

Neural Circuits Underlying Imitation Learning of Hand Actions: An Event-Related fMRI Study

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Summary

The neural bases of imitation learning are virtually unknown. In the present study, we addressed this issue using an event-related fMRI paradigm. Musically naive participants were scanned during four events: (1) observation of guitar chords played by a guitarist, (2) a pause following model observation, (3) execution of the observed chords, and (4) rest. The results showed that the basic circuit underlying imitation learning consists of the inferior parietal lobule and the posterior part of the inferior frontal gyrus plus the adjacent premotor cortex (mirror neuron circuit). This circuit, known to be involved in action understanding, starts to be active during the observation of the guitar chords. During pause, the middle frontal gyrus (area 46) plus structures involved in motor preparation (dorsal premotor cortex, superior parietal lobule, rostral mesial areas) also become active. Given the functional properties of area 46, a model of imitation learning is proposed based on interactions between this area and the mirror neuron system.

Introduction

Imitation is the capacity of individuals to learn to do an action from seeing it done (Thorndike, 1898; see Meltzoff and Prinz, 2002). Imitation implies *learning* and requires a *transformation* of a seen action into an ideally identical motor action done by the observer.

The neural mechanisms subserving imitation learning are largely unknown. Insight, however, into the possible

mechanisms underlying them comes from the discovery, in the monkey, of a particular type of neuron that discharges both when individuals perform a specific goal-directed action and when they observe another individual doing a similar action (“mirror neurons;” Gallese et al., 1996; Rizzolatti et al., 1996a). In the monkey, mirror neurons are found in the premotor area F5 and in the inferior parietal lobule (see Rizzolatti et al., 2001).

A series of electroencephalographic (EEG), magnetoencephalographic (MEG), transcranial magnetic stimulation (TMS), and brain imaging studies (e.g., Fadiga et al., 1995; Grafton et al., 1996; Rizzolatti et al., 1996b; Decety et al., 1997; Grèzes et al., 1998, 2003; Hari et al., 1998; Cochin et al., 1999; Nishitani and Hari, 2000, 2002; Strafella and Paus, 2000; Gangitano et al., 2001; Manthey et al., 2003; Johnson-Frey et al., 2003; Buccino et al., 2004) showed that a mirror neuron system exists also in humans. As in the monkey, two key regions form it: the caudal part of the inferior frontal gyrus (IFG) and the adjacent premotor cortex and the rostral part of the inferior parietal lobule (see Rizzolatti et al., 2001).

Although the human mirror neuron system is similar to that of the monkey in many respects, it has certain properties that are lacking or are poorly developed in the monkey. It is activated by the observation of intransitive actions (not only by goal-directed actions as in the monkey) (e.g., Fadiga et al., 1995; Iacoboni et al., 1999; Maeda et al., 2002) and by action pantomimes (Grèzes et al., 1998, 2003; Buccino et al., 2001), and it appears to code the time course of the observed action (Gangitano et al., 2001). It is plausible that the highly developed capacity of humans, in contrast to nonhuman primates (see Visalberghi and Fragaszy, 2001), to learn by imitation may be accounted for, at least in part, by the evolution of these properties.

What is the role of mirror neurons in imitation? Mirror neurons “resonate” in response to the elementary motor acts (e.g., finger lifting, precision grip) that form the observed action. It has been postulated that, through this mechanism, an observed action is subdivided into its elementary components and coded motorically. When the action to be imitated corresponds to an elementary act already present in the mirror neuron system, this act can be immediately forwarded to other structures and replicated. In this type of imitation, no actual learning is involved. When imitation, however, requires the learning of a novel motor pattern or a novel motor sequence, a further mechanism is required. It has been suggested that this learning mechanism consists in a recombination of the “resonated” motor acts into a new motor pattern or a new motor sequence (Byrne, 2002; Rizzolatti, 2003).

There is strong evidence that the mirror neuron system plays a fundamental role in immediate imitation of a motor act already present in the observer’s repertoire. Using functional magnetic resonance imaging (fMRI), Iacoboni et al. (1999) showed that the pars opercularis of IFG, one of the key regions of the mirror neuron system, is activated more strongly in the case of an imitative motor act (finger lifting) than when the same motor act

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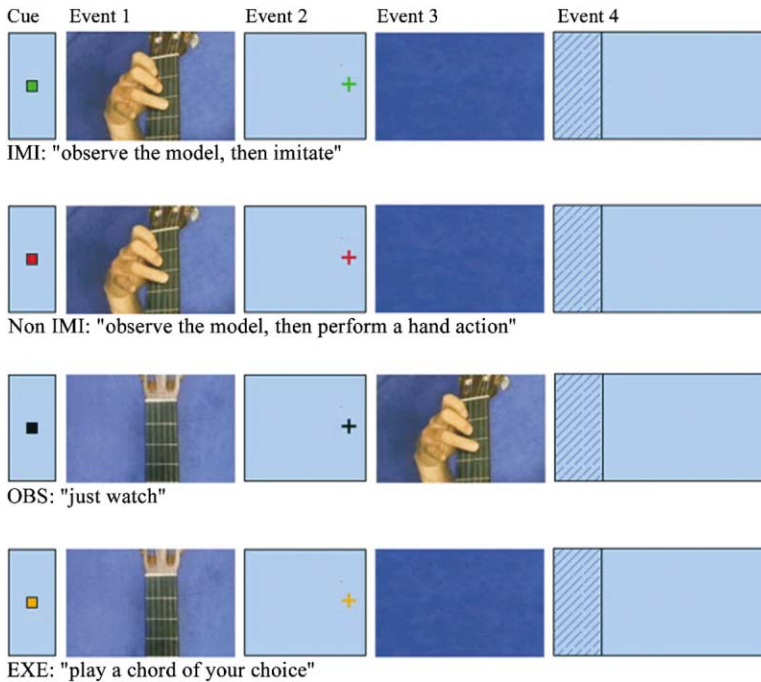


Figure 1. The Events Forming the Four Experimental Conditions IMI, Non-IMI, OBS, and EXE Are Graphically Illustrated

Each condition began with the presentation of a cue (a square) of different color according to the experimental condition. The purpose was to prompt participants on the task to perform. Subsequently, the events illustrated occurred one after the other. In each condition, Event 3 was preceded by the appearance of a cross of the same color of the square. The cross was presented at the end of Event 2. Its disappearance from the screen was the signal for participants to start the required task. Participants were instructed to reposition their hands on the guitar neck immediately after the task completion. For this reason, the first 2 s of Event 4 (crossing lines) were removed from the analysis. Duration of the events: Cue = 2 s; Event 1 = 4–10 s; Event 2 = 2–8 s; Event 3 = 7 s; Event 4 = 6–12 s. Abbreviations: IMI, imitation; Non-IMI, nonimitation; OBS, observation; EXE, execution.

is executed in response to a symbolic or spatial cue. Subsequent fMRI (Koski et al., 2002, 2003; Grèzes et al., 2003) and MEG (Nishitani and Hari, 2000, 2002) studies confirmed the involvement of the mirror neuron system in imitation of simple motor acts.

The neural basis of immediate imitation was also investigated by Tanaka and coworkers in two studies in which they asked volunteers to imitate finger and arm postures (Tanaka et al., 2001; Tanaka and Inui, 2002). Unlike the experiments just reviewed, the postures to be imitated were rather complex. In the first study, they found an activation of the supramarginal gyrus, particularly strong when a meaningless hand posture was contrasted with a symbolic one. In the second study, they compared imitation of hand versus arm postures. The results showed activation of the IFG and inferior parietal lobule for imitation of finger postures and of the superior parietal lobule for imitation of arm postures.

Although these studies represent an interesting attempt to address the issue of the neural basis of immediate imitation of complex postures, possibly requiring a rearrangement of the elementary motor acts, their results failed to define consistently the cortical circuits involved in this process. Furthermore, because the stimuli used by these authors, although unfamiliar to the participants, were consistently imitated correctly (Tanaka and Inui, 2002), these experiments only marginally addressed the issue of imitation-based learning.

There is agreement among the ethologists that one can properly speak of imitation ("true imitation") only when learning (not just the repetition of an action already present in the imitator's motor repertoire) occurs (Byrne, 1995; Tomasello and Call, 1997). As previously discussed, in true imitation, the underlying mechanism should consist of two distinct steps: the coding of the elementary motor acts present in the action to be imitated by mirror neurons and a recombination of these coded acts in such a way that the observed action can be replicated.

The aim of the present experiment was to define the neural substrates of "true imitation" and, possibly, to establish the structure responsible for the recombination of elementary motor acts in a novel motor pattern. To this end, musically naive participants (nonguitar players) were asked to observe complex, unfamiliar hand actions (guitar chords played by an expert guitarist) and, after an interval, to replicate them as accurately as possible. In contrast to previous studies, we used an imitation paradigm where model observation and imitation were separated by a preparatory interval. The use of an event-related fMRI design allowed us to analyze the temporal progression of activations from action observation to its execution. It is important to stress that our aim was not to study the mechanism underlying long-term consolidated learning but to assess the cortical areas involved in the translation of an observed novel motor pattern into an ideally identical execution of it.

In addition, the activations in the imitation task were compared with three other conditions: a mere observation condition, an execution condition in which participants had to execute guitar chords of their own choice, and a condition in which subjects performed nonimitative actions after observing guitar chords. These conditions allowed us to assess whether observation of action without any subsequent motor requirement and observation in order to imitate share the same neural circuits, to establish at what extent the neural circuits underlying motor imitative actions overlap with those of similar actions internally generated, and finally to define the cortical areas mediating the execution of actions that do not match the observed model.

Results

Figure 1 shows an overview of the experimental conditions. Imitation (IMI) was the basic experimental condition. The other conditions were nonimitation (Non-IMI),

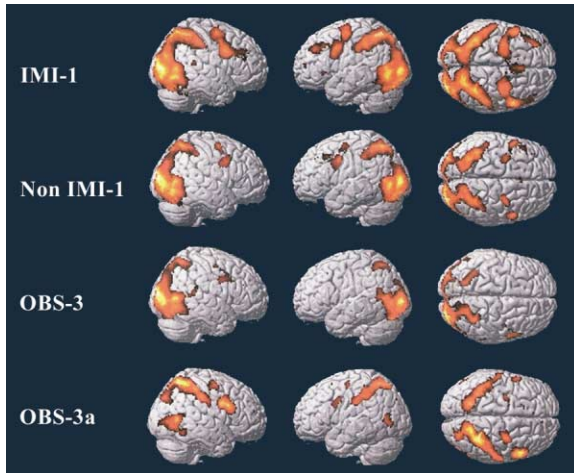


Figure 2. Cortical Areas Activated during the Event in Which Participants Observed the Guitarist Executing the Guitar Chords

This event was present in the conditions IMI, Non-IMI, and OBS (see Figure 1). In IMI-1, Non-IMI-1, and OBS-3, the contrast is with Event 4 (baseline); in OBS-3a, the contrast is with Event 1 (observation of the moving guitar neck). The numbers following each condition indicate the event number (e.g., IMI-1 = first event of condition IMI, OBS-3 = third event of condition OBS). Abbreviations as in Figure 1.

observation (OBS), and execution (EXE). Each condition consisted of four events (Events 1, 2, 3, and 4). In the text and figures, the different events are indicated by the condition they belong to, followed by their order number (e.g., IMI-1, first event of condition IMI; OBS-3, third event of condition OBS).

The results will be presented by comparing the events of various conditions that are physically identical but differ cognitively.

Observation of Guitar Chords

The observation of a guitar chord, made by an expert guitarist, was the initial event of IMI (IMI-1). The observation of a guitar chord was also present as the first event in Non-IMI (Non-IMI-1) and as the third event in OBS (OBS-3). In Non-IMI, the instruction was to observe the model and to execute subsequently a hand action on the guitar neck not related to guitar playing (grasp-release of the guitar neck, rhythmical covering, or gentle scratching of the fretboard). In OBS, the instruction was to observe the model without any subsequent request of motor behavior. Observation events were contrasted with the baseline (Event 4, blank screen) (see Figure 1).

The results are shown in Figure 2 and local maxima of the activated foci in Table 1.

In IMI-1 there was, in addition to a bilateral activation of visual occipital and temporal areas, a bilateral, left prevalent activation of the inferior parietal lobule slightly extending into the superior parietal lobule, and of two foci in the premotor cortex. The first of these foci was located in the ventral part of the precentral gyrus and slightly invaded the pars opercularis of the IFG, while the second one lay more dorsally in the precentral gyrus. There was also a marked activation of the middle prefrontal gyrus and a clear, bilateral activation of mesial areas, basically corresponding to the pre SMA.

In Non-IMI-1, the activation pattern was similar to that found in IMI-1, but its intensity and extent were less marked. The mesial activation was absent. These activa-

Table 1. Local Maxima of Activated Foci, Expressed in Montreal Neurological Institute Standard Brain and Talairach Coordinates, during the Event Observation in the Conditions IMI, Non-IMI, and OBS

Anatomical Region	Left							Right						
	MNI			TAL				MNI			TAL			
	x	y	z	x	y	z	Z	x	y	z	x	y	z	Z
IMI-1														
Precentral gyrus (PMv)/pars opercularis	-52	8	34	-51	9	31	5.78	56	6	36	55	7	33	5.64
Precentral gyrus (PMv/PMd)	-28	-8	60	-28	-5	56	4.94	28	-6	58	28	-3	54	4.66
Pre SMA								6	10	50	6	12	45	5.31
Intraparietal sulcus (caudal)	-32	-60	56	-32	-56	54	5.62	26	-64	56	26	-59	55	5.87
Superior parietal lobule	-24	-74	44	-24	-70	44	5.39							
Inferior parietal lobule (rostral)	-46	-36	40	-46	-33	38	4.95	52	-32	44	51	-29	42	4.5
	-56	-24	36	-55	-22	34	4.54							
Middle frontal gyrus (caudal)	-40	28	42	-40	29	37	3.90	46	34	32	46	34	28	3.59
Middle frontal gyrus (rostral)	-32	40	32	-32	40	27	4.51							
Basal ganglia	-24	2	12	-24	2	11	4.20	24	8	4	24	8	3	3.48
Cerebellum	-20	-44	-40	-20	-44	-31	3.69							
Non-IMI-1														
Precentral gyrus (PMv)/pars opercularis	-48	2	34	-48	4	31	4.65	56	6	36	55	7	33	4.63
Precentral gyrus (PMv/PMd)	-24	-8	46	-24	-6	43	5.21	36	0	52	36	2	48	3.97
Intraparietal sulcus (caudal)	-32	-62	60	-32	-57	58	5.60	28	-60	60	28	55	58	5.03
Inferior parietal lobule (caudal)	-32	-48	50	-32	-44	48	5.21							
Inferior parietal lobule (rostral)	-50	-34	48	-50	-31	46	3.42	44	-38	46	44	-35	44	4.27
Middle frontal gyrus (caudal)	-46	22	40	-46	23	36	3.86							
OBS-3														
Precentral gyrus (PMv)/pars opercularis	-58	10	30	-58	11	27	3.64	58	2	32	57	3	29	4.11
Intraparietal sulcus (caudal)	-30	-60	60	-30	-55	58	3.90	36	-54	58	36	-50	56	4.41
	-18	-66	52	-18	-62	51	4.18							

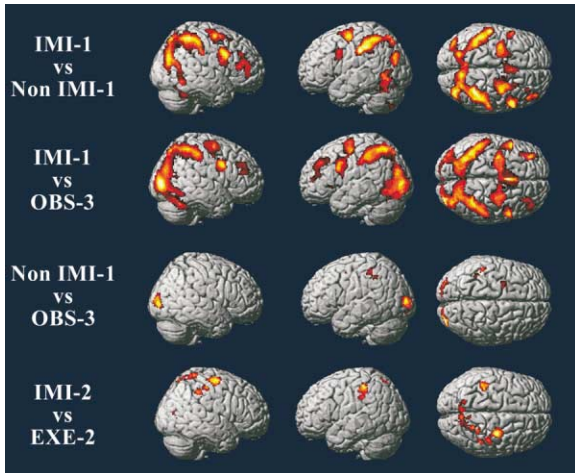


Figure 3. Direct Comparison between Identical Events in Different Conditions

Conditions and events used for the contrasts are indicated on the left side of the figure.

tion differences were statistically confirmed by direct comparison between IMI-1 and Non-IMI-1 (see Figure 3, upper row).

In OBS-3, there also was a bilateral activation of the visual occipital and temporal areas and of the posterior part of the inferior parietal lobule, plus a weak activation of the right ventral premotor cortex. Direct comparison between IMI-1 and OBS-3 confirmed the stronger activation in the IMI condition (Figure 3, second row). In contrast, almost no difference in activation was found in the comparison of Non-IMI-1 versus OBS-3 (Figure 3, third row).

The lack of activation of the rostral sector of the inferior parietal lobule and the weak activation of the premotor cortex in OBS-3 is rather surprising. It is well established that the parieto-premotor circuit is active during the mere observation of hand actions (see Discussion). This lack of activation may have resulted from a cancellation effect due to the contrast with the baseline (Event 4). At the beginning of Event 4, the participants repositioned their hands on the guitar neck. In order to avoid a possible motor contamination (see Experimental Procedures), we eliminated from the analysis the first 2 s of this event (see Figure 1 and Experimental Procedures). In addition, Events 4 where video-recordings showed overt movements after 2 s period (see above) were removed. Despite these procedures, some residual motor activity might have been present in some baseline events, and, because of common circuits underlying action observation and execution, this motor activity could have determined the lack of activation in OBS-3. To check for this possibility, OBS-3 was contrasted with OBS-1 (observation of a moving guitar neck).

The results are shown in Figure 2 (OBS-3a). The new contrast showed a clear activation of the whole inferior parietal lobule and of the ventral part of the precentral gyrus, extending into the pars opercularis of the IFG. The activation pattern during mere observation was, therefore, qualitatively similar to that found in IMI-1 and Non-IMI-1, although less intense. A further difference

with these conditions, and in particular with IMI-1, was the absence of any prefrontal and mesial cortical activation.

Pause before Action Execution

The second event in IMI and Non-IMI was the pause event. During this event, participants had to prepare themselves either to imitate the observed action (IMI-2) or to execute actions not related to guitar playing (Non-IMI-2).

The results are presented in Figure 4 and Table 2. The difference between the two conditions is striking. In IMI-2, brain activity is extremely high. In contrast, in Non-IMI-2 the cortex seems to be almost at rest.

The pattern of activation in IMI-2 was similar to that found in IMI-1, but without the activation of visual areas. In spite of this basic similarity, some interesting differences are worth noting. First, the peak activation in the inferior parietal lobule shifted rostrally, corresponding now to the arm/hand representation of this lobule. Second, there was an increase of the superior parietal lobule activation. Third, there was a shift, on both sides, of the dorsal precentral focus into dorsal direction occupying now a considerable sector of the cortex above the superior frontal sulcus. Fourth, there was an activation of the ventral-most part of the precentral sulcus previously absent. Fifth, although the frontal activation partially overlapped that found in IMI-1, there was an increase in its extension and strength bilaterally. The focus of the activation was now dorsal to the pars triangularis of the IFG. Sixth, there was a dramatic increase of the mesial wall activations.

In Non-IMI-2, although the cortex was poorly active, activation was present on the mesial cortical wall in correspondence of pre SMA and the adjacent cingulate gyrus. Two small activations were also present in the left frontal lobe (Figure 4, Non-IMI-2).

In addition to the two conditions mentioned above, also during EXE-2 participants waited for action execu-

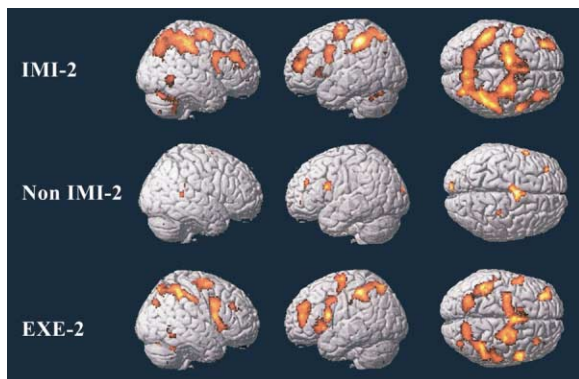


Figure 4. Cortical Areas Activated during the Pause Event in the Different Experimental Conditions

All contrasts with Event 4. In IMI-2, after seeing the action model (guitar chord), participants had to rehearse it in order to imitate it later. In Non-IMI-2, after seeing the model, participants had to plan the execution of one of three previously learned nonchord hand actions on the guitar neck. In EXE-2, after seeing the action model, participants had to freely choose a chord to execute later. Abbreviations and conventions as in Figure 2.

Table 2. Local Maxima of Activated Foci, Expressed in Montreal Neurological Institute Standard Brain and Talairach Coordinates, during the Event Pause in the Conditions IMI, Non-IMI, and EXE

Anatomical Region	Left							Right							
	MNI			TAL				Z	MNI			TAL			
	x	y	z	x	y	z	x		y	z	x	y	z	Z	
IMI-2															
Inferior frontal gyrus (Pars opercularis)								54	12	8	53	12	7	3.69	
Precentral gyrus (PMv)/pars opercularis	-58	10	34	-57	11	31	5.01	56	6	28	55	7	25	4.71	
Precentral gyrus (PMv/PMd)	-24	-10	58	-24	-7	54	5.20	26	-10	54	26	-7	50	5.24	
Pre SMA	-12	-6	66	-12	-3	61	5.15								
Anterior cingulate	-8	4	48	-8	6	44	4.21	8	10	44	8	12	40	4.38	
Insula	-38	22	6	-38	22	4	4.02								
Postcentral gyrus								52	-30	42	51	-27	40	5.13	
Intraparietal sulcus	-8	-68	60	-8	-63	58	4.49	18	-70	56	18	-65	55	4.19	
Inferior parietal lobule (rostral)	-38	-32	36	-38	-29	35	4.28	40	-40	36	40	-37	35	5.28	
Middle frontal gyrus (caudal)	-36	42	34	-36	42	29	4.81	46	18	30	46	19	27	3.56	
Middle frontal gyrus (rostral)	-32	48	12	-32	47	9	4.23								
Basal ganglia	-28	2	0	-28	2	0	3.59	24	2	2	24	2	2	4.23	
Cerebellum	-24	-72	-50	-24	-72	-38	4.04	24	-70	-50	24	-70	-39	4.58	
Non-IMI-2															
Precentral gyrus (PMv)/pars opercularis	-58	10	26	-57	11	23	4.99								
Pre SMA	-2	0	58	-2	3	53	3.97	10	2	56	10	5	51	3.42	
Anterior Cingulate	-6	4	48	-6	6	44	3.84								
Prefrontal cortex (rostral)	-38	42	28	-38	42	24	3.63								
Basal ganglia	-28	0	0	-28	0	0	3.78	28	4	4	28	4	3	3.81	
EXE-2															
Inferior frontal gyrus (pars opercularis)	-56	8	16	-55	8	14	5.58	52	6	16	51	7	14	4.99	
Precentral gyrus (PMv)/pars opercularis	-54	4	36	-53	6	33	4.59	58	6	34	57	7	31	4.37	
Precentral gyrus (PMv/PMd)	-24	-10	52	-24	-7	48	4.35	28	-12	52	28	-9	48	4.37	
Pre SMA								2	4	54	2	6	49	4.54	
								0	8	50	0	10	46	4.56	
Anterior Cingulate	-12	8	32	-12	9	29	3.71								
	-8	8	46	-8	10	42									
Insula	-38	20	0	-38	19	-1	4.18								
Postcentral gyrus	-56	-26	40	-55	-23	38	3.76	56	-20	38	55	-18	36	4.11	
Intraparietal sulcus	-26	-68	58	-26	-63	57	4.24	38	-54	52	38	-50	50	3.76	
								16	-70	56	16	-65	55	4.27	
Inferior parietal lobule (rostral)	-42	-38	46	-42	-35	44	5.52	38	-40	42	38	-37	41	4.42	
Middle frontal gyrus (caudal)	-30	42	28	-30	42	24	5.34								
Middle frontal gyrus (rostral)	-40	44	4	-40	43	2	4.60								
Basal ganglia	-24	8	8	24	8	7	4.80	28	-2	8	28	-2	7	4.68	

tion but, in this case, after seeing a moving guitar neck instead of a chord model. The results are shown in the lower part of Figure 4. The pattern was strikingly similar to that observed in IMI-2, but with a less intense activation of the prefrontal lobe on the right side. Direct comparison IMI-2 versus EXE-2 confirmed this finding (Figure 3, bottom row).

Action Execution

Participants performed an action on the guitar neck during the third event of IMI, Non-IMI, and EXE. In IMI-3, they had to replicate the observed chords. In Non-IMI-3, they had to make actions not related to guitar playing. In this condition the participants observed the chords made by the guitar player but had to disregard them. Finally, in EXE-3 they had to play chords of their choice (no model was presented in Event 1 in this condition).

The results are shown in Figure 5 and Table 3. The activations were remarkably similar in all three conditions. In all of them there was a very strong activation of the *right* primary sensory-motor areas, extending into

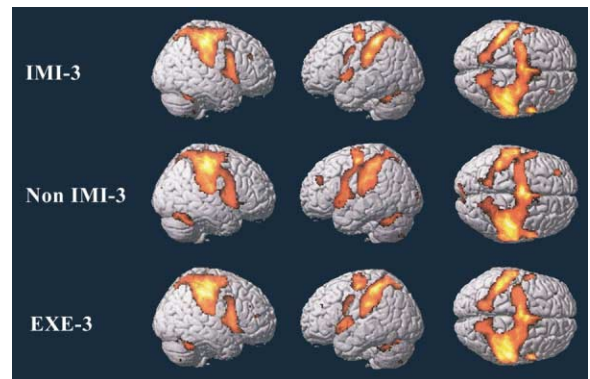


Figure 5. Cortical Areas Activated during the Execution of the Required Action

In IMI-3 and EXE-3 they executed chords on the guitar neck; in Non-IMI-3 they executed one of following actions: covering the strings, grasping, or gentle scratching of the guitar neck. Contrasts with Event 4. Abbreviations and conventions as in Figure 2.

Table 3. Local Maxima of Activated Foci, Expressed in Montreal Neurological Institute Standard Brain and Talairach Coordinates, during the Event Execution in the Conditions IMI, Non-IMI, and EXE

Anatomical Region	Left							Right							
	MNI			TAL				Z	MNI			TAL			
	x	y	z	x	y	z	x		y	z	x	y	z	Z	
IMI-3															
Precentral gyrus (PMv)/pars opercularis	-60	8	24	-59	9	22	3.92	56	6	24	55	7	22	5.32	
Precentral gyrus (PMv)	-56	-2	40	-55	0	37	4.97								
Precentral gyrus (PMv/PMd)								20	-14	58	20	-11	54	5.20	
Insula	-46	0	4	-46	0	4	4.61								
Precentral gyrus								42	-14	58	42	-11	54	7.19	
Postcentral gyrus								40	-28	60	40	-24	56	5.22	
Intraparietal sulcus	-18	-68	60	-18	-63	58	4.47								
Inferior parietal lobule (rostral)	-60	-22	30	-59	-20	29	4.99	50	-36	52	50	-32	50	5.45	
Middle frontal gyrus (caudal)								32	36	30	32	36	26	3.58	
Cerebellum	-28	-54	-26	-28	-53	-19	4.96	30	-48	-30	30	-48	-23	4.71	
Non-IMI-3															
Precentral gyrus (PMv)/pars opercularis	-58	6	20	-57	7	18	5.61	58	6	32	57	7	29	4.64	
	-52	6	8	-51	6	7	4.76								
Precentral gyrus (PMv)	-54	-2	40	-53	0	37	4.37	56	-4	38	55	-2	35	4.35	
Insula	-40	-4	4	-40	-4	4	4.17								
Precentral gyrus								42	-14	58	42	-11	54	7.19	
Postcentral gyrus								48	-18	58	48	-15	54	5.94	
								50	-28	48	50	-25	45	5.49	
Intraparietal sulcus	-14	-62	66	-14	-57	64	4.39	8	-56	70	8	-51	67	4.61	
Inferior parietal lobule (rostral)	-58	-34	34	-57	-31	33	4.45	58	-34	44	57	-31	42	4.56	
Prefrontal cortex (caudal)	-30	44	28	-30	44	24	3.86								
Basal ganglia	-28	0	6	-28	0	5	4.50	24	-4	8	24	-3	8	4.99	
Cerebellum	-24	-66	-24	-24	-65	-17	4.30	26	-66	-20	26	-65	-14	5.11	
EXE-3															
Precentral gyrus (PMv)/pars opercularis	-60	8	24	-59	9	23	4.76	54	8	12	53	8	11	4.96	
								56	8	24	55	9	22	4.93	
Precentral gyrus (PMv)	-58	2	38	-57	4	35	4.69								
Insula								48	10	0	48	10	0	4.34	
Precentral gyrus	-38	-14	56	-37	-11	52	7.12								
Postcentral gyrus								54	-24	44	53	-21	42	5.59	
								42	-26	60	42	-22	56	5.46	
Intraparietal sulcus	-42	-40	58	-42	-36	55	5.66	18	-72	52	18	-67	51	4.25	
	-12	-64	64	-12	-59	62	5.21								
Inferior parietal lobule (rostral)	-58	-18	20	-57	-18	18	5.03	52	-32	44	51	-29	42	5.45	
Basal ganglia	-28	2	8	-28	2	7	4.28	24	-4	8	24	-3	7	5.13	
Cerebellum	-28	-58	-34	-28	-58	-26	4.43	38	-50	-30	38	-50	-23	4.88	

the superior parietal lobule. These activations are to be related to the fact that participants used their left hand to perform the required actions.

The activation of the posterior part of the inferior parietal lobule in the right hemisphere observed in the previous events tended to disappear, while the rostral parietal activation (most likely corresponding to primary sensory cortices, SI) was strong. In addition, there was an activation of the secondary somatosensory area (SII). The right premotor activations located in the precentral gyrus decreased, while a large activation of the ventral-most part of the precentral gyrus near the sylvian fissure and including the insula appeared. The right prefrontal activations were virtually absent. The *left* hemisphere activations did not differ much in the three conditions.

Observation of a Moving Guitar Neck

Participants observed guitar neck motion in the first event of OBS and EXE (OBS-1 and EXE-1, respectively). In OBS-1 the participants had no subsequent actions

to execute, while in EXE-1, after seeing the guitar neck motion, the participants had to execute guitar chords of their choice.

The results are shown in Figure 6. The observation of the guitar neck motion (OBS-1) determined activation of visual areas only. As compared with the observation of biological motion (IMI-1, Non-IMI-1, and OBS-3), no activation was observed in either the parietal or frontal lobe.

In EXE-1, the same stimulus produced activations in the posterior part of the inferior parietal lobule and in the dorsal part of the precentral gyrus, posterior to the medial frontal gyrus, in the left hemisphere and, more ventrally, in the same gyrus in the right hemisphere. A further activation was found in the prefrontal lobe, especially on the left. These activations indicate that, although there was no other request other than that of observing the moving guitar neck, participants were already activating endogenously some of the areas that became active in EXE-2 and EXE-3.

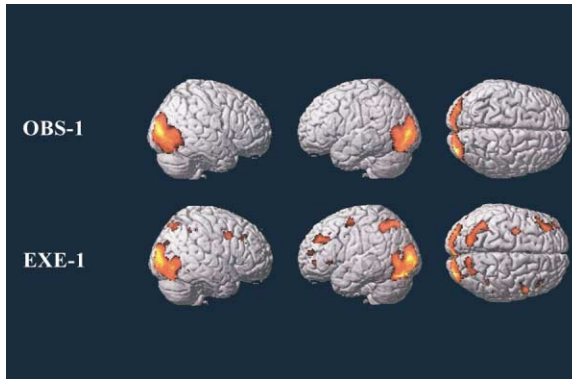


Figure 6. Cortical Areas Activated during the Observation of the Moving Guitar Neck in OBS-1 and EXE-1
Contrasts with Event 4. Abbreviations and conventions as in Figure 2.

Discussion

Imitation is a complex cognitive function that implies learning a novel motor pattern or a novel motor sequence. The aim of the present study was to define the circuit underlying this function and assess whether the mirror neuron system is an essential part of this circuit.

The results showed that the mirror neuron system is indeed at the core of imitation-based learning. They also indicate that during imitation learning, the activity of the mirror neuron circuit is under control of the middle frontal lobe (area 46) and anterior mesial cortical areas. In the following discussion, we will first examine the activations in the mirror neuron system, and then we will discuss the role of the other cortical areas active during imitation.

Mirror Neuron System and Imitation

During all phases of IMI, a strong activation was found in the rostral part of the inferior parietal lobule and the ventral premotor cortex plus the pars opercularis of the inferior frontal gyrus (IFG).

Anatomical and functional data from monkey experiments indicate that the inferior parietal lobule is formed by two sectors: a rostral sector related to somatosensory, visual, and motor domains (Leinonen and Nyman, 1979; Leinonen et al., 1979; Hyvarinen, 1982; Gallese et al., 2002) and a caudal one essentially related to the visual modality and the control of eye movements (Mountcastle et al., 1975; Hyvarinen, 1982; Andersen, 1987; Colby and Goldberg, 1999; Constantinidis and Steinmetz, 2001). Recent studies showed that the rostral sector of the inferior parietal lobule contains mirror neurons (K.J. Fogassi et al., 1998, *Soc. Neurosci.*, abstract; Gallese et al., 2002).

These data suggest that the activation of the rostral sector of the inferior parietal lobule, found in the present experiment, is related to the activation of mirror neurons coding the motor acts forming the observed chords. It is interesting to note that the rostral inferior parietal lobule activation was more pronounced in IMI-2, where the volunteers had to maintain in memory the chord model, than in EXE-2, where they had to choose the

chord freely. It is likely that this activation difference reflects the coding of information taken from the model, necessary for imitation.

The activation of the caudal sector of the inferior parietal lobule, also found in the present experiment, is probably related to the involvement of this sector in higher-order visual functions. It is plausible that the activation of this sector reflects interactions between objects and eye or hand/arm movements directed toward them.

Data from previous fMRI experiments are consistent with this interpretation. The observation of actions done by others using hand, mouth, or foot also determined a rostral and a caudal activation in the inferior parietal lobule (Buccino et al., 2001). Unlike the caudal activation, the rostral one was somatotopically organized, with the hand representation largely corresponding to that found in the present experiment.

During all phases of IMI, two activation sites were found in the premotor cortex: one was located ventrally, the other dorsally. The functional interpretation of the ventral activation is straightforward. This activation, which includes the dorsal part of the pars opercularis of IFG and the adjacent precentral gyrus, is constantly found during hand action observation (see Rizzolatti et al., 2001). Furthermore, the same region is active during finger movements or object grasping (Fink et al., 1997; Krams et al., 1998; Binkofski et al., 1999; Iacoboni et al., 1999; Ehrsson et al., 2000; Gerardin et al., 2000) and hand motor imagery (Grafton et al., 1996; Gerardin et al., 2000). This ventral activation most likely corresponds, therefore, to the sector of ventral premotor cortex (PMv), where hand actions are represented.

It is more difficult to assign the dorsal precentral activation to a specific physiological region. There are two possibilities. The first is that the dorsal activation corresponds to the dorsal premotor cortex (PMd). The second is that this activation is located in PMv, but in that part where proximal arm movements are represented.

In a previous study (Rizzolatti et al., 2002), we suggested that in humans the border between ventral and dorsal premotor cortex lies at the level of the upper border of the frontal eye field, approximately at Z level 50 in Talairach coordinates (see Paus, 1996; Corbetta, 1998; for more recent fMRI data, see Kimmig et al., 2001). If this view is accepted, the activation found in the present study includes both the dorsal part of PMv and PMd. It is interesting to note that in OBS-3 (observation without further motor instruction) and in Non-IMI-1 (observation with the instruction to perform actions different from the observed ones), the entire premotor activation was located below Z 50, while in IMI-1 the activation expanded dorsally and straddled the superior frontal sulcus. A possible interpretation is that, when there is an instruction to imitate, besides coding the action model (in PMv), the individuals start to mentally prepare the proprioceptive and motor execution aspects of the required action. PMd would mediate this motor preparation.

In conclusion, the rostral inferior parietal lobule and PMv, including the pars opercularis of IFG, appear to represent the circuit that “translates” the observed actions into the motor representation of the same actions. In contrast, activation of PMd most likely reflects motor

preparation. It might, however, also represent an activation of a dorsal sector of the mirror neuron system, as suggested by Grèzes et al. (2003).

During action observation event, activations in the two key sectors of the mirror neuron system (rostral inferior parietal lobule and PMv plus posterior IFG) were also found in OBS and Non-IMI. In both conditions they were weaker than during IMI. There are two possible, not mutually exclusive, explanations for stronger activation of the mirror neuron system during IMI as compared to Non-IMI and OBS. The first one is that the subjects paid more attention to the observed action when they had to subsequently imitate it than when this request was absent. The second explanation is that the stronger activation of the mirror neuron system during IMI was due to the fact that, in this condition, this system has to maintain specific information on the model over time and to rearrange, through the intervention of other centers, the “resonated” motor act representations into a novel motor pattern.

The line between these two explanations is very tenuous. It is well known that attentive observation of actions leads to activation of the observer’s motor system, sometimes producing an imitative overt behavior. Darwin, for example, noted that spectators that look attentively at motor performances often do overt movements, similar to those they are observing. Recently, experimental evidence was provided that the observation of motor actions primes the execution of similar actions (Craighero et al., 2002; Vogt et al., 2003). Regardless, however, of what is the major factor determining the stronger activation of the mirror neuron system during IMI as compared to the other conditions, what is important here is that the *same circuit* (mirror neuron system) that is active during mere action observation mediates also imitation-based learning.

Other Neural Structures Active during Imitation

Besides activation of the inferior parietal lobule and premotor areas, during IMI activations were found also in the prefrontal lobe, the anterior mesial cortices, and the superior parietal lobule.

In the prefrontal lobe two distinct activations were found. One was located in the caudal part of the middle frontal gyrus, and the other more rostrally in the same gyrus. The caudal activation was present only during IMI-1. Although it is difficult to assign a specific role to this area in the context of the present experiment, a possibility is that, as suggested by Buchel et al. (1998), this area is involved in top-down attentional processes.

The rostral activation, most likely located in area 46, was strong during IMI-2, but was present also during EXE-2. Based on monkey experiments, this prefrontal area has been considered the cortical region underlying working memory (Fuster and Alexander, 1971; Funahashi et al., 1990; see Fuster, 1995). According to Goldman-Rakic and coworkers, the dorsal sector of the lateral frontal lobe (area 46) is involved in the spatial aspects of working memory, while the adjacent ventral area is involved in object working memory (see Goldman-Rakic, 1995; Levy and Goldman-Rakic, 2000). Various authors challenged this view. According to Petrides (1994, 2000), the basic memory functions are carried

out in the temporal and parietal cortices and not in the frontal lobe. The frontal lobe intervenes on information reaching it from these cortical regions for higher order memory processing, with a distinction between the ventral sector, carrying out more elementary memory functions, and the dorsal one, involved in more complex functions like the “monitoring” of remembered information. A different view was advanced by Passingham and coworkers (Passingham et al., 2000; Rowe et al., 2000) and Owen (2000). According to them, the ventral sector of the prefrontal cortex is mostly related to associative conditional learning, while area 46 is involved in the selection of the target of the response, both in working memory and free selection tasks.

While the classical working memory interpretation may easily account for area 46 activation during IMI-2, it cannot explain the activation of the same frontal sector during EXE-2, where participants had to freely select a chord of their own choice. This finding suggests that area 46 was activated in our experiment not so much to maintain information during the delay period before execution, but to select the motor acts appropriate for the experimental task. This interpretation is close to that proposed for area 46 by Passingham and coworkers (Rowe et al., 2000; see also Jenkins et al., 1994).

Previous experiments showed that mere hand action observation typically does not lead to the activation of the mesial cortical areas (e.g., Rizzolatti et al., 1996b; Grafton et al., 1996; Grèzes et al., 1998; Iacoboni et al., 1999; Buccino et al., 2001; Manthey et al., 2003). The present experiment confirmed this finding. In contrast, a strong activation of these areas was present in the pause phase in all the experimental conditions requiring a subsequent chord execution. It has been postulated that the rostral mesial areas serve as a control system on the activity of the parieto-premotor circuits involved in action initiation (Hikosaka et al., 2000; Sakai et al., 1999; see Rizzolatti and Luppino, 2001). This control is both excitatory and inhibitory (see Alexander and Crutcher, 1990; Rizzolatti et al., 1990; Matsuzaka et al., 1992). It is likely, therefore, that the activation of mesial areas observed in the present study reflects their role in the control of action execution and, in particular, in the necessity to inhibit the selected action until its execution is allowed.

Activation of the superior parietal lobule was previously reported in studies in which participants observed actions with the aim to imitate them later on (Grèzes et al., 1998) and in tasks in which participants observed an action and imitated it online (Iacoboni et al., 1999; Tanaka et al., 2001; Tanaka and Inui, 2002). Some authors suggested that the superior parietal lobule activation plays a key role in imitation (Grèzes et al., 1998; see, however, Decety et al., 2002, stressing the importance of the inferior parietal lobule in imitation). In the present experiment, activation of the superior parietal lobule was found in all conditions in which the participants were required to do an action, regardless of whether it was related or not to the imitation of the model. On the basis of this finding and considering also the fundamental role of the superior parietal lobule in proprioception demonstrated in nonhuman primates (Mountcastle et al., 1975; see also Lacquaniti et al., 1995), we are inclined to interpret its activation as due

to a proprioceptive representation of an action that the individual is ready to execute.

Conclusions

The strong activation of the mirror neuron system in all phases from action observation to action execution indicates that the core process in imitation, i.e., the translation of an action visually coded into an ideally identical action done by the observer, relies on this circuit. This finding contradicts imitation accounts assuming distinct stages for visual and motor representation of action (for review, see Vogt, 2002).

The most likely interpretation for the mirror neuron system activation found in the present experiment is that, during imitation, the observed actions, visually processed in higher order visual areas (see Allison et al., 2000; Jellema et al., 2002), cause the corresponding motor representations in PF and in PMv to resonate (Rizzolatti, 2003). The resonance of these elementary motor representations in the mirror neuron system is not, however, sufficient for learning by imitation. A selection and recombination of these motor elements is necessary to obtain an action congruent to the model. The present data suggest that these processes occur inside the mirror neuron circuit, very likely under the orchestrating role of area 46.

In conclusion, the results of the present experiment identified the core circuit involved in vision-to-action translation. They also showed that other areas, and in particular area 46, play an important role in learning novel hand actions. This "minimalistic" interpretation of the anatomical basis of imitation does not exclude that in imitation conditions where other aspects of the action to be imitated (such as a sequence or rhythm) are fundamental, a crucial role is played also by neural structures other than those evidenced in the present study.

Experimental Procedures

Subjects

Twelve healthy, right-handed volunteers (six males and six females; ages 19 to 37 years, mean, 27 years) participated in the study. Three additional subjects were excluded from the analysis due to large head movements (>5 mm, $n = 2$) or poor quality of imitations ($n = 1$). All subjects had normal or corrected-to-normal visual acuity. They gave their written informed consent to the experimental procedure, which was preventively approved by the local Ethical Committee.

Design and Experimental Conditions

The experiment began with a practice session outside the MRI scanner, which was followed by the main experimental session. This consisted of four conditions presented in quasirandom order: execution of chords after model observation (IMI), execution of "non-chord" movements after seeing the model (Non-IMI), action observation (OBS), and execution of chords without seeing a model (EXE).

Each experimental condition consisted of four events (see Figure 1). Before the start of each trial, a colored square that cued the required task was presented for 2 s.

Condition 1: IMI

Green Cue. Event 1: participants were required to carefully observe a video clip showing the hand of a guitar player that repeatedly performed the same guitar chord, in order to subsequently imitate it. Event 2: blank (blue) screen. During the last second of Event 2, a cross of the same color as the square was shown in the center of the screen to remind participants of the task and to indicate that Event 3 was about to start. Event 3: participants imitated the

previously seen chord with their left hand. Event 4: blank screen. At the beginning of this event, the participants placed their hand in the rest position (see below) on the guitar neck located inside the scanner. Subsequently they kept their hand still on the guitar neck. The crossed line in Figure 1 indicates the period (2 s) during which the subject repositioned their hand in the rest position.

Condition 2: Non-IMI

Red Cue. All events were the same as in Condition 1, except for Event 3. During this event, participants had to perform one of three "nonchord" actions, which they had learned during the practice session.

Condition 3: OBS

Black cue. Event 1: participants saw a video clip showing a guitar neck that moved gently in the horizontal plane (amplitude 6% of image width). Event 2 was as in Condition 1. Event 3: a video sequence was presented showing the right hand of a guitar player performing two different chords on a guitar neck, each pressed twice. Participants were instructed to carefully observe the presented sequence. Event 4 was as in Condition 1.

Condition 4: EXE

Yellow Cue. All events were the same as in Condition 3, except for Event 3, where participants were asked to perform a guitar chord of their own choice while the screen showed a curtained, dark blue background. Participants started performing the self-selected chord when the yellow cross had disappeared and repeated this two or three times until the end of Event 3.

In order to be able to analyze the three main events (Events 1, 2, and 3) of each experimental condition separately, we used an event-related design. Events 1, 2, and 4 were presented in different ("jittered") durations across trials, and tasks were varied from one trial to the next. The scanning session was divided into four blocks of 16 trials each. Each block was divided into four subblocks that contained one exemplar of each condition.

Apparatus and Stimuli

A wooden guitar neck (height 20 cm) was placed in vertical orientation next to the participant's left thigh so that it could be comfortably held throughout the scanning periods. In order to reduce tactile exploration, strings were removed and only five frets were present. During all nonactive events (Events 1, 2, and 4, and throughout Condition 3), participants placed their index, middle, and ring finger in a rest position on frets 1, 2, and 3, respectively, on the far side of the fretboard (near the leg). Stimuli were presented via a Sony PX20 data projector onto a translucent, vertical screen located above the participant's chest. This was visible, via a mirror, in a distance of approximately 27 cm above the participant's head. Presentation Software (Neurobehavioral Systems, Inc.) was used for display of the color cues (2° visual angle) and video clips (448 × 336 pixels, 25 frames per second, 25° horizontal and 19° vertical visual angle). All clips were recorded using a classical guitar played by a skilled guitarist (SV). He used his right hand so that the chords appeared as a mirror image of the participant's left hand. (Being a left-handed guitarist, he played chords with his right hand.) This perspective was chosen in order to preserve spatial compatibility between the model's and the imitator's hand. Further, we have verified, in a behavioral pilot study, that in this perspective, the chords are imitated more accurately and with shorter latencies than when displaying the model in an anatomically matched but spatially incompatible perspective (see also Koski et al., 2003).

In all video clips, the model's fingers moved from the rest position to the chord, pressed the chord, lifted just above the fretboard, and pressed the chord again. This resulted in a rhythmical press-release pattern of 2 s duration that continued throughout the display event. Participants were instructed to perform the chords in the same rhythmical manner. All chords involved either two or three fingers, each on a different string and using only the upper three frets, and no chord involved the small finger. The participants did not see their hand during scanning. No chord was shown twice to a participant throughout the practice and main sessions. For later scoring, the participant's hand was videotaped during the scanning session, synchronous with an image of the displayed stimuli. Event 4 was the baseline for most contrasts, so particular attention was paid to the motor behavior of participants during this event. Specifically, the

first 2 s of this event were routinely removed from the analysis because over this time participants repositioned their hand on the fretboard. Furthermore, the whole event was removed when the videorecords showed movements of the participants in the Event 4 following the initial first 2 s.

For the practice session, the scanner setup, as described above, was replicated in a separate room. Subjects were lying on a bed, and stimuli were presented on an Eizo 18" flat panel display that was mounted approximately 60 cm above the participant's head. The model stimuli could be swapped against a life image of the participant's hand, providing visual feedback during the first part of the practice session.

Instruction and Procedure

At the beginning of the practice session, participants were introduced to the guitar fretboard, to the hand's rest position, and to the rhythmical press-release pattern in which all chords were to be performed. In a first practice block, eight imitation trials were performed that were similar to the IMI trials of the main experiment but involved a guitar neck with strings and visual feedback of the hand during imitation. Participants were instructed to observe the model chords attentively and to reproduce the chords with maximal accuracy. In order to improve accuracy, they were allowed to make online corrections. This block was followed by six trials in which imitation trials alternated with "nonchord" trials to prepare participants for Condition 2 (Non-IMI). During Event 3 of these trials, participants were instructed to perform one of three familiar actions, namely grasp-release of the guitar neck, rhythmical covering, or gentle scratching of the fretboard. In a further block of six imitation trials, a guitar neck without strings was used, and online visual feedback was no longer available. Finally, a full block of 16 trials was run, which exactly resembled the procedure in the main experiment. For the EXE condition, participants were asked not to use the same chord across trials, but also not to excessively engage in inventing complex, novel chords. The practice session lasted about 30 min and was directly followed by the main scanning session.

Functional Magnetic Resonance Imaging

Functional MR data were acquired with a 1.5T Siemens Sonata whole-body scanner with echoplanar imaging (EPI) capability using the standard radio-frequency head coil. Multislice T2*-weighted echo-planar images were obtained from a gradient-echo sequence with the following parameters: echo time TE = 66 ms, repetition time TR = 3 s, flip angle = 90°, field of view FOV = 200 mm, slice thickness = 4 mm, interslice gap = 0.4 mm, in-plane resolution = 3.125 × 3.125 mm². The 30 slices covered the whole brain from the cerebellum through to the vertex. On average, 37 ± 9 EPI-volumes were acquired per event per condition in all participants. A T1-weighted anatomical MRI was also acquired for each subject using the 3D MP-RAGE (magnetization-prepared, rapid acquisition gradient echo) sequence with the following parameters: TE = 3.93 ms, TR = 2200 ms, inversion time TI = 1200 ms, flip angle = 15°, FOV = 240 mm, slice thickness = 1.5 mm, matrix = 180 × 256, number of sagittal slices = 128.

Data Processing and Statistical Analysis

The entire data analysis was performed with SPM99 (Statistical Parametric Mapping software; The Wellcome Department of Imaging Neuroscience, London, UK; <http://www.fil.ion.ucl.ac.uk>) running on MATLAB (The Mathworks, Inc., Natick, MA). The first four images of each run were discarded, because they cover the time period the MR signal needs to reach a steady state. The preprocessing steps were (1) realigning the images to correct for movement artifacts, (2) adjusting the slice timing to the middle slice to compensate for the differences in acquisition time of the individual slices, (3) coregistering the anatomical image to the mean functional image, and (4) normalizing all images to standard stereotactic space (Montreal Neurological Institute, see SPM software) with a voxel size of 2 × 2 × 2 mm³ for the functional images. Thereafter, the functional data sets were smoothed with a Gaussian kernel of 10 mm for group analysis.

The statistical analysis was performed in two levels. In the first level for each subject, the onsets and durations of each of the stimuli

were modeled in a General Linear Model (GLM) according to the stimulus types. The design matrix was composed of 12 regressors according to the experimental conditions (Events 1, 2, and 3 of the four conditions IMI, Non-IMI, OBS, EXE) for each session. The regressors were convolved with the canonical hemodynamic response function (HRF), and 12 additional regressors per session were included in the GLM to account for voxel intensity variations due to absolute and differential head movement. In the second level, corresponding contrast images of the first stage for each subject were entered into one-sample t tests ("random effects analysis," Friston et al., 1999). The results reported are significant at $p_0 < 0.001$ (p_0 = uncorrected for multiple comparisons).

The stereotactic coordinates of the local maxima within areas of significant activity change were determined for all stimulus types. The anatomical localization of these local maxima and clusters was assessed by reference to a standard stereotactic atlas (Talairach and Tournoux, 1988) after appropriate coordinate transformation.

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