

Common and Differential Neural Mechanisms Supporting Imitation of Meaningful and Meaningless Actions

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Abstract

■ Neuropsychological studies indicate that, after brain damage, the ability to imitate meaningful or meaningless actions can be selectively impaired. However, the neural bases supporting the imitation of these two types of action are still poorly understood. Using PET, we investigated in 10 healthy individuals the neural mechanisms of imitating novel, meaningless actions and familiar, meaningful actions. Data were analyzed using SPM99. During imitation, a significant positive correlation ($p < .05$, corrected) of regional cerebral blood flow with the amount of meaningful actions was observed in the left inferior temporal gyrus only. In contrast, a significant positive correlation ($p < .05$, corrected) with the amount of meaningless movements was observed in the right parieto-occipital junction. The direct categorical comparison of imitating meaningful (100%) relative to meaningless (100%) actions showed differential increases in neural activity ($p < .001$, uncorrected) in the left inferior temporal gyrus, the left parahippocampal gyrus, and the left angular gyrus. The reverse categorical comparison of imitating meaningless (100%) relative to meaningful (100%) actions revealed differential increases in neural activity ($p < .001$, uncorrected) in the superior parietal cortex bilaterally, in the right parieto-occipital

junction, in the right occipital-temporal junction (MT, V5), and in the left superior temporal gyrus. Increased neural activity common to imitation of meaningless and meaningful actions compared to action observation was observed in a network of areas known to be involved in imitation of actions including the primary sensorimotor cortex, the supplementary motor area, and the ventral premotor cortex. These results are compatible with the two-route model of action imitation which suggests that there are at least two mechanisms involved in imitation of actions: a direct mechanism transforming a novel action into a motor output, and a semantic mechanism, on the basis of stored memories, that allows reproductions of known actions. Our results indicate that, in addition to shared neural processes, the direct and the semantic mechanisms that underlie action imitation also draw upon differential neural mechanisms. The direct mechanism underlying imitation of meaningless actions differentially involves visuospatial transformation processes as evidenced by activation of areas belonging to the dorsal stream. In contrast, imitation of meaningful actions differentially involves semantic processing as evidenced by activation of areas belonging to the ventral stream. ■

INTRODUCTION

In recent years, neuroscientists have become increasingly interested in imitation of individual behavior. In particular, functional brain imaging studies have given us new insights into the neural mechanisms which sustain imitation of simple movements such as finger lifting (e.g., Iacoboni et al., 1999) that could be either directed at a target or not (Koski, Wohlschläger, et al., 2002), symbolic and nonsymbolic finger configurations (Tanaka, Inui, Iwaki, Konishi, & Nakai, 2001), or movements involving manipulation of small 3-D

objects (Decety, Chaminade, Grèzes, & Meltzoff, 2002; Grefkes, Weiss, Zilles, & Fink, 2002). Other studies (Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti, Fadiga, Matelli, et al., 1996) employed observation and execution of simple goal-directed actions both as stimulus and response. The areas activated in common in the latter studies were the left inferior frontal gyrus and frontal operculum (Iacoboni et al., 1999; Grafton, et al., 1996; Rizzolatti, Fadiga, Matelli, et al., 1996), the left superior temporal sulcus (STS), the left inferior parietal lobule, and the rostral part of the left supplementary motor area (SMA; Grafton et al., 1996; Rizzolatti, Fadiga, Matelli, et al., 1996). Interestingly, in a PET study in which subjects were asked to watch hand stimuli without doing anything (baseline), to immediately copy hand movements (execute-only condition, E), to prepare for the copying response (prepare-only condition,

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P), and to prepare plus execute the hand movements (prepare + execution condition, PE), Krams, Rushworth, Deiber, Frackowiak, & Passingham (1998) found an increase in regional cerebral blood flow (rCBF) in Broca's area when either the PE or the P conditions were compared with the baseline or E conditions. These authors thus suggested that the involvement of Brodmann's area 44 is not related to movement per se, but more specifically to the preparation of *copied* movements.

Given the activation of parts of Broca's area, it has been suggested that this region represents the human homologue of macaque area F5, which contains bimodal neurons that discharge when the animal *sees* an action as well as when it *performs* the same action (i.e., the so-called mirror neurons; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). Altogether, these findings have been taken as evidence for the existence of a unique neuromechanism supporting visuomotor mapping in action imitation (see, for instance, Goldenberg & Hagmann, 1997).

The direct mapping approach is, however, only one possible way to account for imitation of actions. Other views have been put forward to explain some findings that cannot easily be accommodated by direct mapping theories. To account for children (as well as adults) making errors in imitating ear-hand movements, Bekkering, Wohlschläger and colleagues argued that imitation implies decomposition and reconstruction of actions according to a hierarchy of goals (Wohlschläger, Gattis, & Bekkering, 2003; Wohlschläger, & Bekkering, 2002; Bekkering, Wohlschläger, & Gattis, 2000). Rumiati and Tessari (2002), on the other hand, have claimed that the goal-directed theory of imitation should be integrated within a two-route model for the reproduction of actions (see Figure 1). These authors found that healthy volunteers imitated meaningful actions (MF) better than meaningless actions (ML) and argued that this advantage was due to MF actions having their goals stored in long-term, semantic memory (i.e., the semantic route). In contrast, ML actions, which have no pre-stored goals in semantic memory, can be reproduced *only* using the direct route (from visual analysis to action working memory, i.e., bypassing semantic processing). The use of a direct, nonsemantic mechanism for reproducing ML actions puts greater demands on the short-term/working memory system.

To our knowledge, so far only two studies have investigated indirectly the neural bases of imitation of complex MF and ML actions (Grezes, Costes, & Decety, 1998; Decety, Grezes, et al., 1997). Here we will refer only to the latter study because, although comparable in most aspects to the former, its design contains also the necessary baseline condition (i.e., perception of stationary hands). In Grezes et al. (1998), perception of both MF and ML actions with the aim to imitate was associated with activation of a common network of

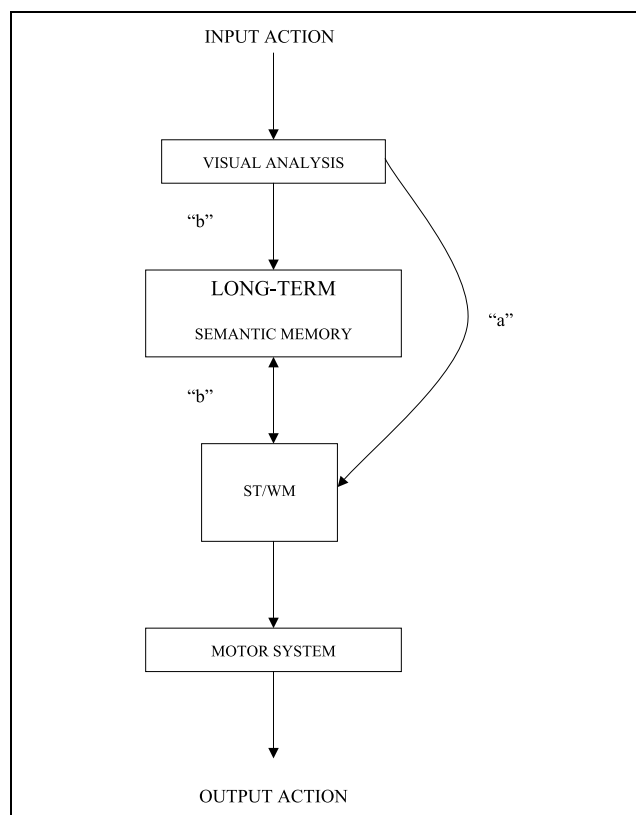


Figure 1. This flowchart reproduces simplified two-route model for action imitation. Following the visual analysis, known MF actions automatically activate the selection of the semantic, indirect mechanism ("b"). The direct mechanism is selected in order to imitate novel ML actions but also to reproduce both MF and ML actions presented intermingled ("a"). ST/WM = short-term/working memory.

regions in the dorsal pathway bilaterally extending to the dorsolateral premotor cortex and the right cerebellum. Additional activations were located in the SMA and in the orbito-frontal cortex bilaterally when subjects perceived MF actions. In contrast, during observation of MF and ML actions without any aim, activation of a common set of regions in the ventral and dorsal stream was found. In addition, MF actions enhanced the neural activity of the inferior frontal and fusiform gyri in the left hemisphere, and ML actions in the dorsal pathway bilaterally and the right cerebellum.

Further evidence for putative differential mechanisms supporting the imitation of MF and ML actions stems from clinical neuropsychology. It is well known that after left brain damage, patients with ideomotor apraxia (hereafter IMA) may be selectively impaired in imitating actions (Liepmann, 1905). Analogous with models of language production, Rothi, Ochipa, and Heilman (1991) postulated the existence of different neural mechanisms for imitating either MF or ML actions: the ML actions can be imitated using a direct (i.e., sublexical) route, whereas the lexical-semantic route can be selected to reproduce MF actions. Although the direct

route connects the visual analysis to the innervatory patterns, the semantic route comprises different processing stages, including the action input lexicon, the semantic system, and the action output lexicon, before accessing to the innervatory patterns (this stage is in common with the direct route).

Goldenberg and Hagmann (1997) described two apraxic patients, LK and EN, who showed an impairment in imitating ML but not MF acts. In addition, in both patients, the replication of hand positions on a manikin was defective too. Given the association of the two deficits (i.e., imitation on themselves and on a manikin), the authors argued that, besides a damage to the direct route, these two patients suffered from a faulty knowledge about the structure of the human body. Because lesions in the two patients overlapped in the inferior portion of the left angular gyrus (BA 39), the authors suggested that the lesion of this area was responsible for causing apraxia in both patients. In contrast, Bartolo, Cubelli, Della Sala, Drei, and Marchetti (2001, patient MF) reported a patient with a large left fronto-temporo-parietal lesion, who performed poorly on all tests of gesture production except for imitation of meaning-less actions.

According to the model depicted in Figure 1, the deficit in imitating ML actions (Goldenberg & Hagmann, 1997) could be caused by an interruption of the direct visuomotor mechanism that converts input into output actions directly (Rothi et al., 1991). On the other hand, the deficit in reproducing MF actions reported by Bartolo et al. (2001) was interpreted by the authors as due to a damage occurring along the semantic route. Why wasn't this patient using the direct mechanism for reproducing MF actions?

The patient described by Bartolo et al. (2001) was able to recognize the meaningful actions suggesting that the action input lexicon and the semantic system proper were spared. Recognizing the meaning of the presented actions selected the semantic route automatically; once the semantic route was selected, the patient could not switch from the semantic to the direct, spared route in order to reproduce the meaningful action; as a consequence, she made errors in imitating meaningful actions. Bartolo et al. argued that the patient's breakdown along the semantic route should occur *after* the semantic system, in accessing (or within) the action output lexicon. All these processing components (i.e., action input lexicon, semantic system, action output lexicon) belong to the semantic route and have no contact with the direct route.

Overall, these neuropsychological studies cannot help to identify the neural bases that support the imitation of MF and ML actions due to typically rather large lesion size, disconnection (or distance) effects, and associated neuropsychological deficits.

The model proposed by Rothi et al. (1991) is, however, helpful in suggesting possible different imitation

processes depending on the nature of the stimulus (i.e., MF or ML). Tessari and Rumiati (2004) argued that, besides the content of the stimulus, there are also other factors influencing imitation. They found that the composition of the experimental list (i.e., whether MF and ML actions are presented mixed or in blocks), the fact of knowing the composition of the list (i.e., knowing whether there will be mixed or blocked presentation of MF and ML actions), and the relative proportion of the two types of stimuli (MF and ML actions) in the list all influence the selection of the mechanisms that are used to imitate MF and ML actions. Importantly, when MF and ML actions were presented in separate blocks, healthy subjects imitated MF actions better than ML actions. In contrast, when presenting mixed MF and ML actions, subjects imitated MF and ML actions with the same accuracy. Tessari and Rumiati argued that in the blocked condition, MF actions are imitated using the fast semantic route, and ML actions are reproduced using the slower nonsemantic, direct route. In the mixed condition, however, subjects try to switch between the semantic and nonsemantic route at the beginning of the block but soon revert to the direct route for imitating both MF and ML actions as it allows the reproduction of both types of actions. Furthermore, the more ML movements there are in the stimulus list, the earlier the subjects tend to use the direct, nonsemantic strategy for the remaining stimuli (both MF and ML movements). Therefore, the selection of the imitation strategy highly correlates with the composition of the stimulus list.

Similarly to the study of Tessari and Rumiati (2004) with healthy subjects imitating under time pressure, studies with brain-damaged patients also failed to find an advantage in imitation of MF over ML actions when presented intermingled (Toraldo, Reverberi, & Rumiati, 2001; De Renzi, Motti, & Nichelli, 1980). It is plausible that the left-brain-damaged patients in Toraldo et al. (2001) and De Renzi et al. (1980) imitated MF and ML actions with the same accuracy because they applied the nonsemantic, direct mechanism that allows both types of action to be translated into a motor output.

The main aim of the present study was to investigate the neural mechanisms associated with imitation of MF and ML actions. The design specifically aimed at revealing parametric modulation of rCBF in the brain areas sustaining imitation of these two types of action. Based on the imaging studies reviewed above (Iacoboni et al., 1999; Grezès et al., 1998; Decety, Grezès, et al., 1997; Grafton et al., 1996; Rizzolatti, Fadiga, Matelli, et al., 1996), we expected the dorsal visuomotor stream to be activated predominantly when subjects imitated ML actions and the ventral visuoperceptual stream, plus a possible involvement of the dorsal visual pathway, when they imitated MF actions. These predictions were based on the assumption that imitation of ML actions can be supported by direct visuomotor transformation only (i.e., the nonsemantic, direct route),

whereas imitation of MF actions can rely on both the direct and the semantic routes from vision-to-action. Although the direct route might be located in the dorsal stream, the semantic route could be supported by the ventral pathway.

RESULTS

PET Imaging

The categorical comparison of all parametric conditions, that is, all conditions in which subjects *imitated* MF and/or ML actions, versus the condition in which subjects only *observed* MF and ML actions (*baseline*), revealed a neural network of areas known to support imitation of actions ($p < .05$, corrected): the primary sensorimotor cortex, the (ventral) premotor cortex, the SMA, the parieto-occipital junction, and the primary visual cortex. Furthermore, activations were observed in the left thalamus and insular cortex as well as in the right cerebellum (see Table 1).

A significant positive correlation ($p < .05$, corrected) of neural activity with the amount of MF movements was observed in the left inferior temporal cortex, namely, the left inferior temporal gyrus only (Table 2a, Figure 2). In contrast, a significant positive correlation with the amount of ML movements was observed in the right parieto-occipital junction only (Table 2b, Figure 3).

For categorical comparison of MF and ML conditions, the statistical threshold was reduced to $p < .001$, uncorrected, as the reduced number of observations

Table 1. Relative Increases in Brain Activity during *Imitation* of Either MF or ML Movements Compared to *Observation* of MF and ML Movements (i.e., All Experimental Conditions versus Baseline)

| Region | Side | x | y | z | t |
|-----------------------------|------|-----|-----|-----|------|
| Primary sensorimotor cortex | L | -32 | -24 | +68 | 28.0 |
| Supplementary motor area | L | -6 | -14 | +52 | 17.8 |
| Ventral premotor cortex | L | -58 | +2 | +34 | 7.2 |
| Primary visual cortex | | 0 | -76 | +16 | 7.4 |
| Parieto-occipital junction | L | -12 | -86 | +34 | 6.4 |
| | R | +14 | -84 | +38 | 5.9 |
| Insular cortex | L | -42 | +6 | +4 | 7.5 |
| Thalamus | L | -18 | -18 | +8 | 9.5 |
| Cerebellum | R | +14 | -54 | -16 | 18.9 |

$p < .05$ (corrected for multiple comparisons). Note that there is no significant activation of the occipito-temporal junction (MT/V5) in this comparison. For each region of activation, the coordinates in standard stereotactic MNI space are given referring to the maximally activated focus within an area of activation as indicated by the highest t value. x = distance (mm) to right (+) or left (-) of the midsagittal plane; y = distance anterior (+) or posterior (-) to vertical plane through the anterior commissure; z = distance above (+) or below (-) the intercommissural (AC-PC) plane.

Table 2. Brain Regions Whose Activity Correlated Significantly with the Type of Movement to be Imitated (i.e., the Ratio of MF and ML Movements)

| Region | Side | x | y | z | t |
|--|------|-----|-----|-----|-----|
| (a) Regions positively correlated with the amount of MF movements | | | | | |
| Inferior temporal gyrus | L | -56 | +2 | -30 | 5.0 |
| (b) Regions positively correlated with the amount of ML movements | | | | | |
| Parieto-occipital junction | R | +10 | -86 | +32 | 5.6 |

$p < .05$ (corrected for multiple comparisons). For further explanations, see Table 1.

available for this analysis also meant reduced sensitivity. The direct categorical comparison of meaningful (100% MF) relative to meaningless (0% MF) actions revealed ($p < .001$, uncorrected; extent threshold of 30 voxels) differential increases in neural activity associated with MF movements in the left inferior temporal gyrus, the left parahippocampal gyrus, and the left angular gyrus (see Table 3a and Figure 4).

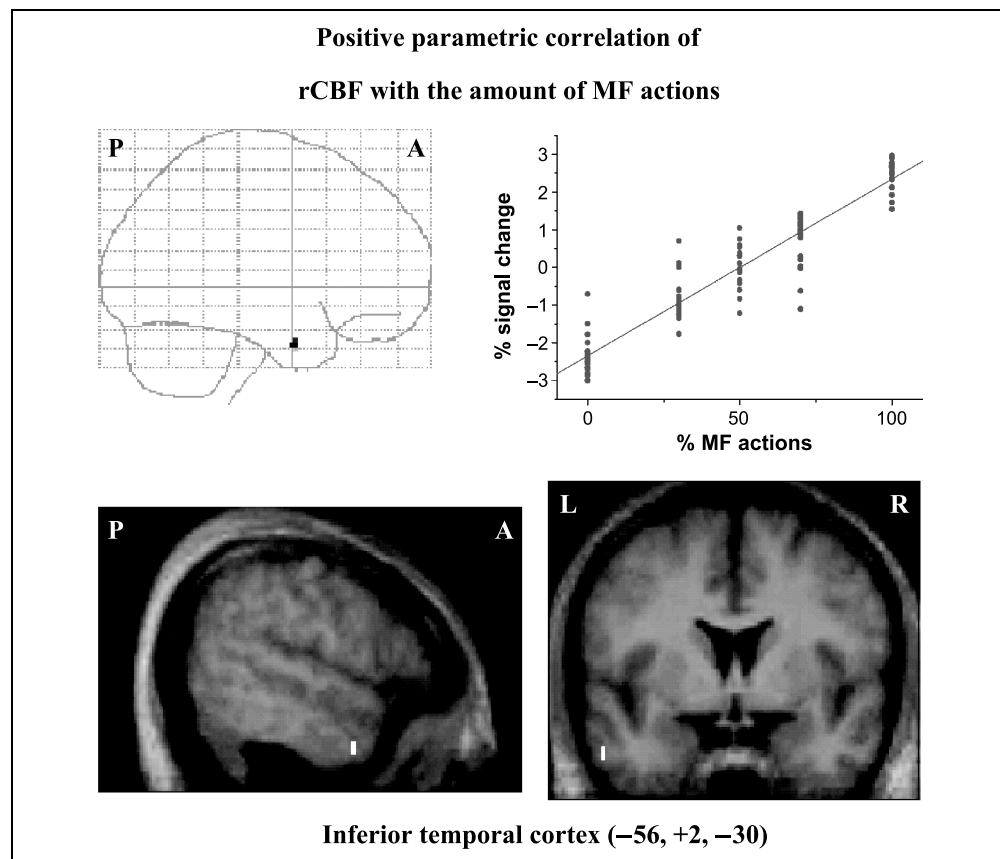
The reverse categorical comparison of meaningless (0% MF) relative to meaningful (100% MF) revealed ($p < .001$, uncorrected; extent threshold of 30 voxels) differential increases in neural activity associated with ML movements in the right parieto-occipital junction, in the superior parietal cortex bilaterally, and in the right occipito-temporal junction (MT, V5) (see Table 3b and Figure 5). An additional differential activation was observed in the left superior temporal gyrus.

Behavioral Results

As there was no significant difference between the scores of the two raters (all $\kappa > 0.7$ on Cohen's Kappa), the analyses reported below were carried out on the mean scores. A first analysis conducted on the overall correct imitation of MF and ML actions with Percentage as a factor (with five levels: MF 100%–ML 0%, MF 70%–ML 30%; MF 50%–ML 50%; MF 30%–ML 70%; MF 0%–ML 100%) revealed that imitation performance significantly improved as a function of the proportion of MF actions in the respective conditions [MF 100%–ML 0% = 89%; MF 70%–ML 30% = 87%; MF 50%–ML 50% = 82%; MF 30%–ML 70% = 81.6%; MF 0%–ML 100% = 79%, $F(4,36) = 2.68$, $p < .05$].

In a second analysis, the main effect of Percentage was tested separately for MF and ML actions. A significant main effect for MF but not for ML actions [$F(3,27) = 5.33$, $p < .05$, and $F(3,27) = .97$, $p > .05$, respectively], was found. This result indicates that the subjects' ability to imitate MF actions improved as a function of the number of MF actions to be imitated during each block of trials; in contrast, the subjects' ability to imitate ML

Figure 2. Activity in the left inferior temporal cortex positively correlates with the amount of MF actions to be imitated. In the upper right corner, the linear regression between the percentage of rCBF signal change in the left inferior temporal cortex (mean adjusted data for the 10 subjects; y-axis) and the amount of MF actions (for the five experimental conditions; x-axis) is shown ($y = 0.047 * x - 2.341, r = .945$). In the left upper corner, the sagittal $SPM_{(z)}$ map is shown as through-projection onto a representation of standard stereotactic space (Talairach & Tournoux, 1988). The lower row display shows the sagittal (left) and coronal (right) $SPM_{(z)}$ map superimposed upon the structural group mean MR image that had been spatially normalized into the same stereotactic space (Talairach & Tournoux, 1988). The level of the sagittal and coronal sections was selected to show the local maximum within the activated brain area. The exact coordinates of the local maximum within the area of activation and its t statistics are given in Table 2a. R = right; L = left; A = anterior; P = posterior.



actions did not vary across the experiment (see Figure 6), dependent upon the context.

A direct comparison between 100% MF and 100% ML conditions confirmed that subjects were more accurate when imitating MF actions [one-tailed paired t test with Bonferroni correction, $t(9) = 7.88, p < .001$; mean 100% MF = 89%, mean 100% ML = 79%; SD : MF = 8.72, ML = 9.13). Likewise, in the 100% MF condition, subjects performed significantly better than in the 50% MF and in 30% MF, but not compared to the 70% MF condition [one-tailed paired t test with Bonferroni correction, $t(9) = 4.54, p = .001, t(9) = 4.90, p = .001$, and $t(9) = .67, p > .05$, respectively]. No empirical differences were found when comparing imitation performance of ML actions across the different conditions (all comparisons $F < 1$; see Figure 6).

An analysis by items (MF and ML actions) was carried out to assess whether a learning effect had occurred during the experiment. This would correspond to an improvement of the subjects' accuracy for a given item across repetitions. In order to achieve this, the average slopes for all MF and ML actions across subjects were

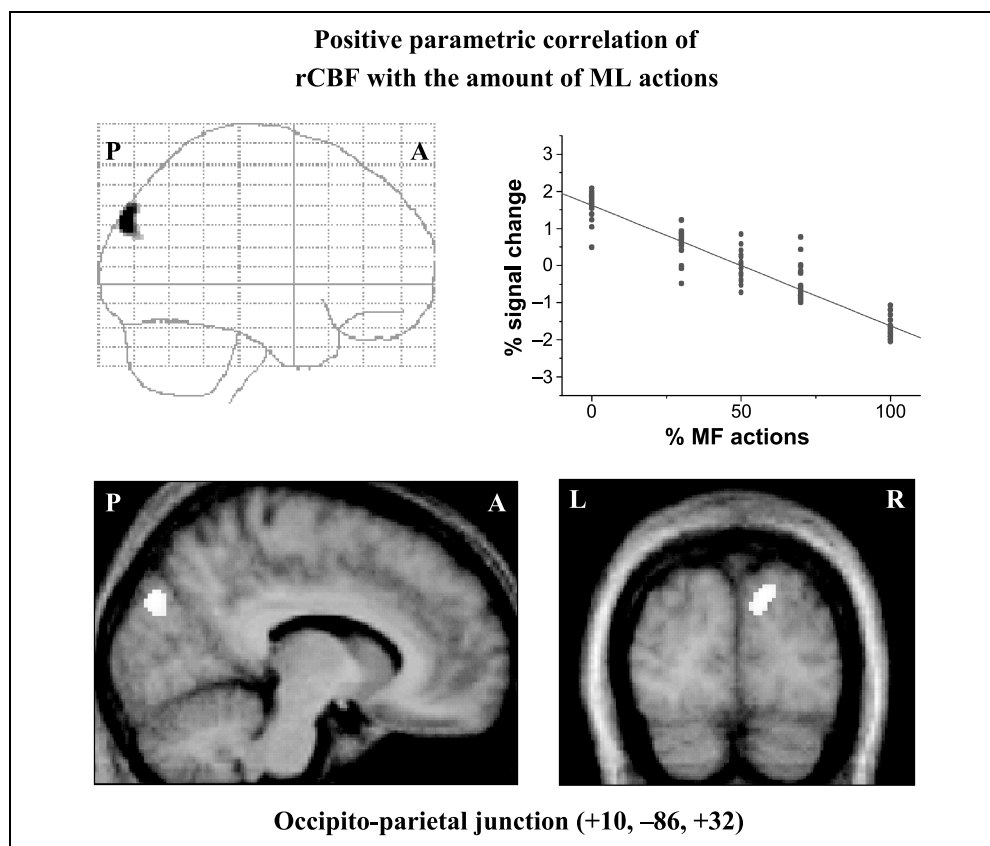
calculated and then compared to a nonincreasing function. None of the comparisons was found to be significant (all t test, $p > .05$).

DISCUSSION

The design of the present study was specifically aimed at revealing the parametric modulation of rCBF (as an index of neural activity in a brain area) related to imitation of either MF or ML actions.

Neuropsychological attempts to analyze the neural bases of action imitation have proven difficult because of typically rather large lesions, disconnection (or distance) effects, and additional deficits, for instance, impaired ability to pantomime the use of objects, apraxia of object use, and action and object agnosia (see also Marshall & Fink, 2003). In contrast, imaging studies of action imitation may shed light on the neural mechanisms subserving imitation. So far, however, functional imaging of action imitation has been limited to reproduction of different types of single finger movements (e.g., Koski, Wohlschläger, et al., 2002; Tanaka, Inui,

Figure 3. Activity in the right parieto-occipital junction positively correlates with the amount of ML actions to be imitated. In the upper right corner, the linear regression between the percentage of rCBF signal change in the right parieto-occipital junction (mean adjusted data for the 10 subjects; y-axis) and the amount of MF actions (for the five experimental conditions; x-axis) is shown ($y = -0.032 * x + 1.623$, $r = -.945$). In the left upper corner, the sagittal SPM_(z) map is shown as through-projection onto a representation of standard stereotactic space (Talairach & Tournoux, 1988). The lower row display shows the sagittal (left) and coronal (right) SPM_(z) map superimposed upon the structural group mean MR image, that had been spatially normalized into the same stereotactic space (Talairach & Tournoux, 1988). The level of the sagittal and coronal sections was selected to show the local maximum within the activated brain area. The exact coordinates of the local maximum within the area of activation and its *t* statistics are given in Table 2b. R = right; L = left; A = anterior; P = posterior.



Iwaki, Konishi, & Nakai, 2001; Iacoboni et al., 1999), and of movements necessary to manually explore simple 3-D objects (Decety, Chaminade, et al., 2002), or has not yet required subjects to actually imitate actions (with the exception of Rumiati et al., 2004). Instead, subjects were asked to observe actions with the intention to imitate those actions later (Grezes et al., 1998; Decety, Grezes, et al., 1997).

In our study, the observation of differentially modulated brain areas depending upon whether more MF or ML actions were imitated strongly supports the hypothesized task-dependent selection of differential neural mechanisms for imitation of either MF and ML actions, as suggested by behavioral studies with healthy subjects (Tessari & Rumiati, 2004; Rumiati & Tessari, 2002) and brain-damaged patients (Bartolo et al., 2001; Goldenberg & Hagmann, 1997). We predicted differential activations predominantly in the dorsal stream, the more ML actions were imitated. In this situation, subjects need to rely on a direct, nonsemantic mechanism (see Figure 1), which permits a direct translation of any action seen into a motor output by visuospatial and

visuomotor transformations known to rely on parieto-occipital and parietal areas. In contrast, when subjects imitated more MF actions, the predicted differential activations were in the ventral stream, as MF actions are likely to involve semantic processing.

Overall, our results are in good agreement with those models of vision for action which predict a role of the ventral stream (as well as of the inferior parietal cortex, as in the view of Glover, 2004) in the production of acquired but not novel actions (see Rossetti, Pisella, & Vighetto, 2003; Jeannerod, 1994).

Neural Bases of Imitation of MF and ML Actions

The positive correlation (Table 2, and Figures 2 and 3) of rCBF as an index of regional neural activity with the increasing amount of MF actions in the left inferior temporal gyrus indicates that this area is specifically involved in the imitation of MF actions. On the other hand, the neural activity centered upon the right parieto-occipital junction (positive correlation of rCBF with increasing amount of ML actions) was specifically influ-

Table 3. Relative Increases in Brain Activity during Imitation of MF and ML Movements

| Region | Side | x | y | z | t |
|---|------|-----|-----|-----|-----|
| (a) Main effect of MF movements (100% MF > 0% MF) | | | | | |
| Inferior temporal gyrus | L | -56 | +2 | -30 | 4.3 |
| Angular gyrus | L | -42 | -62 | +34 | 3.8 |
| Parahippocampal gyrus | L | -24 | -18 | -32 | 3.8 |
| (b) Main effect of ML movements (0% MF > 100% MF) | | | | | |
| Parieto-occipital junction | R | +12 | -86 | +34 | 5.1 |
| Superior parietal cortex | L | -34 | -50 | +66 | 4.3 |
| | L | -22 | -66 | +60 | 3.4 |
| Superior parietal cortex | R | +14 | -60 | +72 | 4.2 |
| Occipito-temporal junction (MT/V5) | R | +48 | -62 | -4 | 3.8 |
| Superior temporal gyrus | L | -60 | -38 | +18 | 3.7 |

$p < .001$ (uncorrected, extent threshold of 30 voxels). Brain regions showing relative rCBF increases associated with each comparison of interest. 100% MF: experimental condition 1 with only meaningful movements as stimuli for imitation. 0% MF: experimental condition 5 with only meaningless movements as stimuli for imitation. For further explanations, see Table 1.

enced by imitation of ML actions. These findings are consistent with the view that the direct and semantic mechanisms involved in imitation rely on differential neural mechanisms.

The direct categorical comparison of MF actions relative to ML actions was associated with differential increases in neural activity in three regions of the left hemisphere, two of which belong to the ventral stream (i.e., the inferior temporal gyrus and the left parahippocampal gyrus), the other one (i.e., the left angular gyrus) to the ventral branch of the dorsal stream as suggested by Milner and Goodale (1995) and more recently by Rizzolatti and Matelli (2003). These more extended activations, too, are in good agreement with the hypothesis that MF actions preferentially draw upon the ventral stream (i.e., the semantic route), but may also involve the dorsal stream that enables individuals to reproduce all sorts of movements (i.e., the direct route).

In contrast, the reverse categorical comparison of ML relative to MF actions indicated that imitation of ML actions was associated with differential increases in neural activity in the right parieto-occipital junction, the superior parietal cortex bilaterally, the right occipito-temporal junction (MT, V5), and the left superior temporal gyrus. Regions sustaining action imitation in our study are broadly consistent with the activations observed by Grèzes et al. (1998) when subjects perceived actions with the aim to later imitate them, irrespective of stimulus content. If one considers ML and MF actions in terms of unfamiliar and familiar actions, respectively,

then another interesting comparison can be made with the results from a subsequent study of Grèzes, Costes, and Decety (1999). The authors required subjects to observe learned and unknown ML actions with or without the purpose of imitating them, in addition to observing stationary hands as a control (*baseline*). They found that, irrespective of the subjects' intentions, some brain areas were modulated by the degree of visuomotor learning the subjects underwent. More specifically, as the ML actions became familiar to the subjects, a reduction of neural activity in motion-related areas within the dorsal stream, together with an activity increase within the inferior parietal cortex and the frontopolar cortex, was observed.

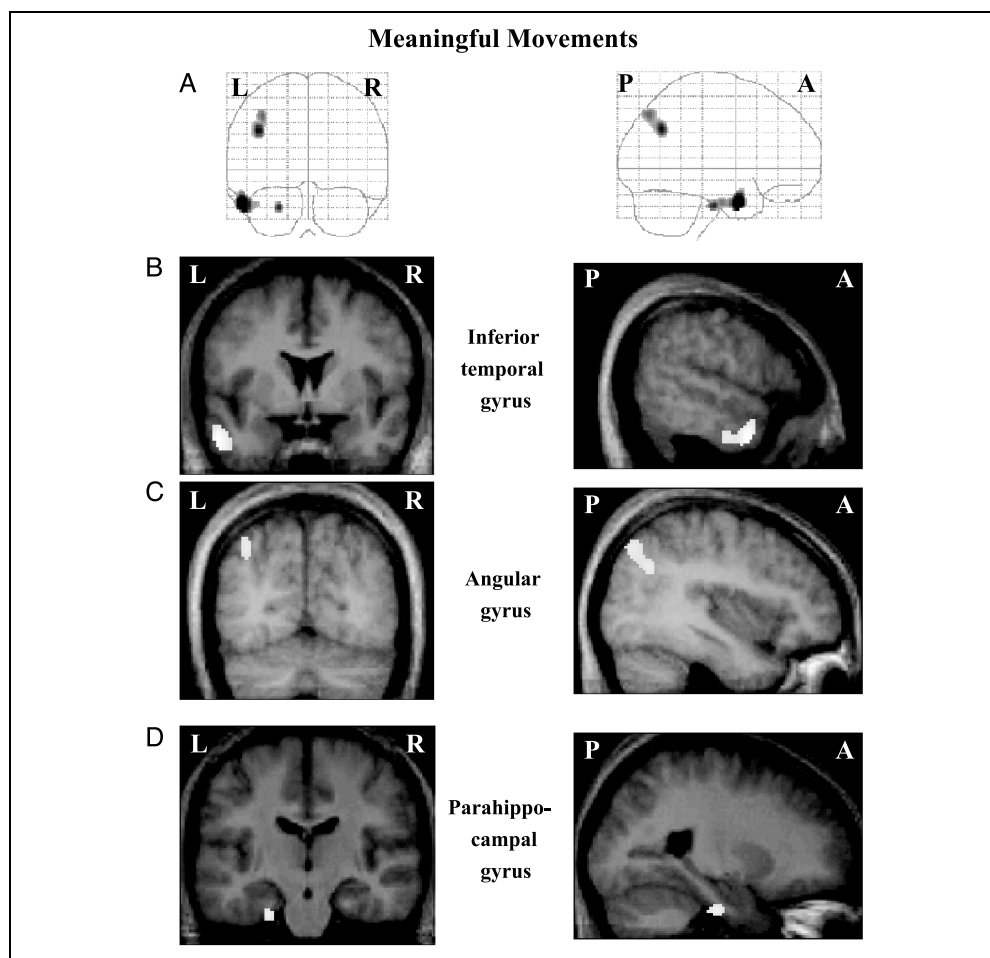
Our findings, however, are more difficult to reconcile with neuropsychological data reported by Goldenberg and Hagmann (1997). They described two patients whose lesions in the left hemisphere overlapped in the angular gyrus (BA 39), and showed a deficit in imitating ML movements. This contrasts with our observation in the direct categorical comparison of MF actions relative to ML actions where the angular gyrus was activated.

It is, however, important to keep in mind that the angular gyrus is a large region which is unlikely to subservise one function or psychological process only. Functional imaging has revealed that the human inferior parietal cortex, of which the angular gyrus is a part consists—as in the macaque—of a mosaic of functionally different subareas (e.g., anterior intraparietal area [AIP], see Grefkes et al., 2002, and ventral intraparietal area [VIP], see Bremner et al., 2001). Therefore, it is conceivable that these subareas within the human inferior parietal cortex may be involved in different cognitive processes during action imitation, so that the rather large lesions in neurological patients, with their additional distance effects, may lead to other deficit patterns than the fine-scaled imaging data would predict. To clarify this issue, more neuropsychological studies in which the patients' lesions are carefully reconstructed and normalized to a common template are needed to compare the neuropsychological deficits due to lesions with the activation patterns from imaging studies. Even if larger numbers of neuropsychological lesion data were available, one should keep in mind, however, that “nothing has so obscured the problem of cerebral localization as correlations between grossly localized pathology and manifest symptoms on the one hand and localization of basic psychological functions” (Von Monakow, 1911).

Imitation versus Observation

The comparison of all parametric conditions, that is, all conditions in which subjects *imitated* MF and/or ML actions, versus the condition in which subjects only *observed* MF and ML actions (*baseline*), revealed activations in the expected motor areas (Fink, Frackowiak,

Figure 4. Areas with relative increases of rCBF during the imitation of MF actions. In the upper row (A), the coronal (left) and sagittal (right) SPM_(z) maps are shown as through-projection onto representations of standard stereotactic space (Talairach & Tournoux, 1988). The other rows (B to D) display the coronal (left) and sagittal (right) SPM_(z) maps superimposed upon the structural group mean MR image that had been spatially normalized into the same stereotactic space (Talairach & Tournoux, 1988). The level of the sagittal and coronal sections was selected to show the local maxima within the activated brain areas: left inferior temporal gyrus (B), left angular gyrus (C), and left parahippocampal gyrus (D). The exact coordinates of the local maxima within the areas of activation and their *t* statistics are given in Table 3a. R = right; L = left; A = anterior; P = posterior.



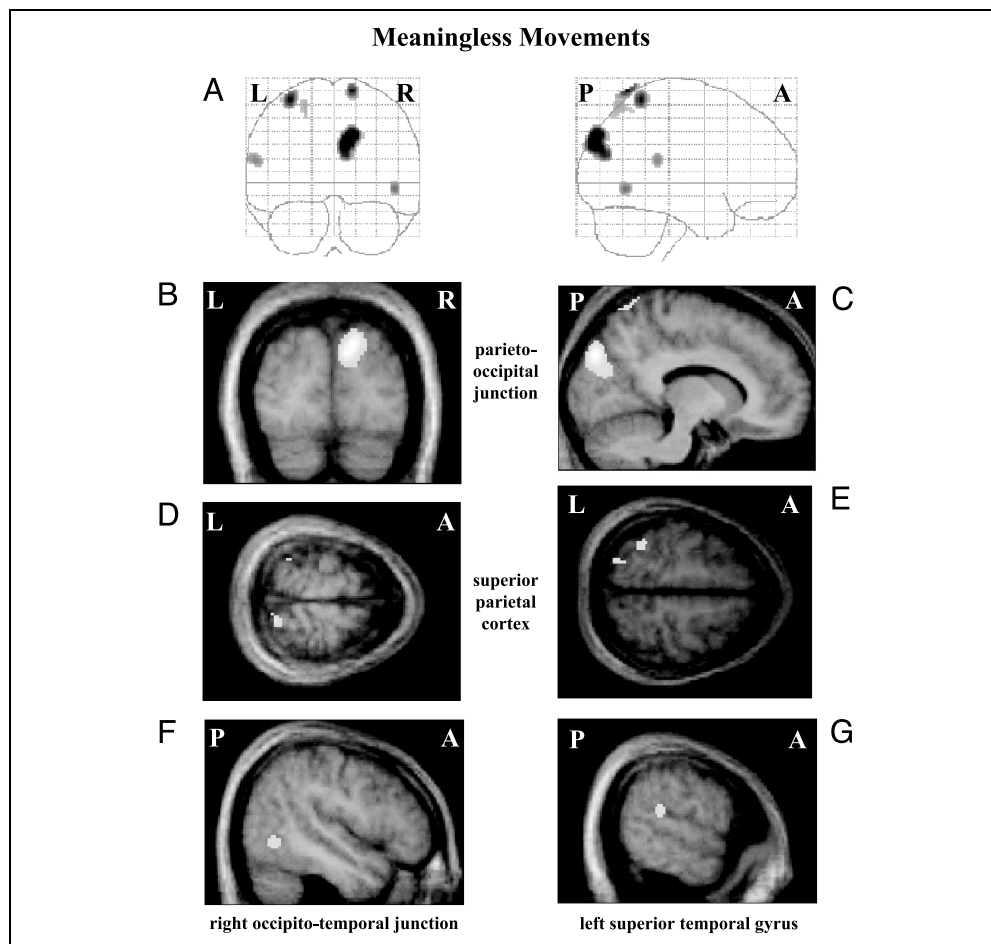
Pietrzyk, & Passingham, 1997): left primary sensorimotor cortex, left premotor cortex, left SMA, the primary visual cortex, as well as an bilateral activation of the parieto-occipital junction. Additional activations were found in the right cerebellum, the left thalamus, and the left insular cortex (see Table 1). This network of regions supporting action imitation relative to observation of both MF and ML actions is also comparable with what was previously described in two studies by Grèzes et al. (1998, 1999). In the first study (Grèzes et al., 1998), subtracting the baseline condition (i.e., static hands) from the four conditions of interest (observation of MF actions with or without the intention to imitate; observation of MF and ML actions without any aim) revealed neural activations in several areas, irrespective of either the nature of the stimuli (MF or ML actions) or the purpose of perception (with or without the intention to imitate): These areas included V5 (held to reflect hand movement analysis), the superior occipital gyrus, and the parietal cortex (considered to be related to the spatial analysis of bodily actions). Consistently, in the second study (Grèzes et al., 1999), a common network involving the dorsal stream was engaged in all conditions when compared with stationary hands (baseline condition).

The similarities between the activations found in the studies by Grèzes et al. (1998, 1999) and those reported in our study suggest that motor representations are implicated not only in action execution but also in action perception (Grèzes & Decety, 2001). Furthermore, the network of brain regions underlying perception of actions (Grèzes et al., 1998, 1999) and imitation (this study) overlaps with the network of brain areas found to be activated when subjects performed mental simulation of actions (e.g., Decety, Kawashima, Gulyas, & Roland, 1992). This suggests that we do use our motor knowledge to understand actions performed by others (Blakemore & Decety, 2001). This view is also in keeping with the role that the human mirror neuron system is suggested to play in imitation (see Buccino, Binkofski, & Riggio, 2004, for a recent review) that includes visual processing of the observed movements as well as motor simulation.

Imitation of MF and ML Actions

Subjects were more accurate in imitating MF than ML actions when they were presented in blocks (100% MF vs. 0% MF). As a corollary finding, the more MF

Figure 5. Areas with relative increases of rCBF during the imitation of ML actions. In the upper row (A), the coronal (left) and sagittal (right) $SPM_{\{z\}}$ maps are shown as through-projection onto representations of standard stereotactic space (Talairach & Tournoux, 1988). The other displays show the respective coronal (B), sagittal (C, F, G), and transverse (D, E) $SPM_{\{z\}}$ maps superimposed upon the structural group mean MR image, that had been spatially normalized into the same stereotactic space (Talairach & Tournoux, 1988). The level of the coronal, sagittal, and transverse sections was selected to show the local maxima within the activated brain areas: right parieto-occipital junction (B), right parieto-occipital junction and right superior parietal cortex (C), right superior parietal cortex (D), two activation foci in the left superior parietal cortex (E), right occipito-temporal junction (F), and left superior temporal gyrus (G). The exact coordinates of the local maxima within the areas of activation and their t statistics are given in Table 3b. R = right; L = left; A = anterior; P = posterior.



actions there were in a block of trials, the better the subjects imitated them. Note, however, subjects' imitation of either MF or ML actions did not improve across repetitions. These behavioral findings are consistent

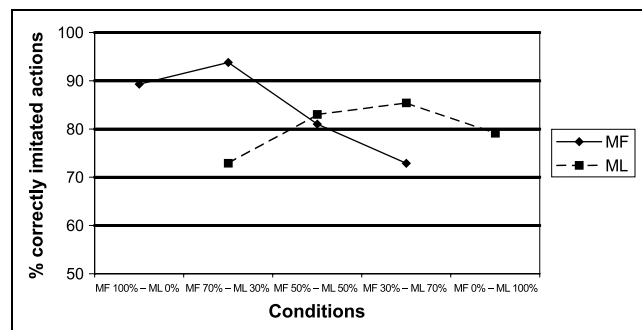


Figure 6. The percentages of subjects' correct imitative responses are plotted separately for MF and ML actions. On the x -axis, the five different conditions correspond to the differences in relative proportions of MF and ML actions (1: MF 100%–ML 0%; 2: MF 70%–ML 30%; 3: MF 50%–ML 50%; 4: MF 30%–ML 70%; 5: MF 0%–ML 100%). For each subject, each value was averaged across two repeats.

with the activations revealed by the parametric design. The key regions subserving imitation of MF and ML actions, respectively, are the left inferior temporal gyrus and the right parieto-occipital junction. These were the only areas where a significant positive correlation of neural activity with the amount of either MF or ML actions was observed. It is likely that these two regions play different roles according to the goal at hand. The left inferior temporal gyrus seems to be involved in action encoding and in attributing the semantic value of an action in the context of imitation. In contrast, the right parieto-occipital junction may act as a visuospatial short-term memory whose role becomes more critical when subjects are required to imitate actions for which no predefined meaning (hence, motor schema) exists.

Conclusions

The present study indicates that different aspects of action imitation rely not only on a common network of brain regions, as implied by other neuroimaging

studies (Koski, Wohlschläger, et al., 2002; Decety, Chaminade, et al., 2002; Tanaka et al., 2001; Iacoboni et al., 1999), but also on specific differential neural mechanisms selectively activated depending upon whether the actions to imitate carry a meaning or not (see also Grezès et al., 1998; Decety, Grezès, et al., 1997). Both our behavioral and functional imaging data also suggest that during action imitation we do not simply map the action seen directly into a motor output, as a restrictive interpretation of the direct mapping hypothesis would predict. Instead, we rely on differential neural mechanisms as a function of the content of actions and of the context in which they appear.

METHODS

Subjects

Ten healthy right-handed male subjects (mean age = 26 years, $SD = 1.9$), with no history of neurological or psychiatric illness, gave informed consent. We studied only male volunteers in order to avoid the normal variation in brain size and shape between the sexes. Handedness was assessed with the Edinburgh Inventory Test (Oldfield, 1971). The study was approved by the ethics committee of the University Hospital of the RWTH Aachen, Germany. Permission to administer radioactivity was obtained from the responsible federal authorities in Germany.

Experimental Design

A parametric design was adopted where the relation of MF to ML actions in the list of stimuli used as triggers for imitation in a given block of trials was varied. The proportion of MF and ML actions had five levels, which constituted the five experimental conditions of interest (i.e., imitation) (C1: 100% MF–0% ML; C2: 70% MF–30% ML; C3: 50% MF–50% ML; C4: 30% MF–70% ML; and C5: 0% MF–100% ML). Subjects were informed that they were going to be presented with MF and ML actions, but they were not given the actual composition of the lists in a given block of trials. In all conditions, subjects observed the actions shown on the screen and imitated them right away with their right arm. In the baseline condition (B), intermingled MF and ML actions (50% MF and 50% ML) had to be observed only (without the requirement of subsequent imitation). All five imitation conditions (C1, C2, C3, C4, and C5) and the baseline condition (B) were repeated twice per subject in a counterbalanced order, giving a total of 120 observations (i.e., PET rCBF measurements were performed, 12 rCBF scans per subject, 10 subjects). The order of conditions was counterbalanced within and across subjects. For all imitation conditions, task performance was recorded with a video camera during PET scanning and later scored independently

by two experienced raters who were not aware of the aims of the study and scored subjects' performance in a different order from that which was originally performed by the subjects during scanning. Raters, who studied the list of stimuli prior to the scoring, viewed only the imitated actions and were also not aware of the composition of the list (i.e., the ratio of MF and ML actions in the list). An action was scored as either correct or incorrect.

Stimuli and Procedure

Two sets of 30 MF and 30 ML actions were used to create the subsets of stimuli to be presented in the six conditions of the study. Thus, in the conditions other than 50% MF and 50% ML (C3 and B), some actions (in the 70%–30% conditions) or all (in the 100% conditions) were presented more than once. MF actions were pantomimes of use of objects such as hammering or writing. All pantomimes required the involvement of only one limb and contained both distal (i.e., hand) and proximal (i.e., arm) movement components. ML actions were derived from MF actions, in that they involved about the same muscles but were performed in a different plane or axis. The actions shown as stimuli were performed by a model using the left arm/hand. This procedure was chosen based on the evidence that humans have a preference for specular and not anatomical imitation. Thus, when the actor moves the left hand, the imitator has a preference to move the right hand (see Koski, Iacoboni, Dubeau, Woods, & Mazziotta, 2003; Bekkering et al., 2000). All the actions obtained by this procedure were video-recorded and then presented on a PC monitor placed in front of the participants at a distance of 0.7 m (eye-to-monitor distance).

Measurements of rCBF were taken using an ECAT HR+ PET scanner (CTI Siemens, Germany) and ^{15}O -butanol using standard technology and procedures previously described in detail (see e.g., Weiss, Marshall, Zilles, & Fink, 2003; Weiss et al., 2000).

During the rCBF measurements, subjects viewed first a black fixation cross in the center of a white screen for 15 sec, followed by the sequence of trials lasting 90 sec. Each action was presented for 1 sec with an interstimulus interval (ISI) of 0.5 sec, (i.e., 60 actions were shown in a block of trials). Halfway through the ISI (i.e., after 0.25 sec), a beep went off to inform the subject that the following trial was about to start. All actions performed by the subjects were considered for the subsequent scoring.

Prior to the experiment proper, eight healthy subjects, who did not take part in the PET experiment, were required to perform the imitation task in experimental conditions comparable to those used in the scanner. This was done in order to ascertain whether the laying position allowed the subjects to imitate the pantomimes within the time window used in the original behavioral

study by Tessari and Rumiati (2004). As their accuracy was similar to that of subjects in the study of Tessari and Rumiati, it was decided that the same timing and procedure be maintained also for the PET study.

Imaging Processing and Statistical Analysis

Following standard image preprocessing (including image realignment, image normalization into standard stereotactic space, and smoothing), statistical analyses were performed using SPM99 (www.fil.ion.ucl.ac.uk/spm). For each pixel, across all subjects and all scans, the mean relative rCBF values were calculated separately for each of the main effects. Comparisons of the means were made using the *t* statistic and thereafter transformed into normally distributed *Z* statistics. The resulting set of *Z* values constituted a statistical parametric map (SPM_{Z} map). For the contrasts of interest, the significance of these statistical parametric maps was assessed by comparing the expected and observed distribution of the *t* statistic under the null hypothesis of no differential activation effect on rCBF. The level of significance applied for the respective analyses is stated in the Results section.

For all statistical comparisons of interest, the stereotactic coordinates of the pixels of local maximum significant rCBF changes within areas of significant relative rCBF change associated with the specific comparisons were determined. The anatomical localization of these local maxima was assessed by reference to a standard stereotactic atlas (Talairach & Tournoux, 1988). Additional validation of this method of localization was obtained after superimposition of the SPM_{Z} maps on the group mean magnetic resonance (MR) image calculated after each individual's MR image had been stereotactically transformed into the same standard stereotactic space.

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REFERENCES

Bartolo, A., Cubelli, R., Della Sala, S., Drei, S., & Marchetti, C. (2001). Double dissociation between meaningful and meaningless gesture production in apraxia. *Cortex*, *37*, 696–699.

Bekkering, H., Wohlschäger, A., & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *Quarterly Journal of Experimental Psychology*, *53A*, 153–164.

Blakemore, S. J., & Decety, J. (2001). From the perception of action to the understanding of intention. *Nature Reviews Neuroscience*, *2*, 561–567.

Bremmer, F., Schlack, A., Shah, N. J., Zafiris, O., Kubischik, M., Hoffmann, K., Zilles, K., & Fink, G. R. (2001). Polymodal motion processing in posterior parietal and premotor cortex: A human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron*, *29*, 287–296.

Buccino, G., Binkofski, F., & Riggio, L. (2004). The mirror neuron system and action recognition. *Brain and Language*, *2*, 370–376.

De Renzi, E., Motti, F., & Nichelli, P. (1980). Imitating gestures: A quantitative approach to ideomotor apraxia. *Archives of Neurology*, *37*, 6–10.

Decety, J., Chaminade, T., Grèzes, J., & Meltzoff, A. N. (2002). A PET exploration of the neural mechanisms involved in reciprocal imitation. *Neuroimage*, *15*, 265–272.

Decety, J., Grèzes, J., Costes, M., 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.

Decety, J., Kawashima, R., Gulyas, B., & Roland, P. E. (1992). Preparation for reaching: A PET study of the participating structure in the human brain. *NeuroReport*, *3*, 761–764.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, *91*, 176–180.

Fink, G. R., Frackowiak, R. S., Pietrzyk, U., & Passingham, R. E. (1997). Multiple nonprimary motor areas in the human cortex. *Journal of Neurophysiology*, *77*, 2164–2174.

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

Glover, S. (2004). Separate visual representations in the planning of control of action. *Behavioral Brain Sciences*, *27*, 3–29.

Goldenberg, G., & Hagmann, S. (1997). Tool use and mechanical problem solving in apraxia. *Neuropsychologia*, *36*, 581–598.

Grafton, S. T., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Location of grasping representation in humans by positron emission tomography: 2. Observation compared to imagination. *Experimental Brain Research*, *112*, 103–111.

Grefkes, C., Weiss, P. H., Zilles, K., & Fink, G. R. (2002). Crossmodal processing of object features in human anterior intraparietal cortex: An fMRI study implies equivalencies between humans and monkeys. *Neuron*, *35*, 173–184.

Grèzes, J., Costes, N., & Decety, J. (1998). Top-down effect of strategy on the perception of human biological motion: A PET investigation. *Cognitive Neuropsychology*, *15*, 553–582.

Grèzes, J., Costes, N., & Decety, J. (1999). The effects of learning and intention on the neural network involved in the perception of meaningless actions. *Brain*, *122*, 1875–1887.

Grèzes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping*, *12*, 1–19.

Iacoboni, M., Wood, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, *286*, 2526–2528.

Jeannerod, M. (1994). The representing brain. Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, *17*, 187–245.

- Koski, L., Iacoboni, M., Dubeau, M., Woods, R. P., & Mazziotta, J. C. (2003). Modulation of cortical activity during different imitative behaviors. *Journal of Neurophysiology*, *89*, 460–471.
- Koski, L., Wohlschläger, A., Bekkering, H., Woods, R. P., Dubeau, M., Mazziotta, J. C., & Iacoboni, M. (2002). Modulation of motor and premotor activity during imitation of target-directed actions. *Cerebral Cortex*, *12*, 847–855.
- Krams, M., Rushworth, M. F. S., Deiber, M.-P. Frackowiak, R. S. J. & Passingham, R. E. (1998). The preparation, execution and suppression of copied movements in the human brain. *Experimental Brain Research*, *120*, 386–398.
- Liepmann, H. (1905). Die linke Hemisphere und das Handeln. *Münchener medizinische Wochenschrift*, *49*, 2322–2326, 2375–2378.
- Marshall, J. C., & Fink, G. R. (2003). Cerebral localization: Then and now. *Neuroimage*, *20*, S2–S7.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.
- Oldfield, E. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, *3*, 131–141.
- Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D., & Fazio, G. (1996). Localization of grasp representation in humans by PET: Observation versus execution. *Experimental Brain Research*, *111*, 246–252.
- Rizzolatti, G., & Matelli, M. (2003). Two different streams from the dorsal visual system: Anatomy and functions. *Experimental Brain Research*, *153*, 146–157.
- Rossetti, Y., Pisella, L., & Vighetto, A. (2003). Optic ataxia revisited: Visually guided action versus immediate visuomotor control. *Experimental Brain Research*, *153*, 171–179.
- Rothi, L. J. G., Ochipa, C., & Heilman, K. M. (1991). A cognitive neuropsychological model of limb praxis. *Cognitive Neuropsychology*, *8*, 443–458.
- Rumiati, R. I., & Tessari, A. (2002). Imitation of novel and well-known actions: The role of short-term memory. *Experimental Brain Research*, *142*, 425–433.
- Rumiati, R. I., Weiss, P. H., Shallice, T., Ottoboni, G., Noth, J., Zilles, K., & Fink, G. R. (2004). Neural basis of pantomiming the use of visually presented objects. *Neuroimage*, *21*, 1224–1231.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. Stuttgart: Thieme.
- Tanaka, S., Inui, T., Iwaki, S., Konishi, J., & Nakai, T. (2001). Neural substrates involved in imitating finger configurations: A fMRI study. *NeuroReport*, *12*, 1171–1174.
- Tessari, A., & Rumiati, R. I. (2004). The strategic control of multiple-routes in imitation of actions. *Journal of Experimental Psychology: Human Perception and Performance*, *30*, 1107–1116.
- Torraldo, A., Reverberi, C., & Rumiati, R. I. (2001). Critical dimensions affecting imitation performance of patients with ideomotor apraxia. *Cortex*, *37*, 737–740.
- von Monakow, C. (1911). Die Lokalisation im Grosshirn. *Journal of Psychology and Neurology*, *17*, 185–200.
- Weiss, P. H., Marshall, J. C., Wunderlich, G., Tellmann, L., Halligan, P. W., Freund, H. J., Zilles, K., & Fink, G. R. (2000). Neural consequences of acting in near versus far space: A physiological basis for clinical dissociations. *Brain*, *123*, 2531–2541.
- Weiss, P. H., Marshall, J. C., Zilles, K., & Fink, G. R. (2003). Are action and perception in near and far space additive or interactive factors? *Neuroimage*, *18*, 837–846.
- Wohlschläger, A., & Bekkering, H. (2002). Is human imitation based on a mirror-neuron system? Some behavioural evidence. *Experimental Brain Research*, *143*, 335–341.
- Wohlschläger, A., Gattis, M., & Bekkering, H. (2003). Action generation and action perception in imitation: An instantiation of the ideomotor principle. *Philosophical Transactions of the Royal Society of London, Series B, Biological Science*, *358*, 501–519.