kind of action. F5 neurons respond also to the sight of a relatively large class of actions under different visual conditions. With regard to their motor properties, however, these neurons are often tuned to a specific action. Thus, it is possible that the inverse-forward model pairing is initially facilitated because a large variety of visual stimuli activate non-selectively STS and F5. This non-selective visual activation, however, can be mapped efficiently only onto few specific motor outputs coded in F5. When an inefficient motor output is selected, it will generate a large error signal in its forward model, and will be assigned 'low responsibility' for that specific visual input. When finally an efficient motor output is selected, a small error signal will be generated and when the prediction of the forward model will also be confirmed by re-afferent feedback, the pair of forward and inverse model will be given 'high responsibility' for that action.

Another question that is worth posing is the following: within each region (STS, human inferior frontal or macaque F5, human posterior parietal or macaque PF) are the areas receiving inputs and producing outputs the same or different? In other words, how does the functional architecture of inverse and forward models map onto neural structures, and above all onto mirror neurons? We have recently performed a meta-analysis of some fifty fMRI datasets obtained in normal volunteers performing hand action imitation and observation (Molnar-Szakacs et al., 2002). We have observed that in the dorsal sector of pars opercularis of the inferior frontal gyrus (the human homologue of F5) there is an area that is active during both action observation and imitation, whereas in the ventral sector of pars opercularis of the inferior frontal gyrus there is an area that is active during imitation but not during action observation. One way of looking at these

findings is that the dorsal sector represents the *mirror* sector of pars opercularis, whereas the ventral sector is simply a premotor area. Another way of looking at it, however, is that the dorsal sector of pars opercularis receives the STS input of the visual description of the observed action and produces the motor plan that forms the output of the inverse model, whereas the ventral sector of pars opercularis produces the efferent copy of the motor command to be sent back to STS and used by the forward model to predict the sensory consequences of the imitative action.

In STS, the meta-analysis that we performed shows that the areas active during imitation and during action observation overlap completely. This suggests that the same STS area produces the visual description of the action used as input by the inverse model and receives the efferent copy of the motor command used by the forward model.

### 3. A way to language

Language is the house of Being.  
Martin Heidegger, *Being and Time*, 1927

#### *a. The essential role of Broca's area in imitation of finger movements*

Some neuro-anatomical considerations suggest that area F5 of the macaque brain is the evolutionary precursor of Brodmann area 44 of the human brain (von Bonin and Bailey, 1947; Petrides and Pandya, 1994; Rizzolatti and Arbib, 1998). Brodmann area 44 (BA 44) is a cytoarchitectonic area that maps probabilistically onto pars opercularis of the inferior frontal cortex (Mazziotta et al., 2001a; Mazziotta et al., 2001b), an area that we have seen strongly implicated in imitation and belonging to what we call the minimal

neural architecture for imitation. BA 44 is part of Broca's area (some authors assimilate Broca's area to BA 44 only), the most important cortical region for language processing in the human brain. The simultaneous involvement of BA44 in language and imitation, and the evolutionary anatomical considerations that I will address below, suggest functional links between imitation and language. A discussion of these possible links will be the focus of the whole section 3 of this chapter.

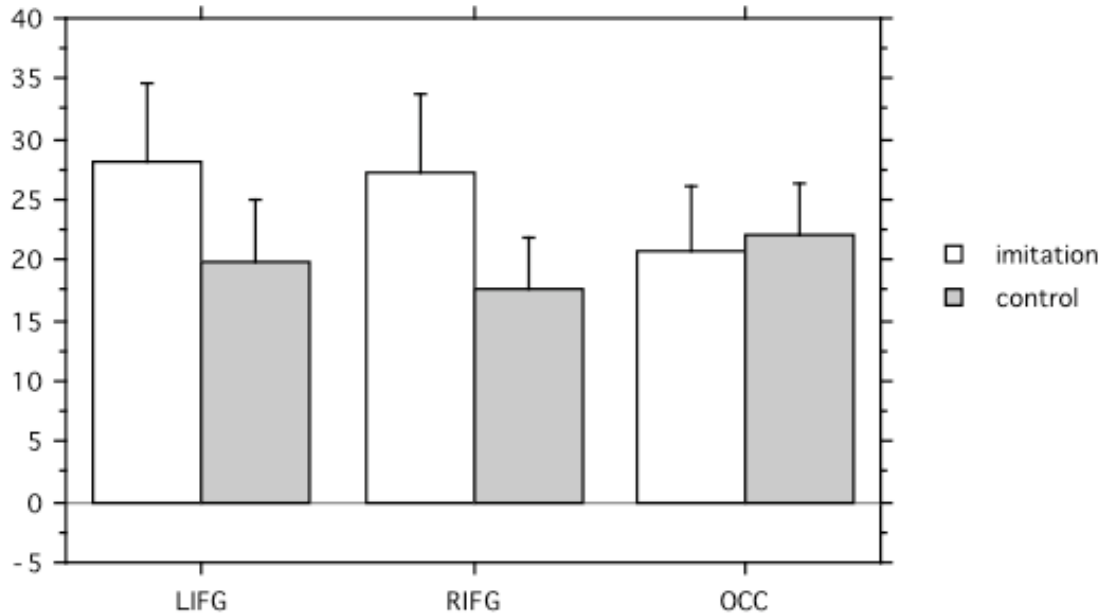
In the macaque frontal lobe, there exists a major sulcus that divides the granular prefrontal cortex anteriorly with the agranular motor and premotor cortex posteriorly. This sulcus is called the arcuate sulcus, since its shape resembles the shape of an arc. It has been suggested that the evolutionary process has evolved the dorsal sector of the arcuate sulcus of the macaque brain into the superior frontal sulcus of the human brain. The same process would have evolved the ventral sector of the arcuate sulcus into the inferior frontal sulcus of the human brain. Area F5 is located ventrally to the arcuate sulcus, and its human homologue would also be located ventrally with respect to the inferior frontal sulcus. Thus, one would expect to find the human homologue of area F5 in the inferior frontal gyrus. And one would likely find it relatively posteriorly located, sitting just in front of the premotor cortex represented in the precentral gyrus, given that F5 is a rostral premotor area. If one then considers the cyto-architecture of F5, which is devoid of a granular layer, one would expect the human homologue of F5 to be an agranular cortical area. If one considers all these things, the most likely candidate as human homologue of F5 is BA 44 (Rizzolatti and Arbib, 1998; Geyer et al., 2000). In fact, BA 44 is the rostralmost agranular cortical field in the inferior frontal gyrus, and is located right anteriorly to the ventralmost sector of the precentral gyrus. If BA 44 were

the human homologue of macaque F5, then one would expect that from a physiological standpoint these two areas share some features. In terms of motor representation of body parts, F5 in the macaque contains a representation for hand movement and a representation for mouth movements. Thus, one would expect also motor representation for the hand and the mouth in BA 44. In fact, several imaging studies have reported activation in BA 44 for motor tasks engaging the hand (Krams et al., 1998; Binkofski et al., 1999; Iacoboni et al., 1999; Ehrsson et al., 2000) and the mouth (Fox et al., 2001). This also means that in an imaging experiment on, say, imitating foot movements, one should NOT expect to observe activation of BA 44, if this activation reflects the motor aspect of BA 44, and not its linguistic (supposedly disembodied) one.

The activation studies that we have performed on hand imitation have demonstrated that a sector of pars opercularis is activated during imitation and observation of hand action. Its activity is also modulated by the type of imitation (specular versus anatomical), and also by goal-oriented imitation. Our meta-analysis of hand imitation (Molnar-Szakacs et al., 2002) points to the dorsal sector of pars opercularis as the sector of Broca's area with these characteristics. Also, a meta-analysis on language tasks (Chein et al., submitted) suggest that the dorsal sector of pars opercularis is a critical language region. The convergence of the empirical data is impressive, and suggests shared neural structures for imitation and language. It could be objected, however, that the activation observed during imitation in Broca's area is simply due to some kind of silent and maybe unconscious verbalization (Heyes, 2001). This objection does not really explain why there should be more verbalization in some imitative conditions but not in others. It also does not explain why the observation of

hand movements activate Broca's area but the observation of foot movements does not. At any rate, the silent verbalization hypothesis cannot be dismissed too lightly.

To test the contrasting hypotheses of Broca's area involvement in imitation due to silent verbalization or else due to mirror activity for hand or mouth movements, we used repetitive transcranial magnetic stimulation (rTMS). This technique allows one to create some kind of temporary, transient lesion in the brain area stimulated (Walsh and Cowey, 2000). We stimulated pars opercularis of the inferior frontal gyrus during imitation of hand actions and during a control visuo-motor task. We also stimulated a control site. If Broca's activation in imaging studies of imitation is only due to an epiphenomenal silent verbalization, then producing a transient lesion in pars opercularis should not affect the imitative performance. If, in contrast, Broca's area is essential to imitation, then producing a transient lesion in pars opercularis should have an effect on imitation. And if this effect reflects impairment in functional processes that are specific to imitation and to BA 44, then performance in the control task should be unaffected by the stimulation of pars opercularis, and performance in the imitation tasks should be unaffected by stimulation of the control site. The results we obtained in a recent rTMS study performed in our lab are consistent with the hypothesis of an essential role of Broca's area, namely BA 44, in imitation (Figure 5).



**Figure 5.** Percent errors in imitation (white bars) and control task (grey bars). LIFG: left inferior frontal gyrus (pars opercularis). RIFG: right inferior frontal gyrus (pars opercularis). OCC: control site in occipital cortex. There is a reliable increase in error rate for rTMS over the left and right pars opercularis during imitation only.

The possibility remains that the effect we observed is language-mediated, such that one has to name a finger movement in order to imitate it. However, this is quite unlikely, if one looks at human development. In fact, infants can imitate much earlier than they can talk (Meltzoff and Moore, 1977). If Broca's area has an essential role in imitation, then it must be concluded that this area is not exclusively dedicated to language processing. It also suggests an evolutionary continuity between action recognition, imitation, and language.

*b. Warping chimp brains onto homo brains*

The three areas that form what we call the minimal neural architecture for imitation are all located around a major sulcus of the human brain, the Sylvian fissure. The cortex around the Sylvian fissure is called perisylvian, and it is known to be extremely important for language. It is possible that the circuit for action recognition in the monkey has evolved to support imitation and subsequently language. From a relatively simple neural mechanism of matching observation and execution of action (*mirror* neurons), more complex functional properties were built and more complex behaviors were supported. If this hypothetical scenario has some plausibility, one should observe across species morphometric changes localized around the Sylvian fissure.

The lab of Karl Zilles has warped MRI of chimpanzees' brains into MRI of human brains. The process of warping the brain of one species into the brain of another can be quantified by mapping the local field deformations determined by the warping algorithm. By doing so, one can obtain a map of the local changes determined by the evolutionary process in the primate brain. What emerges is that the greatest changes can be observed around the Sylvian fissure, thus supporting the hypothesis that the action recognition system of the macaque is the evolutionary precursor of neural systems associated with language in the human brain.

From a functional standpoint, the *mirror* system meets the criterion of the 'parity assumption' between a sender and a receiver of a message, proposed by Alvin Liberman and his motor theory of speech perception (Liberman and Mattingly, 1985; Liberman and Whalen, 2000). Here, what counts for the sender must count for the receiver. Hence, a common code for language perception and language production is necessary. Evidence in favor of such a code in the domain of language has been recently provided by a TMS

study during speech listening. It was found that the listeners' tongue muscles were much more excitable by a single TMS pulse delivered over the motor cortex when they were listening to words that involved strong tongue movements when pronounced (Fadiga et al., 2002). This evidence is clearly compatible with the motor theory of speech perception according to which it is the activation of the articulatory motor gesture that enables the perception of the speech sounds.

Another empirical link between speech perception and the action recognition system of the macaque has been recently provided by single unit data. It has been shown that *mirror* neurons in the macaque area F5 fire not only at the sight of an action, but also at the sound of an action (i.e., breaking a peanut) in the dark (Kohler et al., 2002). These data suggest two things: first, *mirror* neurons have auditory access necessary to implement speech perception. Second, they enable a multimodal representation of action that is not linked to the visual channel only. This may facilitate learning of speech sounds via imitation.

But the question that is typically raised here is: how does one go from a relatively simple action recognition system to the complex symbolic levels reached by human language? In the next section, rather than trying to answer the question, I will look at the plausibility of the question itself and will discuss language not in the abstract forms often studied by mainstream linguistics, but in its daily, embodied form: conversation.

*c. What we talk about when we talk about language*

"I propose that representations exist only in the world and have no meanings, and that meanings exist only in brains without being represented there ... the most common method of assimilation of meanings is in the give and take of conversation"

Walter J. Freeman, *How brains make up their minds*, 2000

Traditionally, linguists have looked at language trying to extrapolate the most formal and abstract aspects of it. As shown in Figure 6 (left side), one can form sentences following what has been called a "tree structure" or "government and binding theory". The main idea behind it is that certain lexemes "govern" or "bind" some other lexemes. Thus, every grammatical sentence (S, top of the tree) consists at least of a *noun phrase* (NP) and a *verb phrase* (VP). NP and VP in turn break down into various "branches". An NP may consist of a *determiner* and an *adjective* and a *noun*, as for instance in the case "the funny guy". A VP may consist of a *verb* (threw) and an NP (the ball) and a *propositional phrase* (to John) which can be further decomposed. The benchmark test of this approach is shown in Figure 6 (right side). The sentence is completely made up, doesn't refer to real things, yet it is still following grammatical rules. This has been taken as evidence in favor of a universal grammar that can be processed similarly by all brains (Chomsky, 1981; Chomsky, 1986a; Chomsky, 1986b, 1990, 1997, 1999). So, the issue here would be: how can such a formalized structure emerge from a relatively primitive action recognition system? A type of answer (very vague, admittedly) to this question, provided by others elsewhere (Rizzolatti and Arbib, 1998), is that 'gestures may be a primitive form of grammar'. The problem with both question and answer is that they accept a view of language as a phenomenon that can be essentially reduced to formal constructs such as grammar.

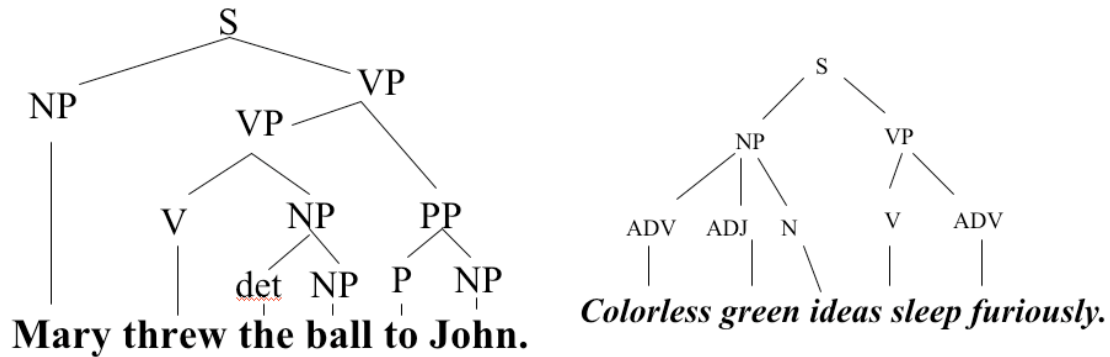


Figure 6

The real question to ask is: how do people talk? Figure 7 shows a transcription of a typical naturally occurring everyday speech. As it can be seen, not only violations of grammar (in *italic*) occur throughout the speech, but most importantly this segment of speech is full of phenomena (the question marks, they indicate sound stretches, hesitation markers, false starts, self-repairs, prosodic emphasis, manipulation of timing and of word rhythm) that are meaningful to both speaker and hearer. These phenomena are not even part of what is studied by traditional linguists. However, Conversation Analysis (CA) has provided a corpus of robust empirical data that well describe these phenomena (Heritage, 1989; Goodwin and Heritage, 1990; Heritage and Roth, 1995; Goodwin, 2000; Goodwin and Goodwin, 2000).

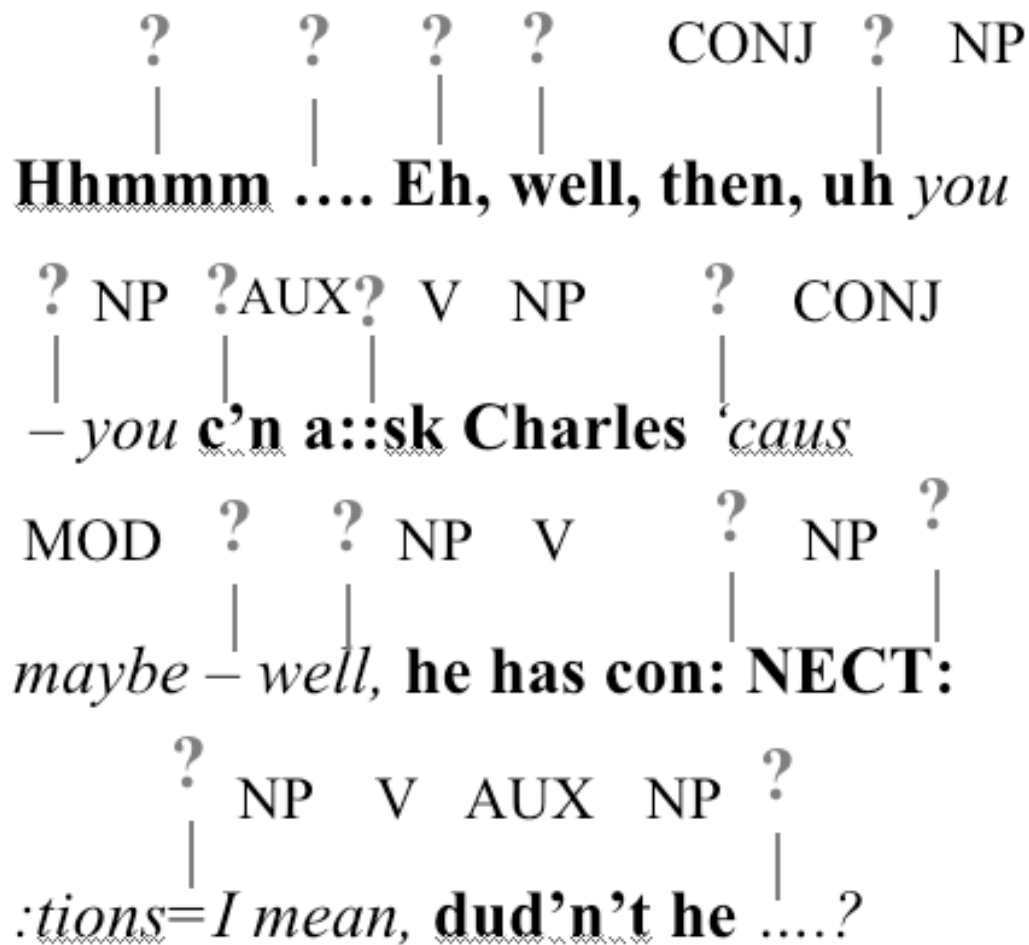


Figure 7

A salient feature of typical conversations that is ignored by traditional linguists is turn-taking. The average transition space from one speaker to another is less than 0.2 seconds, and longer pauses are immediately perceived as violation of temporal norms even by young children. What enables such fast transitions is the hearer's tracking through the stream of the other's speech for the appearance of fairly invariant, transiently appearing opportunities for taking a turn - which are not exclusively grammatical, but rhythmic and pitch contour-intonational as well. CA data shows that the fast transition that typically occurs between sentences is so familiar to both parties as a legitimate point for the other speaker to come in, that elaborate strategies in rhythm, intonation and even

grammar have to be adopted by the original speaker in order to obtain a multi-sentence turn in conversation.

What comes out of CA in its acknowledgement of language as an embodied practice, is that such motoric processes as eye-gaze, body torque, rhythm attunement and simultaneous gesture are part of a social interaction (rather than a "software program" as classical cognitivism advocates) critically dependent on the motor system's facility for temporal orientation and sequence organization and, I propose, dependent also (and plausibly even deriving from) on the action recognition or *mirror* system.

Thus, rather than trying to mimic (oh well...) a traditional grammatical structure in the domain of manual communication (the approach of Rizzolatti and Arbib, 1998), what I advocate here is to consider carefully the incontrovertibly motor elements that are at work in conversation and that human beings must still rely on to choreograph their interactions with each other. The processing of all those motor elements that give meaning to conversations require a fast functional architecture not dissimilar to the one needed in motor control. Here is where forward and inverse modeling and the action recognition system in which *mirror* neurons can coordinate activity between individuals with a simple matching mechanism have a real computational advantage over classical cognitive architectures.

#### **4. Feeling the emotions of others**

##### *a. Empathy and imitation*

Empathy allows the sharing of experiences, needs and goals across individuals, thus playing a fundamental role in social cognition. The functional aspects and corresponding neural mechanisms of empathy, however, are poorly understood. When Theodore Lipps introduced the concept of empathy (*Einfühlung*), he theorized a critical role for the mechanism of *inner imitation* of the actions of others in generating empathy (as cited in (Gallese, 2001)). In support of Lipps' idea, empathic individuals exhibit non-conscious mimicry of the postures, mannerisms, and facial expressions of others (the *chameleon effect*) to a greater extent than non-empathic individuals (Chartrand and Bargh, 1999). Thus, empathy may occur via a mechanism of action representation that modulates and shapes our understanding of the emotional contents of other individuals.

Separate neural systems for emotions and action representation, however, do exist in the primate brain. The limbic system is critical for emotional processing and behavior, and the temporo-parieto-frontal circuit I described above (the minimal neural architecture for imitation) is critical for action representation. Anatomical data suggest that a sector of the insular lobe, the dysgranular field, is connected with the limbic system as well as with posterior parietal, inferior frontal, and superior temporal cortex (Augustine, 1996). This connectivity pattern makes the insula a candidate for relaying action representation information to limbic areas processing emotional content.

*b. The minimal neural architecture for imitation and the limbic system: a role for the insular lobe*

To test this hypothesis, we performed two experiments, a brain imaging

experiment with normal volunteers, and a neuropsychological study with both neurological patients and normal controls. In the brain imaging study we used functional magnetic resonance imaging (fMRI) while subjects were either observing or imitating emotional facial expressions. A modulation of the action representation circuit onto limbic areas via the insula predicts greater activity during imitation, compared to observation of emotion, in the whole network. In fact, *mirror* areas would be more active during imitation than observation because of the simultaneous encoding of the sensory input and planning of the motor output. Within *mirror* areas, the inferior frontal cortex seems particularly important here, given that understanding goals is an important component of empathy. The insula would be more active during imitation because its role of relay would increase, compared to mere observation. Finally, limbic areas would also increase their activity because of the increased motor activity. Moreover, if an action representation mediation is really critical to empathy and the understanding of the emotions of others, then even the mere observation of emotional facial expression should activate brain regions of motor significance. Thus, observation and imitation of emotions should yield substantially similar patterns of activated brain areas, with greater activity during imitation in premotor cortex, especially inferior frontal cortex, in superior temporal cortex, insula, and limbic areas.

The results of the fMRI study confirmed our hypothesis. There was a substantially similar network of activated areas for both imitation and observation of emotion. Among the areas activated during both imitation and observation, the premotor face area, the dorsal sector of pars opercularis of the inferior frontal gyrus, the superior temporal sulcus, the insula, and the amygdala had greater activity during imitation than

observation of emotion.

The peak of activation in primary motor cortex during imitation of facial emotional expressions that we observed in our study corresponds extremely well with the location of the primary motor mouth area as determined by a meta-analysis of published PET studies, by a meta-analysis of original data in 30 subjects studied with PET, and by a consensus probabilistic description of the location of the primary motor mouth area obtained merging the results of the two previously described meta-analyses (Fox et al., 2001). This confirms the robustness and reliability of the data, in spite of the presence of facial motion during imitation. This is due to the fact that, even though motion artifacts were present at individual level, the group analysis got rid of these artifacts because each subject had different kinds of motion artifacts and they were thus eliminated when all the data were considered. In keeping with this, the data also clearly show peaks of activity in pre-SMA face area and the face area of the posterior portion of the rostral cingulate zone (RCZp), that correspond extremely well with the pre-SMA and RCZp face locations as determined by a separate meta-analysis of PET studies focusing on motor areas in the medial wall of the frontal lobe (Picard and Strick, 1996). Thus, our dataset clearly represents the first fMRI demonstration of human primary motor and rostral cingulate face area. With regard to premotor regions, the peaks that we observed correspond well with premotor mouth peaks as described by action observation studies. In fact, robust premotor responses during observation of facial emotional expressions were observed, in line with the hypothesis that action representation mediates the recognition of emotions in others even during simple observation.

The activity in pars opercularis shows two separate foci during imitation, a ventral

and a dorsal peak, but only the dorsal peak remained activated, albeit at significantly lower intensity, during observation of emotion. This pattern, with very similar peaks of activation, was also observed in our fMRI meta-analysis of hand action imitation and observation previously described (Molnar-Szakacs et al., 2002). In the monkey, F5 neurons coding arm and mouth movements are not spatially segregated and our human imaging data are consistent with this observation. Furthermore, the imaging data on imitating facial emotion converge with the data on hand imitation in suggesting that the mirror sector of the human inferior frontal gyrus is located in the dorsal part of pars opercularis.

The anterior sector of the insula was active during both imitation and observation of emotion, but more so during imitation, fulfilling one of the predictions of the action representation mediation to empathy' hypothesis. This is in line with two kinds of evidence available on this sector of the insular lobe. First, the anterior insula seems receiving slow-conducting unmyelinated fibers that respond to light, caress-like touch and may be important for emotional and affiliative behavior between individuals (Olausson et al., 2002). Second, imaging data suggest that the anterior insular sector is important for the monitoring of agency (Farrer and Frith, 2002), the sense of ownership of actions, which is a fundamental aspect of action representation. This confirms a strong input onto the anterior insular sector from areas of motor significance.

The increased activity in the amygdala during imitation compared to observation of emotional facial expression reflects the modulatory role of the action representation circuit onto limbic activity. It has been long hypothesized (Darwin was the first) (Ekman, 1973; Buck, 1980; Ekman, 1999) that facial muscular activity influences people's

affective responses. This is the first demonstration, however, that activity in the amygdala, a critical structure in emotional behaviors and in the recognition of facial emotional expressions of others, increases while subjects imitate the facial emotional expressions of others, compared to mere observation.

To further test the hypothesized mediation of action representation onto limbic activity via insula we also studied the ability to recognize emotions in two groups of ischemic stroke patients and in a control group. We studied patients with insular lesions only, compared to patients with lesions outside the insula. If empathy occurs via action representation modulation of limbic activity that is implemented in the insula, then an insular lesion should impair such mechanism. This predicts greater deficit in recognizing emotion in the group of patients with insular lesions, compared to patients with lesions outside the insula. This is because the insula would be an obligated path in which the modulation of action representation networks must be channeled to reach limbic structures such as the amygdala. This prediction is also met by the empirical data. Although both groups of patients are significantly impaired compared to normals, the deficit in emotion recognition is significantly greater in insular patients compared to stroke patients with lesions outside the insula. The deficit in emotion recognition in non-insular patients may be due to either non-specific effects of the lesions or to some effects onto the action representation network determined by the lesions. The additional evidence of the data obtained in neurological patients is extremely important because activation studies cannot fully determine if an activated area is essential to the task or behavior studied. Recently, repetitive TMS has been used to create transient lesions in normal subjects to test how essential a given activated area is, as we did in our rTMS

study on imitation in Broca's area described above. Repetitive TMS, however, cannot reach deep structures such as the insula. Hence, the clinical data are essential here.

Some preliminary neurological evidence in support of both the anatomical and functional proposal described here has been also described in a patient with a subcortical lesion encompassing also the anterior sector of the insula. This patient had both the inability to detect disgust as presented in many different ways, from non-verbal emotional sounds to prosody to facial expressions, and the inability to experience himself disgust (Calder et al., 2000).

All in all, we understand the feelings of others via a mechanism of action representation shaping emotional content, such that we ground our empathic resonance in the experience of our acting body and the emotions associated with specific movements. As Lipps noted, when I observe a circus performer on a hanging wire, I feel I am inside him (as cited in (Gallese, 2001). In order to empathize, we need a mediation of the representation of the actions associated with the emotions we are witnessing, and a brain network including structures that support communication between action representation circuits and circuits dedicated to emotional processing.

## **5. Conclusion**

The temporo-parieto-frontal circuit described here is the first available neural model of imitation in primates. The anatomical location and the functional properties that this circuit exhibits confirm a key role of imitation in learning and communication. This may not appear as big news to behavioral scientist who have studied imitation for years, and

have observed how imitative abilities are tied to social learning. The novelty, however, resides in the fact that our research program shows how functional properties of a relatively well-developed large scale neural circuit can now inform about the functional characteristics of behavioral domains that remained for a long time impenetrable to a neuroscientific investigation. This information, in turn, can be used to test more general questions in the behavioral sciences, for instance the innateness or learnability of some functions, or the approach humans take to mentalize.

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## References

- Augustine JR (1996) Circuitry and functional aspects of the insular lobes in primates including humans. *Brain Res Rev* 2:229-294.
- Binkofski F, Buccino G, Stephan KM, Rizzolatti G, Seitz RJ, Freund H-J (1999) A parieto-premotor network for object manipulation: evidence from neuroimaging. *Exp Brain Res* 128:210-213.
- Buck R (1980) Nonverbal behavior and the theory of emotion: The facial feedback hypothesis. *Journal of Personality & Social Psychology* 38:811-824.
- Byrne RW, Russon AE (1998) Learning by imitation: a hierarchical approach. *Behav Brain Sci* 21:667-712.
- Calder AJ, Keane J, Manes F, Antoun N, Young AW (2000) Impaired recognition and experience of disgust following brain injury. *Nat Neurosci* 3:1077-1078.
- Chartrand TL, Bargh JA (1999) The chameleon effect: The perception-behavior link and social interaction. *Journal of Personality & Social Psychology* 76:893-910.
- Chein JM, Fissell K, Jacobs S, Fiez JA (submitted) Functional heterogeneity within Broca's area during verbal working memory. *Physiology and Behavior*.
- Chomsky N (1981) Knowledge of language: Its elements and origins. *Philosophical Transactions of the Royal Society of London* 295:223-234.
- Chomsky N (1986a) *Knowledge of language*. New York: Praeger.
- Chomsky N (1986b) Changing perspectives on knowledge and use of language. In: *The representation of knowledge and belief.*, pp 1-58. Tucson, AZ, USA: University

- of Arizona Press.
- Chomsky N (1990) Language and mind. In: *Ways of communicating.*, pp 56-80. New York, NY, US: Cambridge University Press.
- Chomsky N (1997) Language and cognition. In: *The future of the cognitive revolution.*, pp 15-31. New York, NY, US: Oxford University Press.
- Chomsky N (1999) On the nature, use, and acquisition of language. In: *Handbook of child language acquisition.*, pp 33-54. San Diego, CA, US: Academic Press, Inc.
- Decety J, Grezes J, Costes N, Perani D, Jeannerod M, Procyk E, Grassi F, Fazio F (1997) Brain activity during observation of actions: Influence of action content and subject's strategy. *Brain* 120:1763-1777.
- di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G (1992) Understanding motor events: a neurophysiological study. *Exp Brain Res* 91:176-180.
- Dubeau MC, Iacoboni M, Koski L, Markovac J, Mazziotta JC (2001) Topography for body parts motion in the STS region. *Soc Neurosci Abs* 27.
- Ehrsson HH, Fagergren A, Jonsson T, Westling G, Johansson RS, Forssberg H (2000) Cortical activity in precision- versus power-grip tasks: an fMRI study. *J Neurophysiol* 83:528-536.
- Ekman P (1973) *Darwin and Facial Expression: A Century of Research in Review.* Ny: Academic Press.
- Ekman P (1999) Facial Expressions. In: *Handbook of cognition and emotion.*, pp 301-320. Chichester, England: John Wiley & Sons Ltd.
- Fadiga L, Craighero L, Buccino G, Rizzolatti G (2002) Speech listening specifically modulates the excitability of tongue muscles: a TMS study. *Eur J Neurosci*

15:399-402.

Farrer C, Frith CD (2002) Experiencing oneself vs another person as being the cause of an action: the neural correlates of the experience of agency. *Neuroimage* 15:596-603.

Fox PT, Huang A, Parsons LM, Xiong JH, Zamariippa F, Rainey L, Lancaster JL (2001) Location-probability profiles for the mouth region of human primary motor-sensory cortex: model and validation. *Neuroimage* 13:196-209.

Frith CD, Frith U (1999) Interacting minds: A biological basis. *Science* 286:1692-1695.

Gallese V (2001) The 'shared manifold' hypothesis. *Journal of Consciousness Studies* 8:33-50.

Gallese V, Fadiga L, Fogassi L, Rizzolatti G (1996) Action recognition in the premotor cortex. *Brain* 119:593-609.

Geyer S, Matelli M, Luppino G, Zilles K (2000) Functional neuroanatomy of the primate isocortical motor system. *Anat Embryol (Berl)* 202:443-474.

Goodwin C (2000) Action and embodiment within situated human interaction. *Journal of Pragmatics* 32:1489-1522.

Goodwin C, Heritage J (1990) Conversation analysis. *Annual Review of Anthropology* 19:283-307.

Goodwin MH, Goodwin C (2000) Emotion within situated activity. In: *Communication: An arena of development.*, pp 33-53. Stamford, CT, US: Ablex Publishing Corp.

Grafton ST, Arbib MA, Fadiga L, Rizzolatti G (1996) Localization of grasp representation in humans by positron emission tomography. 2. Observation compared with imagination. *Exp Brain Res* 112:103-111.

- Grezes J, Costes N, Decety J (1998) Top-down effect of strategy on the perception of human biological motion: A PET investigation. *Cogn Neuropsychol* 15:553-582.
- Haruno M, Wolpert DM, Kawato M (2001) Mosaic model for sensorimotor learning and control. *Neural Comput* 13:2201-2220.
- Heritage J (1989) Current developments in conversation analysis. In: *Conversation: An interdisciplinary perspective.*, pp 21-47. Clevedon, England: Multilingual Matters, Ltd.
- Heritage JC, Roth AL (1995) Grammar and institution: Questions and questioning in the broadcast news interview. *Research on Language and Social Interaction* 28:1-60.
- Heyes C (2001) Causes and consequences of imitation. *Trends Cogn Sci* 5:253-261.
- Heyes C (2002) Transformational and associative theories of imitation. In: *Imitation in animals and artifacts.*, pp 501-523. Cambridge, MA, US: MIT Press.
- Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G (1999) Cortical mechanisms of human imitation. *Science* 286:2526-2528.
- Iacoboni M, Koski LM, Brass M, Bekkering H, Woods RP, Dubeau MC, Mazziotta JC, Rizzolatti G (2001) Reafferent copies of imitated actions in the right superior temporal cortex. *Proc Natl Acad Sci U S A* 98:13995-13999.
- Ishikura T, Inomata K (1995) Effects of angle of model demonstration on learning of motor skill. *Percept Mot Skills* 80:651-658.
- Jellema T, Baker CI, Oram MW, Perrett DI (2002) Cell populations in the banks of the superior temporal sulcus of the macaque and imitation. In: *The imitative mind: Development, evolution, and brain bases.*, pp 267-290. New York, NY, US: Cambridge University Press.

- Kalaska JF, Caminiti R, Georgopoulos AP (1983) Cortical mechanisms related to the direction of two-dimensional arm movements: relations in parietal area 5 and comparison with motor cortex. *Exp Brain Res* 51:247-260.
- Kawato M (1999) Internal models for motor control and trajectory planning. *Curr Op Neurobiol* 9:718-727.
- Kohler E, Keysers C, Umiltà MA, Fogassi L, Gallese V, Rizzolatti G (2002) Hearing sounds, understanding actions: action representation in mirror neurons. *Science* 297:846-848.
- Koski L, Wohlschläger A, Bekkering H, Woods RP, Dubeau MC, Mazziotta JC, Iacoboni M (2002) Modulation of motor and premotor activity during imitation of target-directed actions. *Cereb Cortex* 12:847-855.
- Koski LM, Iacoboni M, Dubeau M-C, Woods RP, Mazziotta JC (in press) Modulation of cortical activity during different imitative behaviors. *J Neurophysiol*.
- Krams M, Rushworth MFS, Deiber M-P, Frackowiak RSJ, Passingham RE (1998) The preparation, execution, and suppression of copied movements in the human brain. *Exp Brain Res* 120:386-398.
- Lacquaniti F, Guigon E, Bianchi L, Ferraina S, Caminiti R (1995) Representing spatial information for limb movement: role of area 5 in the monkey. *Cereb Cortex* 5:391-409.
- Lieberman AM, Mattingly IG (1985) The motor theory of speech perception revised. *Cognition* 21:1-36.
- Lieberman AM, Whalen DH (2000) On the relation of speech to language. *Trends Cogn Sci* 4:187-196.

- Matelli M, Luppino G, Rizzolatti G (1985) Patterns of cytochrome oxidase activity in the frontal agranular cortex of the macaque monkey. *Behav Brain Res* 18:125-136.
- Mazziotta J, Toga A, Evans A, Fox P, Lancaster J, Zilles K, Woods R, Paus T, Simpson G, Pike B, Holmes C, Collins L, Thompson P, MacDonald D, Iacoboni M, Schormann T, Amunts K, Palomero-Gallagher N, Geyer S, Parsons L, Narr K, Kabani N, Le Goualher G, Boomsma D, Cannon T, Kawashima R, Mazoyer B (2001a) A probabilistic atlas and reference system for the human brain: International Consortium for Brain Mapping (ICBM). *Philos Trans R Soc Lond B Biol Sci* 356:1293-1322.
- Mazziotta J, Toga A, Evans A, Fox P, Lancaster J, Zilles K, Woods R, Paus T, Simpson G, Pike B, Holmes C, Collins L, Thompson P, MacDonald D, Iacoboni M, Schormann T, Amunts K, Palomero-Gallagher N, Geyer S, Parsons L, Narr K, Kabani N, Le Goualher G, Feidler J, Smith K, Boomsma D, Hulshoff Pol H, Cannon T, Kawashima R, Mazoyer B (2001b) A four-dimensional probabilistic atlas of the human brain. *J Am Med Inform Assoc* 8:401-430.
- Meltzoff AN, Moore MK (1977) Imitation of facial and manual gestures by human neonates. *Science* 198:74-78.
- Molnar-Szakacs I, Iacoboni M, Koski L, Maeda F, Dubeau MC, Aziz-Zadeh L, Mazziotta JC (2002) Action observation in the pars opercularis: Evidence from 58 subjects studied with FMRI. *J Cogn Neurosci Suppl* S:F118.
- Montague P, Berns G, Cohen J, McClure S, Pagnoni G, Dhamala M, Wiest M, Karpov I, King R, Apple N, Fisher R (2002) Hyperscanning: Simultaneous fMRI during Linked Social Interactions. *Neuroimage* 16:1159.

- Mountcastle V, Lynch J, Georgopoulos A, Sakata H, Acuna C (1975) Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. *J Neurophysiol* 38:871-908.
- Olausson H, Lamarre Y, Backlund H, Morin C, Wallin BG, Starck G, Ekholm S, Strigo I, Worsley K, Vallbo AB, Bushnell MC (2002) Unmyelinated tactile afferents signal touch and project to insular cortex. *Nat Neurosci* 5:900-904.
- Perrett DI, Emery NJ (1994) Understanding the intentions of others from visual signals: neurophysiological evidence. *Curr Psychol Cogn* 13:683-694.
- Perrett DI, Harries MH, Bevan R, Thomas S, Benson PJ, Mistlin AJ, Chitty AJ, Hietanen JK, Ortega JE (1989) Frameworks of analysis for the neural representation of animate objects and actions. *J Exp Biol* 146:87-113.
- Perrett DI, Harries MH, Mistlin AJ, Hietanen JK, Benson PJ, Bevan R, Thomas S, Oram MW, Ortega J, Brierly K (1990) Social signals analyzed at the single cell level: someone is looking at me, something touched me, something moved! *Int J Comp Psychol* 4:25-55.
- Petrides M, Pandya DN (1994) Comparative architectonic analysis of the human and the macaque frontal cortex. In: *Handbook of neuropsychology* (Boller F, Grafman J, eds), pp 17-58. Amsterdam: Elsevier.
- Picard N, Strick PL (1996) Motor areas of the medial wall: a review of their location and functional activation. *Cereb Cortex* 6:342-353.
- Rilling J, Gutman D, Zeh T, Pagnoni G, Berns G, Kilts C (2002) A neural basis for social cooperation. *Neuron* 35:395-405.
- Rizzolatti G, Arbib M (1998) Language within our grasp. *Trends Neurosci* 21:188-194.

- Rizzolatti G, Luppino G, Matelli M (1998) The organization of the cortical motor system: new concepts. *EEG Clin Neurophysiol* 106:283-296.
- Rizzolatti G, Fogassi L, Gallese V (2001) Neurophysiological mechanisms underlying action understanding and imitation. *Nat Rev Neurosci* 2:661-670.
- Rizzolatti G, Fadiga L, Matelli M, Bettinardi V, Paulesu E, Perani D, Fazio F (1996) Localization of grasp representations in humans by PET: 1. Observation versus execution. *Exp Brain Res* 111:246-252.
- Sakata H, Takaoka Y, Kawarasaki A, Shibutani H (1973) Somatosensory properties of neurons in the superior parietal cortex (area 5) of the rhesus monkey. *Brain Res* 64:85-102.
- Seltzer B, Pandya DN (1994) Parietal, temporal, and occipital projections to cortex of the superior temporal sulcus in the rhesus monkey: a retrograde tracer study. *J Comp Neurol* 343:445-463.
- von Bonin G, Bailey P (1947) *The neocortex of Macaca Mulatta*. Urbana: University of Illinois Press.
- Walsh V, Cowey A (2000) Transcranial magnetic stimulation and cognitive neuroscience. *Nat Rev Neurosci* 1:73-79.
- Wapner S, Cirillo L (1968) Imitation of a model's hand movement: Age changes in transposition of left-right relations. *Child Dev* 39:887-894.
- Wolpert DM, Kawato M (1998) Multiple paired forward and inverse models for motor control. *Neural Networks* 11:1317-1329.