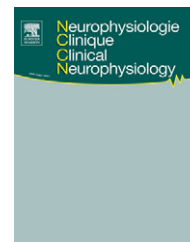


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## REVIEW/MISE AU POINT

# What is “mirror” in the premotor cortex? A review

## Propriétés miroir du cortex moteur : une revue de la littérature

O. Morin<sup>a</sup>, J. Grèzes<sup>b,\*</sup>

<sup>a</sup> Institut Jean-Nicod, UMR 8129, EHESS, CNRS, département d'études cognitives, École normale supérieure, 29, rue d'Ulm, Paris, France

<sup>b</sup> Laboratoire de neurosciences cognitives, UMR 742 Inserm, département d'études cognitives, École normale supérieure, 29, rue d'Ulm, Paris, France

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l'action

**Summary** We review the findings of 24 fMRI studies examining activations in the premotor cortex (Brodmann's areas 6 and 44) during passive observation of actions. We found that such activations regularly occurred. Looking for functional differentiation in the premotor cortex, we found that one parameter was associated with systematic differences in location: this was the presence or absence of targets. Observing biological actions with a physical target, compared to a visual control showing no action at all, consistently activated the ventral premotor cortex (BA 6), and did so significantly more than observing target-less actions (with the same control). In contrast, the activity in BA 44 ("Broca's area") was not modulated by the presence or absence of targets. We propose that the ventral precentral gyrus, and not BA 44, shares the visual properties of "mirror" neurons found in area F5 of the macaque brain.

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**Résumé** Cet article passe en revue les résultats de 24 études en IRMf, en se concentrant plus particulièrement sur le cortex prémoteur (aires de Brodmann 6 et 44) au cours de l'observation passive d'actions. De nombreuses activations au sein des aires de Brodmann 6 et 44 sont trouvées. La recherche d'une différenciation fonctionnelle entre ces deux aires du cortex prémoteur a permis d'identifier un paramètre qui semble avoir une influence systématique sur la localisation des activations ; ce paramètre est l'absence ou la présence d'un but à l'action. L'observation de mouvements biologiques dirigés vers un but active de façon consistante l'aire de Brodmann 6 du cortex prémoteur et ce significativement plus que pendant l'observation de mouvements sans but. En revanche, la présence ou l'absence de but n'a pas d'influence sur la présence d'activations au sein de l'aire 44 de Brodmann (aire dite de Broca). Nous

\* Corresponding author.

E-mail address: [julie.grezes@ens.fr](mailto:julie.grezes@ens.fr) (J. Grèzes).

suggérons que le gyrus précentral ventral (l'aire 6) et non pas l'aire 44 de Brodmann, partage les propriétés visuelles des neurones « miroirs » enregistrés, chez le macaque, dans l'aire F5.  
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## Introduction

Action and perception are not completely segregated in the human brain. Thus, some overlap naturally exists between systems for perceiving actions, and systems for producing them. Since the premotor cortex is one of the key sites of action organization in the human brain, premotor activations are expected to co-occur with action observation. However, there is still considerable debate on: (1) the location; and (2) the functional properties of premotor areas where action meets action perception. The latter question will be easier to explore once the former has been answered. In this paper, we tackle the issue of location, and suggest some clarifications concerning the problem of functional properties.

Viewing actions (in what follows, we shall use that word exclusively in the sense of: motion respecting biomechanical constraints, as performed by a living being) is known to activate several specialized areas. Among these is the superior temporal sulcus (STS) [1]. In humans and monkeys, the STS is consistently and specifically activated by the observation of biological motion alone, independently of contexts or forms [2]. The STS is the visual entry to an important system that was identified in macaques. It is located in the parietal and premotor cortices, and has been called the "mirror system" after the discovery, in monkeys, of parietal and premotor "mirror" cells [3]. These so-called "mirror neurons" were originally found in area F5 of the macaque premotor cortex. They fire both when the monkey sees a goal-directed action, and when the monkey performs some (but in many cases not the same) goal-directed action. The very same action, in the absence of a target object, does not activate the "mirror" neuron. Recently, "mirror" neurons have been shown to react to abstract properties of actions, such as their place in complex motor sequences [4], or the inferred presence or absence of an invisible target [5]. Because of this teleological sensitivity, "mirror" neurons have been attributed a key role in a monkey's understanding of his conspecifics' actions.

Ever since the discovery of "mirror" neurons, researchers have been looking for a human homologue of F5 - that is, one or several brain areas whose conditions of activations match those of "mirror" neurons found in F5. These conditions are: (1) being active during the execution of some target-directed actions; and (2) being active during the observation of some target-directed actions. As of today, the human premotor cortex, which is thought to comprise the precentral cortex (BA 6) and the pars opercularis of the inferior frontal gyrus (BA 44), is considered one of the most likely candidates [6]. Human BA 44 and 6 clearly share many functional and histological properties of the macaque premotor cortex [7,8]. The cytoarchitectonic properties of BA 44 put it clearly aside from BA 45, and move it closer to BA 6 as a premotor area. Furthermore, almost everyone agrees that the ventral part of BA 6 in humans bears much resemblance with the macaque ventral premotor cortex, both anatomically [9] and functionally [10]. Whether or not we can go

further in speculating homologies is a matter of considerable controversy: some see BA 44 as the human homologue of macaque area F5 [11], but others disagree [12]. BA 44 has become the centre of attention in the research concerning a putative mirror system in humans. BA 44 forms part of Broca's area, which is crucially (though not exclusively nor exhaustively - see [13]) involved in language production [14]. The possibility that it could host mirror-neurons is tantalizing. The visual and motor properties of BA 44, as revealed by functional neuroimaging studies, are thought to speak in favour of this view.

First, BA 44 has been found to play a role in the preparation [15] and execution [16,17] of target-directed actions, and particularly of grasping [18,19] a type of gesture for which many "mirror" neurons show a clear preference. BA 44 also seems to be involved in imitation of finger movements [20], although it is unclear to what extent this is the case [21-23]. If it was the case, some think that it would count as a proof that BA 44 is a mirror-neuron area. However, as far as we know, macaque "mirror" neurons are not involved in any kind of imitation, and the executed and observed behaviours they react to are not necessarily similar.

Second, many authors reported activations in BA 44 when subjects viewed a movement that was performed by another human being. However, these activations are puzzling for several reasons. First, they are found both for target-directed and target-less actions, which is not what we should expect from a mirror-neuron-like area. Second, they have proven very difficult to replicate [24,25], and they are quite difficult to locate precisely, because of the anatomical variability of BA 44, whose location varies a lot from one individual to another [26]. BA 44 is delicate to identify on the basis of individual sulcal borders alone [27] - and even these are not investigated by most neuroimaging studies. In a meta-analysis of activations found in Broca's area, [28] it was shown that only the most dorsal fringe of BA 44 was activated during action observation. In their 2001 meta-analysis of PET studies [29], Grèzes and Decety failed to report any activation in BA 44 for action observation; nevertheless, they found that the premotor cortex was activated by action observation. This led them to propose that the precentral cortex (BA 6), and not Broca's area, might be the cortical area exhibiting "mirror" properties for action observation, which in turn makes it a likely homologue of F5. Their meta-analysis, however, took only PET studies into account, which made the data vulnerable to technical limitations.

In this mini-review, we put Grèzes and Decety's hypothesis to the test, this time with fMRI studies, whose spatial resolution is superior. We analyzed activations associated with action observation in the inferior frontal gyrus (BA 44) and the precentral cortex (BA 6).

## Methods

Twenty-four fMRI studies, published from 1999 to 2007, were analyzed [30-49,19,20,24,25]. Only studies performed with

healthy volunteers were included (one study – [49] – also involved autistic subjects, but only healthy subjects' activations were taken into account). Since our goal was to locate visuomotor activity in the premotor cortex as precisely as possible, we restricted our choice to those studies that provided MNI or Talairach coordinates.

We picked up all the contrasts comparing activations elicited by the observation of an action made by a living being with another visual stimulus. Stimuli used in the studies were all films (not photographs) depicting real actions. Contrasts that lacked a visual control – even a rudimentary one, such as a grey background – were not taken into account (the contrasts we had to cast aside for this reason supported our main finding concerning the difference between BA 44 and BA 6 regarding the preference for goals). Only contrasts measured over the whole brain were analyzed, except two [45]. This left us with 40 contrasts in 19 studies.

In all studies, subjects were asked to watch the action and the control visual stimulus; in six studies, subjects had to perform some low-level attentional task (like *n*-back matching). In all other studies subjects simply watched passively. Studies in which subjects were asked to imagine themselves performing the action, and contrasts in which the subject observed the action in order to plan another (or the same) action, were not taken into account.

Contrasts were sorted into three main groups. One first group gathered five contrasts that compared an observed biological action with another action that was not perceived as biological (according to subjects), either because it was unrecognizable, or because it was artificially distorted. Contrasts in which biological action was not recognized were discarded. This was the "biological versus non biological" group. The second group gathered all contrasts ( $n = 12$ ) that compared an observed action with another observed action. This group was the "action versus action" group. The last group gathered all contrasts (23) that compared an observed action with an action-less visual stimulus (either a neutral background or a still picture of the observed action video). This group was the "action versus no action" group.

In each of these three groups, a difference was made between contrasts that used a goal-directed action as their main stimulus, and contrasts that used an action without a target as their main stimulus. A "goal", here and in the following, is an independent physical target that the effector reaches at the end of the action.

For each contrast, the MNI coordinates of all frontal activations were analyzed using SPM anatomy toolbox (Statistical parametric mapping, <http://www.fil.ion.ucl.ac.uk/spm>). Talairach coordinates were transformed before analysis. Only activations found in the premotor cortex that is, in the precentral cortex (BA 6) and in the inferior frontal gyrus (IFG, BA 44), are given and discussed in this paper. IFG activations found in BA 45 are mentioned only when relevant. Activations are signalled as falling in BA 6 or BA 44 when SPM anatomy toolbox located them in one of these areas with a probability of 30% or more. Activations recognized by Anatomy Toolbox as falling in the pars opercularis of the inferior frontal gyrus, but not in BA 44, are mentioned as belonging to the inferior frontal gyrus, but not in BA 44.

## Results and discussion

Overall, more than half of our contrasts (27/40) found activations in the premotor cortex, whether in BA 6, BA 44, or in both. Activations were not found to be especially lateralized, both generally and for individual categories of contrasts. BA 6 and BA 44 did not differ in this respect. Some aspect of action observation seems to recruit the premotor cortex in a very diverse array of conditions. This commonplace finding is coherent with a more general observation: perception, even of nonbiological visual stimuli, very often has a motor component, which can be observed in the premotor cortex [50]. Motor involvement in visual perception is not limited to action perception, and explanations based on mirror neurons are not the only available option. In the detailed analysis that follows, however, we can try to find what caused these cases of premotor involvement in action perception.

### Biological versus nonbiological actions

Five studies [45–47,36,38] contrasted the observation of biological actions to the observation of non-biological actions. None of the actions used in the contrasts were goal-directed; four of them used point-light biological motion stimuli, as designed by Johansson [51]. Point-light stimuli are an excellent means of assessing the sensitivity of a region to biological motion, since it presents in a reliable and recognizable way all the dynamic information that characterizes living beings in motion, minus all kinds of configural information (such as form or place) that one might use to reconstruct a gesture without paying attention to its dynamic properties. The other one [36] used a video of a moving finger contrasted with a video of a moving pair of scissors. None of these contrasts revealed any activation in the precentral cortex (BA 6). The study by Costantini et al. [36], that did not make use of point-light biological motion, found activation in the IFG (BA 44). Only one out of four studies that employed point-light biological motion stimuli found activation in our region of interest. PET studies (for example [52]) also failed to show motor activity following biological motion observation. This may be explained by a lack of sensitivity of the apparatus used: the scanner in Saygin et al. [45] was much more powerful (4T).

However, another explanation may be that the premotor cortex is not sensitive to biological motion *per se*. Several fMRI and PET studies found activations in the inferior frontal gyrus (BA 44) when contrasting actions that were not perceived as biological with actions that were perceived as biological. Three studies [38,53,36] found activations in BA 44 for biomechanically impossible hand actions contrasted with mechanically impossible, nonbiological movements.

### Action versus action

Thirteen contrasts in six studies [39–44] contrasted an action (or a sequence of movements) with another action (or sequence of actions) that differed from the first because it was put in a different context (two contrasts), because it was viewed from another perspective (two contrasts), because the motor sequence was not the same although

the effector remained the same (five contrasts) or, lastly, because the effector was different although the motor sequence did not vary much (three contrasts). This latter category will be examined in the "somatotopy" section, in the next part.

According to an influential hypothesis, the involvement of the premotor cortex in action observation is due to the role the mirror-neuron system plays in action understanding, which means the extraction of things like goals, agency, or a specific type of action, from visual information. If that was the case, one should expect premotor activations not only when action observation is compared with observation of "no action" stimuli, but also when comparing the observation of different actions (highlighting some specific type of action), or of the same gesture within different contexts (suggesting different higher-order objectives), or of the same action viewed from different perspectives (which might suggest different kinds of agency).

#### Same action, different context

If the premotor cortex (or part of it) was the human homologue of a mirror-neuron system, it should be sensitive to the context of an action, just as mirror-neurons are [4,5]. The data we surveyed here speak against this view. Two studies [39,41] compared the condition of seeing a gesture in a certain context with the condition of seeing it outside that context. In Iacoboni et al. [39], two different contexts were tested (one was a table prepared for breakfast, the other was the same table once breakfast had taken place); in Koski et al. 2002 [41], symbolic target-like dots were added in videos representing short intransitive finger movements. None of these two studies found any activation in our region of interest. Iacoboni et al. [39] found several activations in the inferior frontal gyrus, most of them falling squarely in BA 45, none in BA 44.

#### Same action, different perspective

One contrast, in Jackson et al.'s study [40], compared videos of a gesture seen from first-person perspective, with videos of the same gesture seen from third-person perspective. A second contrast made the reverse comparison. No activation was found in the inferior frontal gyrus (BA 44). Only the first contrast (first person versus third person activation) revealed activation in the precentral gyrus (BA 6).

#### Same effector, same object, different action sequence

Five contrasts in two studies [42,43] compared videos showing complex sequences of goal-directed movements with other complex sequences of movements that differed in the way they were organized; this could be because the objects used were different or used in different ways, or in a different order. These contrasts were devised to reveal sensitivity to the more abstract properties of actions. Two of these contrasts found activations both in the premotor cortex and the inferior frontal gyrus (BA 44); two others found activations in the precentral cortex (BA 6) only. One found no activation at all.

Taken together, these results are inconclusive. We cannot rule out some kind of premotor involvement in judging or classifying actions – for example, in Manthey et al. [43]. But a systematic association of the premotor cortex with

our understanding of goals and agency is difficult to support with the present data.

#### Action versus no action

Twenty-three contrasts in nine studies [31–34,37,19,24,40,48] compared activations associated with making subjects observe actions with activations provoked by visual stimuli that presented no movement. A first set of studies used, as a control, a still image of the action (or simply of the effector) that was shown as a dynamic stimulus in the experimental condition. All other studies contrasted an action with a rudimentary visual baseline, such as a grey background or a fixation cross. The results for these two sets are presented together. Nine contrasts out of 22 used a goal-directed action as the main action stimulus: these will be discussed along with the others.

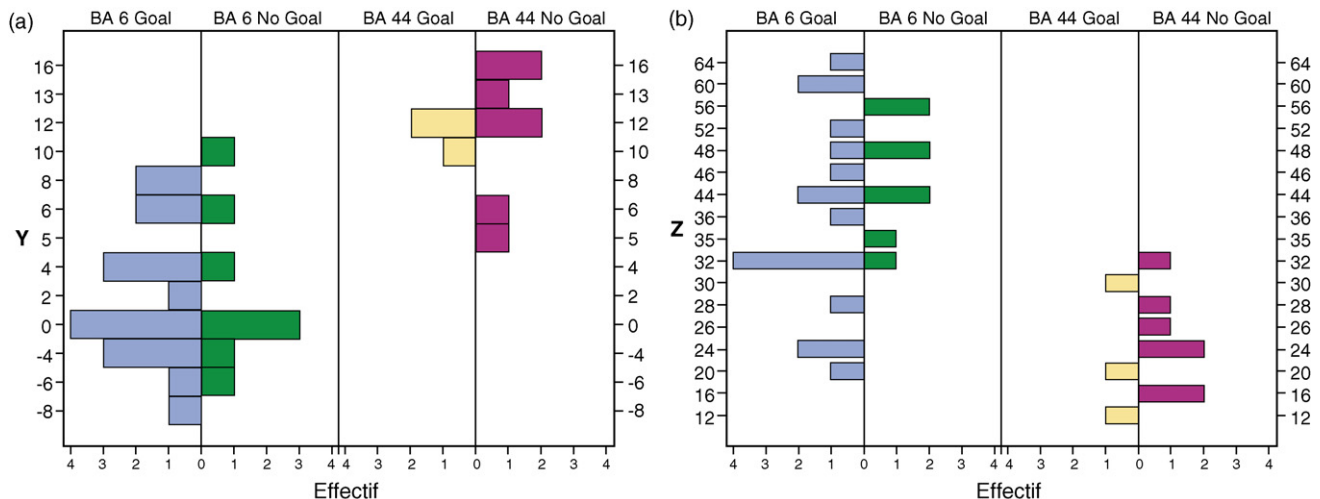
#### Somatotopy along BA 6 and BA 44

In the "action versus action" group, Sakreida et al. [44] contrasted actions made with distal effectors (mouth and fingers) with actions made with more proximal effectors (such as ankles or knees), and with even more proximal ("axial") effectors, such as shoulders or waist muscles. The pattern of activations they found showed activations in BA 44 alone in the "distal versus proximal and axial" contrast, and BA 6 in the other two, suggesting that action observation in the premotor cortex is indeed somatotopically organized in a dorsoventral arrangement, the distal movements being represented more dorsally and the proximal movements (such as those involving fingers and lips) more ventrally.

In the 23 contrasts of this group, three studied finger movements, eight studied mouth movements, and four studied hand-arm actions, two studied feet actions, one, leg actions, and two, whole-body actions. Three contrasts, that did not compare a specific part of the body with another, were not taken into account. The localization of activations in BA 6, BA 44, the precentral cortex or the inferior frontal gyrus, was not found to be influenced by the kind of effectors shown. Activations associated with viewing fingers or mouth actions did not involve the inferior frontal gyrus (BA 44) more than activations associated with viewing less distal effectors. In particular, no activation whatsoever was found in BA 44 for the observation of finger movements (tested in [34,48,24]). If any, activations associated with observing leg and whole-body actions are slightly more often located in the inferior frontal gyrus (BA 44), than those provoked by mouth or finger actions (see for example [48]). Our data do not seem to follow the familiar somatotopic pattern. This is all the more surprising since one study of this group [34] found exactly the same kind of somatotopy as was evidenced in [44]. We can only conclude that somatotopic distributions, though undeniably present, are highly task-dependent, idiosyncratic, and consequently likely to be destroyed when pooling together results from different protocols.

#### Activations in the inferior frontal gyrus (BA 44)

Eight out of 23 contrasts found activation in Brodmann's area 44 associated with seeing biological actions, as opposed to visual stimuli presenting no action. BA 44 activations were



**Figure 1** Bar charts representing the number of activations found during the observation of actions as a function of the presence or the absence of a goal, in the precentral area 6 and in the inferior frontal area BA 44. a: the activations are presented according to their Y; and b: their Z-axis coordinates. The location of BA 6 activations (blue and green) is posterior to BA 44 (yellow and purple) on the Y-axis, and dorsal to BA 44 on the Z-axis. In the two left bar charts (a), the number of activations (*effectif*) found in BA 6 for goal-directed actions (blue) and for non goal-directed actions (green) is presented as a function of the Y coordinate. In the two right bar charts (a), the number of activations (*effectif*) found in BA 44 for goal-directed actions (yellow) and for non goal-directed actions (purple) is presented as a function of the Y-coordinate. The same applies for the bar chart in (b). One can see how the presence of goals during action perception influences the number of activations in the premotor cortex (BA 6), not in BA 44.

Figure 1 Les diagrammes à barres représentant le nombre d'activation ont trouvé pendant l'observation des actions en fonction de la présence ou de l'absence d'un but, dans le secteur precentral 6 et dans le BA inférieur 44 de secteur frontal. Les activation sont présentées selon leur Y (a) et leur axe de Z coordonne (b). L'endroit du BA 6 activation (bleues et vertes) est postérieur au BA 44 (jaune et pourpre) sur l'axe de Y, et la dérive dorsale au BA 44 sur l'axe de Z. Dans les deux diagrammes à barres laissés (a), le nombre d'activation (*effectif*) trouvées en BA 6 pour des actions but-dirigées (bleues) et pour des actions non but-dirigées (vert) est présenté en fonction de y. Dans les deux bons diagrammes à barres (a), le nombre d'activation (*effectif*) trouvées en BA 44 pour des actions but-dirigées (jaune) et pour des actions non but-dirigées (pourpres) est présenté en fonction de y. Le même s'applique pour le diagramme à barres en (b). On peut voir comment la présence des buts pendant la perception d'action influence le nombre d'activation dans le cortex de premotor (BA 6), pas en BA 44.

accompanied by activations in the precentral gyrus (BA 6) in all cases except one. The contrast that revealed BA 44 alone presented the subjects with videos of moving feet compared to photographs of still feet. A disputable case of BA 44 activation is found in Beauchamp et al. [31]: they presented their subjects with images of human whole-body actions, and animated tools (such as hammers rocking back and forth). The authors [31] could not dissociate the activations provoked by these two kinds of stimuli in BA 44.

Five (out of 14) non goal-directed stimuli provoked activations in BA 44; three (out of 9) goal-directed action stimuli provoked activations in BA 44. Therefore, goals do not appear to have a significant effect on BA 44 activations (chi square test: 0.014, d.f. 1,  $P$ -value 0.907 – Pearson, uncorrected).

#### Activations in the precentral gyrus (BA 6)

Fourteen out of 23 contrasts found activations in Brodmann's area 6 for seeing action. Eight of these contrasts revealed BA 6 in isolation, that is, unaccompanied by activations in BA 44. Thus, while activations in BA 44 are strongly associated with activations in BA 6, the reverse association does not hold.

BA 6 activations for the whole group were equally present in the right and left hemisphere, and located on average at

$y=0$ ,  $z=41$ , that is probably in the ventral part of the precentral gyrus, at the border with the dorsal part [54]. Out of 14 non goal-directed stimuli, only five provoked activations in Brodmann's area 6. Likewise, in PET studies, activations associated with observing actions without targets, still in the premotor cortex, vary a lot in localization, and prove very difficult to obtain [55–57].

In contrast, all of nine goal-directed action stimuli were associated with ventral activations in BA 6. The presence of goals does seem to have an effect upon activations in BA 6 (chi square: 9.505, d.f. 1,  $P < 0.002$  – Pearson, uncorrected). BA 6 and BA 44 significantly differ from each other in this respect (chi square: 9, d.f. 1,  $P < 0.003$  – Pearson, uncorrected). This effect remains very significant if we consider the inferior frontal gyrus at large (including BA 45). Similarly, if we take into account activations situated in the precentral gyrus that do not fall squarely within BA 6, both the effect of goals, and the difference between the IFG and the precentral gyrus concerning this effect, remain significant. Our calculation gives the same weight to each of the 23 tests, but we could find the same result by looking at the number of activations found for observing goal and non-goal-directed actions in BA 6 and BA 44 (see Fig. 1). This finding is coherent with existing data from PET studies [29,58] that find the precentral gyrus, and not BA 44,

consistently active for goal-directed action observation. Following Grèzes and Decety [29], we suggest that the ventral precentral gyrus shares the visual properties of “mirror” neurons found in F5 in macaques, whereas BA 44 does not.

## Conclusion

Observing actions, as opposed to still pictures or neutral stimuli, activates the premotor cortex, ventral or dorsal, in a majority of studies. One factor makes a systematic difference in the location of these premotor activations, that is, the presence or absence of targets. As could be expected from monkey data, the human ventral premotor cortex is consistently and specifically activated when subjects view goal-directed actions. More surprisingly, this kind of visuomotor activity can be precisely located in ventral BA 6 (around  $z = 41$ ), quite beyond the boundaries of BA 44. Visuomotor activations in this area are reliable and consistent as far as target-directed gestures are concerned, whilst in the inferior frontal gyrus (BA 44), visuomotor activations are much more erratic, and show no sensitivity to the presence of targets. We tentatively conclude that the ventral precentral cortex has the visual properties of F5 “mirror” neurons, contrary to BA 44. However, this conclusion must remain tentative for the moment. Indeed, it can only be proven by further fMRI research comparing the observation of grasping in the macaque and human brains. Relevant fMRI data in macaques have already been provided by Nelissen et al. [59].

If our conclusion proved to be correct, theories speculating that a mirror-neuron-like system gave rise to our language faculty [60] may be found to rest on fragile grounds. Still, we do not wish to minimize the important motor properties of BA 44. These properties are fascinating, as they may represent the missing link between human language and executive functions [61]. It would indeed be interesting to find if either BA 6 or BA 44 are necessary for (and not merely involved in) action recognition; but this is precisely what neuroimaging cannot tell us – studies using lesions, whether in brain-damaged patients or produced by TMS, may provide the answer.

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