Title
Cortical activation during executed, imagined, and observed foot movements

Journal
Neuroreport, 19(6)

ISSN
0959-4965

Authors
Orr, Elizabeth LR
Lacourse, Michael G
Cohen, Michael J
et al.

Publication Date
2008-04-16

DOI
10.1097/wnr.0b013e3282fbf9e0

Cortical activation during executed, imagined, and observed foot movements

Elizabeth L.R. Orr[a,c], Michael G. Lacourse[c,d], Michael J. Cohen[c,b] and Steven C. Cramer[a]

Departments of [a]Neurology & Anatomy & Neurobiology, Reeve-Irvine Research Center, [b]Department of Psychiatry and Human Behavior, University of California, Irvine, [c]V.A. Long Beach Neuroimaging Research Lab and [d]Department of Kinesiology, California State University, Long Beach, CA, USA

Correspondence to Dr Steven C. Cramer, MD, UCI Medical Center, University of California, Irvine, 101 The City Drive South, Building 53 Room 203, Orange, CA 92868-4280, USA
Tel: + 1 714 456 6876; fax: + 1 714 456 8805; e-mail: scramer@uci.edu

Received 25 December 2007; accepted 7 February 2008

Evidence suggests that executed, imagined, and observed movements share neural substrates, however, brain activation during the performance of these three tasks has not yet been examined during lower extremity movements. Functional MRI was performed in 10 healthy right-footed participants during imagined, executed, and observed right ankle movements. Task compliance was high, confirmed via behavioral assessment and electromyographic measurements. Each task was also associated with its own profile of regional activation, however, overall, regional activation showed substantial overlap across the three lower extremity motor tasks. The findings suggest the utility of continued efforts to develop motor imagery and observation programs for improving lower extremity function in a range of clinical settings. *NeuroReport* 19:625–630 © 2008 Wolters Kluwer Health | Lippincott Williams & Wilkins.

Key words: functional MRI, imagery, lower extremity, motor system, observation, therapy

Introduction

Increasing evidence suggests that different modes of cognitive and movement-based practice that are effective for motor learning in a healthy population can, in the setting of neurological disease, be combined to complement and/or supplement physical rehabilitation to restore preexisting motor networks or effectively build new functional networks that compensate for damage or dysfunction. In light of this, an improved understanding of the neurobiology underlying these approaches might have therapeutic implications. Several modes of practice have been suggested as useful in this regard.

One such cognitive learning modality is motor imagery-based mental practice, a technique traditionally used by athletes for performance preparation and motor skill learning [1]. Neuroimaging studies of motor imagery have identified several motor-related regions as robust components of an action simulation circuit, including supplementary motor area (SMA), ventral premotor (PMv), inferior parietal lobule (IPL), superior temporal sulcus, and primary motor cortex [2–4]. In many cases, motor imagery activates the same regions as those related to motor execution [5]. In addition, motor imagery-based mental practice regimes can produce motor system plasticity [6–8].

Simultaneous to these motor imagery studies, a parallel set of studies has provided evidence for a network of cortical regions that is activated during action observation. The neuroanatomical substrate of this 'mirror-neuron system' overlaps with that related to imagery, and includes at least two motor-related regions, IPL and the lower part of the precentral gyrus/inferior frontal gyrus [5,9,10]. Motor observation, as with imagery, has the advantage that when applied therapeutically, movement can be minimized or even removed as desired.

Toward development of a motor learning paradigm for physical rehabilitation, the aim of this study, therefore, was to evaluate within-subject regional motor system activation during movement execution, movement imagery, and movement observation of the lower extremity. The lower extremity is prominently involved in many clinical contexts; however, studies suggesting overlap of regional brain activations across motor execution, imagery, and observation have been focused on the upper extremity, and the functional anatomy of foot movements, furthermore, is not well understood [11–13]. Four subhypotheses were specifically evaluated toward this aim: (i) movement observation activates the same brain regions associated with imagined and executed lower extremity movements; (ii) movement execution, as compared with the other two tasks, activates a larger primary motor cortex (M1) region contralateral to movement; (iii) because movement execution is the only one of these three tasks that generates afferent somatosensory signals, primary sensory cortex was expected to show significantly larger signal during this task; and (iv) activation within SMA was hypothesized to be higher during imagined, as compared with executed or observed foot movement, based on earlier studies of the upper extremity [14].

Methods

Participants

Ten healthy adults participated in this study; each was right-handed [15], right-footed [16], and had no contraindication to MRI scanning. The experiment was conducted with the understanding and written consent of each participant, and was formally approved by local Institutional Review Boards.

Data acquisition

Participants were first introduced to the experimental tasks by watching four customized videos, each with sagittal views of the right foot. The first two videos were shown outside the scanner. Video 1 was designed to help participants understand the primary foot motor task, which was a visually cued ankle plantar-flexion/dorsi-flexion, by showing clips of a right foot in dorsi-flexion hovering above one of 10 objects, then moving in plantar-flexion to crush the object. The 10 objects varied in size and by the force required to execute the crush and were selected on the basis of the results of a pilot study showing participants could accurately rank the force required to crush each of the selected objects; they were an empty liter-size paper bag, an empty 2 liter plastic bag, sponge, pile of twine, a pile of potato chips, banana, metal shelf bracket, empty soda can, copper pipe, and aluminum duct. Video 2 introduced participants to the structure of the visual cueing that was used during functional fMRI sessions. This video-trained participants to alternate blocks of rest with blocks of movement execution. Once a participant demonstrated compliance with the instructions, they moved to the MRI scanner, where video 2 was presented again, followed by videos 3 and 4.

Videos 2–4 were shown during the fMRI scan session. Each was 8.5-min long and consisted of 30-s blocks of rest alternating with 30-s blocks of task performance, starting and ending with rest. In all blocks, a new right foot image was presented every 3 s. Across videos, rest blocks consisted of an image of a foot at rest, with instructions to remain at rest. Video 2 evaluated movement execution; the active state consisted of one of 10 images of a foot hovering above an object, and the instructions were to 'attempt completing the action' of plantar-flexion, to crush each new object with the right foot. Video 3 evaluated imagined movement; the active state consisted of the same foot hovering images as in video 2, but the instructions were to 'imagine completing the action' of crushing the object with the right foot. Video 4 evaluated movement observation; the active state consisted of video clips showing a right foot crushing an object, and the instructions were to 'carefully observe the action.'

Next, electromyography (EMG) data were collected to characterize leg muscle activity during each task. Outside the scanner, with the participant supine, surface EMG leads were attached to bilateral tibialis anterior muscles, with signal filtered (bandpass 30/1000 Hz), amplified, digitalized, and recorded. For logistical reasons, EMG for video 2 was obtained before scanning and videos 3 and 4 after scanning. During all EMG and fMRI, bilateral ankle splints [13] were fitted from lower tibia, restricting movement to 10° of ankle dorsiflexion/plantarflexion, keeping the foot above but not extending beyond the end of the table, and preventing lateral leg rotation and postural compensation.

MRI scanning

Scanning (1.5 T, Philips, Eindhoven, the Netherlands) began with a whole brain high-resolution volumetric anatomical scan (in-plane resolution 0.94 mm^2, slice thickness 1 mm). Three fMRI scans were acquired next, each 8.5-min long, showing videos 2–4, respectively. Each fMRI scan used a gradient-echo echoplanar imaging sequence, had 170 volumes, 28 axial slices of 4-mm thickness with 1-mm gap, (echo times) TE=40 ms, (repetition times) TR=3 s, flip angle=80°, field of view=24 cm, and acquisition matrix 128×128. Owing to the potential asymmetric transfer effects of movement execution on both imagery and observation, the order of fMRI scans was held constant across all participants (execution, imagery, then observation).

Behavioral compliance assessments

Each participant was monitored throughout the fMRI session to verify presence of foot movements during active blocks of video 2 and absence of visible foot movements during active blocks of videos 3–4 as well as all rest blocks. Eye position was monitored during fMRI. Participants were asked immediately after fMRI to name the objects visually presented, self-rate ability to imagine movement, and demonstrate and describe the movements observed.

Data analysis

An activation map was created separately for each participant and each task using Statistical Parametric Mapping2 (SPM2). For each, the first two functional volumes were removed from each task's images because of tissue nonsaturation. Remaining images were realigned, coregistered to the volumetric scan, spatially normalized into Montreal Neurological Institute (MNI) stereotaxic space, and spatially smoothed (8 mm full width at half maximum). Images during active state were contrasted with rest for each participant and task. Regional activation was then evaluated within and between motor-related tasks.

For each of the three motor-related tasks, random effects analysis was used to generate a group map via a voxelwise one-sample t-test across all participants. Next, a paired t-test was used to directly contrast activation in each region of interest (ROI) between each pair of tasks.

Regional activation (using small volume correction, $P<0.01$ uncorrected) was then evaluated in each group map within five motor ROI: M1, dorsal premotor (PMd), PMv, IPL, and SMA, with the first four of these examined in both right and left hemispheres and SMA treated as a single midline ROI. Each ROI was defined by a 12 mm sphere that was centered about coordinates defined from regional activation sites in a separate cohort of healthy controls imaged in an earlier study of execution of the same right foot movement [17]. In each ROI, activation location (X, Y, and Z coordinates in MNI stereotaxic space), magnitude (maximum z score), and volume (cluster size) were noted. When more than one significant cluster was present, location and magnitude were taken from the largest cluster and volume was the sum of all clusters. In addition, for activation volume, a laterality index was calculated, defined as (left−right)/(left+right), where a value of $+1$ indicates activation lateralized completely to the left hemisphere, contralateral to movement; and a value of -1 indicates lateralized completely to the right hemisphere, ipsilateral to movement.

In addition, task-related fMRI signal change was determined in foot region primary motor and primary sensory cortex on the left, contralateral to movement, for each participant, for each task [18]. These regions were defined from activation maps during movement execution in an earlier group of healthy controls [17]. Paired testing (Wilcoxon) was used within subject to directly compare signal change findings across tasks.

For EMG data, the root mean square values were determined for the first 20 s of the first two rest and active blocks. Values for rest cycles were averaged, as were values for active cycles. For each muscle during each task, EMG signal was normalized by dividing active EMG by rest EMG signal within-subject.

For all analyses, nonparametric, two-tailed statistics were used.

Results

The 10 participants were strongly right-footed (score= 1.75±0.37, mean±SD; −2 indicates left-footed; +2, right-footed) and right-handed (1.96±0.13). Participants were 31.2±8.9 years old, with seven males and three females.

Behavioral compliance with task performance was consistently good. Visual inspection by an experimenter during fMRI verified adherence to instructions. EMG recordings obtained outside the scanner were consistent with these observations (Table 1). Right tibialis EMG showed a significant change from rest, that is, the ratio (active EMG/rest EMG) was significantly different from 1, during movement execution, but not during imagery or observation. EMG in right tibialis anterior during execution was significantly greater than on the left; or on the right during the other two tasks ($P<0.05$). In addition, there were no mirror movements, as left tibialis anterior EMG did not significantly deviate from rest for any of the three tasks. When asked immediately after fMRI to self-rate ability to imagine the movements, participants uniformly considered the task to be easy, scoring 9.6±0.7 on a self-rating scale from 1 (hard to imagine) to 10 (easy to imagine). Of the 10 objects displayed during the active epoch of the movement execution task, 8.4±1.2 were recalled after fMRI. All participants were able to accurately demonstrate each of the movements that had been observed during fMRI.

Table 1 EMG results

Condition	Leg	Mean EMG
Executed movement	Right	3.74±2.92
	Left	1.07±0.10
Imagined movement	Right	0.95±0.08
	Left	1.03±0.13
Observed movement	Right	1.00±0.02
	Left	1.00±0.12

EMG values are mean±SD for tibialis anterior on each side. Within-subject, EMG is expressed as (active state)/(rest).
EMG, electromyography.

During movement execution (Table 2 and Figs 1 and 2), all motor areas examined showed significant activation bilaterally, except for PMd. Activation during execution was most prominent in motor areas contralateral to movement, with positive laterality index in each.

During imagined foot movement, all nine motor regions examined showed significant activation, most prominently in SMA, left IPL, and bilateral PMv. The laterality index indicated leftward lateralization for PMd, M1, and IPL but rightward lateralization for PMv. Again, lateralization to the left was most prominent for IPL.

During observed foot movement, significant activation was present in all nine motor regions examined except left M1. Activation was most prominent in bilateral IPL and PMv. The laterality index indicated leftward lateralization for PMd, PMv, and IPL but rightward lateralization for M1.

The above divergent results across individual tasks were also apparent when voxelwise paired testing was used to directly contrast tasks (Table 3). In particular, movement execution showed significantly greater activation (i.e. larger spatial extent) within left M1 than during imagery or observation. Movement imagery showed significantly greater activation within SMA and bilateral PMv than execution or observation. Movement observation showed significantly

Table 2 Regional activation during each of the three lower extremity motor-related tasks

		Executed movement					Imagined movement					Observed movement				
				Coordinates					Coordinates					Coordinates		
Region	Hemisphere	Cluster size	Maximum *z* score	*X*	*Y*	*Z*	Cluster size	Maximum *z* score	*X*	*Y*	*Z*	Cluster size	Maximum *z* score	*X*	*Y*	*Z*
SMA	Bilateral	629	3.67	2	−6	70	848	4.42	4	−6	68	76	2.86	2	0	62
PMv	Right	87	2.75	48	4	0	567	3.55	44	12	−4	166	3.7	−52	16	8
	Left	211	3.23	−50	4	4	494	3.78	−48	8	18	195	4.13	−52	6	22
	Laterality index	0.42					−0.07					0.08				
PMd	Right	0					163	3.2	40	−12	60	31	3.37	36	−8	58
	Left	0					228	3.99	−30	−10	64	125	3.03	−44	−8	60
	Laterality index						0.17					0.60				
M1	Right	193	3.76	2	−12	52	32	2.68	26	−12	62	35	2.95	30	−16	46
	Left	545	5.28	−6	−46	72	49	2.85	−12	−32	62	0				
	Laterality index	0.48					0.21					−1				
IPL	Right	8	2.73	34	−52	48	48	2.87	40	−42	62	271	4.59	32	−54	50
	Left	568	4.86	−54	−32	24	629	3.84	−54	−36	34	569	4.27	−58	−36	36
	Laterality index	0.97					0.86					0.35				

Data are regional analysis of the group map for each task, using small volume correction at $P<0.01$, uncorrected. Activation volume is represented by cluster size; location, by *XYZ* coordinates (in MNI stereotaxic space) of voxel at maximum *z* score; and magnitude, by the maximum *z* score.
IPL, inferior parietal lobule; M1, precentral gyrus; MNI, Montreal Neurological Institute; PMd, dorsal premotor area; PMv, ventral premotor area; SMA, supplementary motor area.

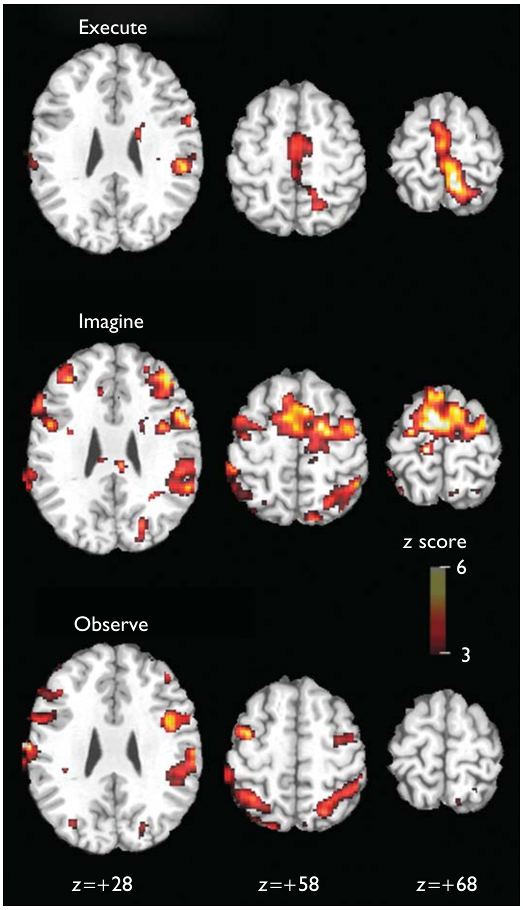

Fig. 1 One sample *t*-tests show the group maps of brain activation during each of the three motor-related tasks. The Montreal Neurological Institute *z* values (at bottom) represent the slice levels depicted.

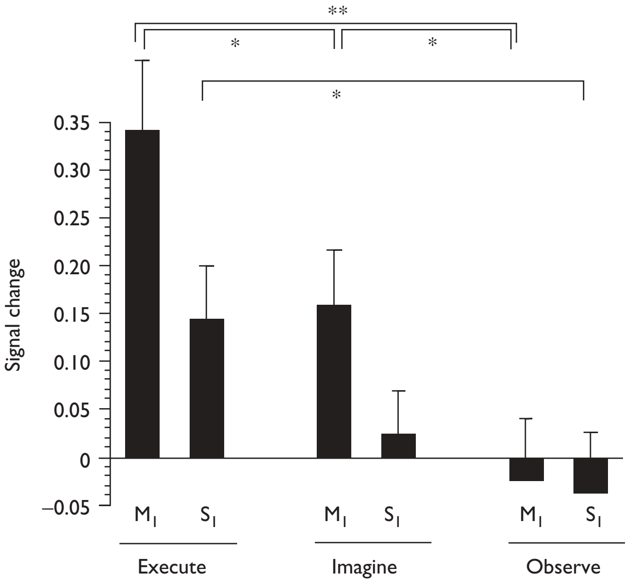

Fig. 2 Task-related signal change, mean ± SEM; the regions of interest are all on the left, and consist of foot M1 (primary motor cortex) or S1 (primary sensory cortex). Paired testing for comparison of tasks significant at $^{*}P<0.05$, $^{**}P<0.005$.

Table 3 Direct contrast of activation across the three tasks

Task contrast	Region	Hemisphere	Cluster size	Maximum z score	Coordinates X	Coordinates Y	Coordinates Z
Execute > imagine	M1	Left	267	4.37	−8	−44	72
	IPL	Left	19	3.04	−50	−26	22
Execute > observe	SMA		376	4.42	0	−8	52
	PMv	Right	51	3.01	46	0	6
	M1	Left	650	5.59	−8	−42	74
	IPL	Right	14	2.86	18	−44	56
		Left	44	3.34	−52	−28	22
Imagine > execute	SMA		116	3.26	−10	−6	66
	PMv	Right	416	3.64	50	20	2
		Left	122	3.16	−56	−4	6
	PMd	Right	489	4.20	30	−18	66
		Left	200	3.61	−44	−22	56
	M1	Right	34	2.88	36	−20	46
	IPL	Right	20	2.77	32	−36	64
		Left	144	3.29	−56	−40	26
Imagine > observe	SMA		599	4.46	4	−6	68
	PMv	Right	353	4.46	58	8	0
		Left	101	3.27	−56	0	6
	PMd	Right	70	3.76	30	−18	66
		Left	6	2.39	−42	−20	54
	M1	Left	137	3.51	−8	−40	74
Observe > execute	PMv	Right	90	4.03	50	18	4
	PMd	Left	98	3.09	−38	−22	68
	M1	Right	20	2.79	34	−22	46
	IPL	Right	233	4.89	38	−50	56
		Left	25	3.04	−56	−34	36
Observe > imagine	IPL	Right	162	4.49	38	−50	56

A voxelwise comparison was performed using paired testing in SPM2. IPL, inferior parietal lobule; M1, precentral gyrus; PMd, dorsal premotor area; PMv, ventral premotor area; SMA, supplementary motor area.

greater activation within right IPL than execution or imagined movement.

Percent signal change, representing magnitude of activation, during each condition (Fig. 2) found left (contralateral) M1 activation during movement execution to be significantly larger than during imagery or observation. Left S1 activation was present during movement execution and essentially absent during imagery and observation, though only the execution-observation contrast was significant.

Discussion

The primary aim of this study was to evaluate the extent of activation overlap in five bilateral brain regions of interest during executed, imagined, and observed lower extremity movements. The results confirm that activation was present in most of the examined motor-related brain regions, during all three motor-related tasks. The findings extend earlier results from the upper extremity to the lower extremity. Specific differences between the three tasks were also measured. Overall, the data support theories that emphasize shared motor system substrates across movement execution, imagery, and observation [5], and extend these theories to the study of lower extremity movements.

Though activation patterns across the three tasks showed many overlapping features, important differences between lower extremity movement execution, imagery, and observation were also found, in both spatial extent and signal magnitude. Specifically, execution was associated with significantly greater extent and magnitude of activation in M1 than during imagery and observation. This finding is consistent with earlier studies of the upper [19] or lower [17] extremity and is likely because M1 is the largest source of corticospinal tract axons driving movement execution [20]. Movement execution was also associated with the largest degree of S1 signal change (Fig. 2), possibly explained by somatosensory feedback that is present during executed but absent during imagined or observed movement, or by the projections that S1 has to M1 and to the spinal cord [20,21]. In addition, PMd activation was absent during movement execution, consistent with earlier studies of the lower extremity [13,17].

Motor imagery is associated with prominent SMA activation for the upper extremity [14] that in some cases is greater than that present during movement execution [22]. In this study, significantly greater activation was found within the SMA and bilateral PMv during movement imagery as compared with observation and execution, suggesting a greater involvement of movement planning networks during motor imagery as versus observation and execution.

This study also addressed the hypothesis that lower extremity movement observation activates the same brain regions as with movement execution and imagery. This question has clinical relevance given the potential use of observation to potentiate motor imagery-based mental practice and subsequent physical rehabilitation. Significant activation was present in all but one of the nine motor regions examined during observed foot movement, supporting the hypothesis. This suggests a potential role of movement observation in modulating lower extremity motor behavior, although this suggestion must be greeted with caution given that significant M1 activation was only seen ipsilateral to observed foot movement (Table 2), and it is contralateral M1 activation that is central to movement generation. Earlier studies of the upper extremity have consistently described bilateral M1 activation with movement observation [23,24]. This finding of only ipsilateral M1 activation with lower extremity observed movement has not been previously described. This finding might simply reflect sparse M1 activation during lower extremity movement observation, being zero contralateral and very small ipsilateral, or this finding might in part relate to differences in the brain organization of upper versus lower extremity movements.

Another finding related to lower extremity movement was that movement observation, as compared with execution and imagery, had significantly greater right IPL activation. This finding may reflect the role attributed to IPL in spatial and memory components of movement planning [3]. In addition, IPL activation is strongest when movement includes an object [25], as was the case in this study. During observation, activation was also relatively prominent in bilateral PMv. This region is a component of the 'mirror neuron system,' which is involved in both action recognition and observational learning, and is active during both the execution and observation of actions [5,9,10]. This suggests that principles of mirror neuron system function also extend to the lower extremity.

Conclusion

Abnormalities in lower extremity motor control are a major source of disability with normal aging, stroke, multiple sclerosis, spinal cord injury, and many other prevalent conditions. These results advance the development of an evidence-based motor learning program to improve function for lower extremity neuromotor rehabilitation by confirming extensive motor network activation during the observation and the imagery of lower extremity movement.

Acknowledgement

This study was supported by grant M01 RR000827-29 from the UC Irvine General Clinical Research Centers Program of the National Center for Research Resources, National Institutes of Health.

References

1. Schmidt RA. Motor schema theory after 27 years: reflections and implications for a new theory. *Res Q Exerc Sport* 2003; **74**:366–375.
2. Decety J. Do imagined and executed actions share the same neural substrate? *Brain Res* 1996; **3**:87–93.
3. Stephan KM, Fink GR, Passingham RE, Silbersweig D, Ceballos-Baumann AO, Frith CD, *et al*. Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *J Neurophysiol* 1995; **73**:373–386.
4. Sharma N, Pomeroy VM, Baron JC. Motor imagery: a backdoor to the motor system after stroke? *Stroke* 2006; **37**:1941–1952.
5. Jeannerod M. Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage* 2001; **14**:S103–S109.
6. Lafleur M, Jackson P, Malouin F, Richards C, Evans A, Doyon J. Motor learning produces parallel dynamic functional changes during the execution and imagination of sequential foot movements. *Neuroimage* 2002; **16**:142–157.
7. Lacourse M, Turner J, Randolph-Orr E, Schandler S, Cohen M. Cerebral and cerebellar sensorimotor plasticity following motor imagery-based mental practice of a sequential movement. *J Rehabil Res Dev* 2004; **41**: 505–524.
8. Cramer SC, Orr EL, Cohen MJ, Lacourse MG. Effects of motor imagery training after chronic, complete spinal cord injury. *Exp Brain Res Exp Hirnforschung* 2007; **177**:233–242.
9. Rizzolatti G, Luppino G. The cortical motor system. *Neuron* 2001; **31**: 889–901.
10. Pomeroy VM, Clark CA, Miller JS, Baron JC, Markus HS, Tallis RC. The potential for utilizing the 'mirror neuron system' to enhance recovery of the severely affected upper limb early after stroke: a review and hypothesis. *Neurorehabil Neural Repair* 2005; **19**:4–13.
11. Buccino G, Binkofski F, Fink G, Fadiga L, Fogassi L, Gallese V, *et al*. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur J Neurosci* 2001; **13**:400–404.
12. Sahyoun C, Floyer-Lea A, Johansen-Berg H, Matthews P. Towards an understanding of gait control: brain activation during the anticipation, preparation and execution of foot movements. *Neuroimage* 2004; **21**: 568–575.
13. Dobkin BH, Firestine A, West M, Saremi K, Woods R. Ankle dorsiflexion as an fMRI paradigm to assay motor control for walking during rehabilitation. *Neuroimage* 2004; **23**:370–381.
14. Porro CA, Cettolo V, Francescato MP, Baraldi P. Ipsilateral involvement of primary motor cortex during motor imagery. *Eur J Neurosci* 2000; **12**: 3059–3063.
15. Oldfield R. The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia* 1971; **9**:97–113.
16. Coren S. The lateral preference inventory for measurement of handedness, footedness, eyedness, and earedness: norms for young adults. *Bull Psychonom Soc* 1993; **31**:1–3.
17. Cramer SC, Lastra L, Lacourse MG, Cohen MJ. Brain motor system function after chronic, complete spinal cord injury. *Brain* 2005; **128**: 2941–2950.
18. Brett M, Anton J-L, Valabregue R, Poline J-B. Region of interest analysis using an SPM toolbox. 8th International Conference on Functional Mapping of the Human Brain, June 2-6, 2002. Sendai, Japan: 2002.
19. Porro C, Francescato M, Cettolo V, Diamond M, Baraldi P, Zuiani C, *et al*. Primary motor and sensory cortex activation during motor performance and motor imagery: a functional magnetic resonance imaging study. *J Neurosci* 1996; **16**:7688–7698.

20. Galea M, Darian-Smith I. Multiple corticospinal neuron populations in the macaque monkey are specified by their unique cortical origins, spinal terminations, and connections. *Cereb Cortex* 1994; **4**:166–194.
21. Soso M, Fetz E. Responses of identified cells in postcentral cortex of awake monkeys during comparable active and passive joint movements. *J Neurophysiol* 1980; **43**:1090–1110.
22. Gerardin E, Sirigu A, Lehericy S, Poline JB, Gaymard B, Marsault C, *et al*. Partially overlapping neural networks for real and imagined hand movements. *Cerebral Cortex* 2000; **10**:1093–1104.
23. Grezes J, Costes N, Decety J. Top-down effect of strategy on the perception of human biological motion: a PET investigation. *Cogn Neuropsychol* 1998; **15**:553–582.
24. Aziz-Zadeh L, Maeda F, Zaidel E, Mazziotta J, Iacoboni M. Lateralization in motor facilitation during action observation: a TMS study. *Exp Brain Res* 2002; **144**:127–131.
25. Faillenot I, Toni I, Decety J, Gregoire MC, Jeannerod M. Visual pathways for object-oriented action and object recognition: functional anatomy with PET. *Cereb Cortex* 1997; **7**:77–85.