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ORIGINAL PAPER

Brain Activation Patterns Characterizing Different Phases of Motor Action: Execution, Choice and Ideation

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Abstract Motor behaviour is controlled by a large set of interacting neural structures, subserving the different components involved in hierarchical motor processes. Few studies have investigated the neural substrate of higher-order motor ideation, i.e. the mental operation of conceiving a movement. The aim of this functional magnetic resonance imaging study was to segregate the neural structures involved in motor ideation from those involved in movement choice and execution. An index finger movement paradigm was adopted, including three different conditions: performing a pre-specified movement, choosing and executing a movement and ideating a movement of choice. The tasks involved either the right or left hand, in separate runs. Neuroimaging results were obtained by comparing the different experimental conditions and computing conjunction maps of the right and left hands for each contrast. Pre-specified movement execution was supported by bilateral fronto-parietal motor regions, the cerebellum and putamen. Choosing and executing finger movement involved mainly left fronto-temporal areas and the anterior cingulate. Motor ideation activated almost exclusively left hemisphere regions, including the inferior, middle and superior frontal regions, middle temporal and middle occipital gyri. These findings show that motor ideation is controlled by a cortical network mainly involved in abstract thinking, cognitive and motor control, semantic and visual imagery processes.

Keywords Movement · Ideation · Motor ideation · fMRI · Finger movement

Introduction

Motor behaviour encompasses a large variety of functional components, which are supported by different neural networks. Bernstein (1996) hypothesized different basilar aspects of action representation, such as chaining structures of movements in combination to attain a goal, adaptive variability of motor elements in a novel context to achieve an objective, recursion as the ability to retrieve previously learned elements that form the substrates for generating an action. Evidence from mapping studies in experimental animals and humans supports the concept of a hierarchical distributed model for motor planning and execution (Grafton and Hamilton 2007), which includes a set of interconnected brain areas that are differentially recruited for different aspects of goal-oriented motor behaviours.

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Based on the cytoarchitectonic maps of the human cerebral cortex, the precentral cortex located anteriorly to the central sulcus (Brodmann area 4) is involved in motor control, whereas the intermediate precentral cortex (Brodmann area 6) located rostrally to the precentral cortex and caudal to the prefrontal lobe is involved in higher-order motor processes, showing that this architectonic organization reflects functional differences. Furthermore, Brodmann area 4 and the caudal part of Brodmann area 6 form a functional entity constituting the primary motor cortex (M1), while the mesial sector of area 6 forms the "supplementary motor area" (SMA) (Rizzolatti and Fogassi 2014). Tanji and Hoshi (2008) have highlighted the central and essential role of the lateral prefrontal cortex in several executive cognitive functions, like information processing, attentional regulation and different aspects of motor control, such as integrative action planning, selective attention for action and in selecting an intended action.

Recent evidence (Drew and Marigold 2015) has also confirmed that the posterior parietal cortex is mainly involved in the planning of movements, whereas the motor cortex contributes primarily to the execution of a movement. Relatedly, animal studies on macaque monkeys have shown that the preparation and planning of actions before execution is accompanied by an increment of neuronal activity in brain regions such as the medial posterior parietal areas (Breveglieri et al. 2014). Taken together, these studies point towards a hierarchical organization of the motor system and illustrate distinct brain structures that are part of this system.

Several studies have investigated the brain substrates of motor imagery, i.e. mental rehearsal in one's mind's eye of a movement, and have found that motor imagery activates to a large extent the same brain networks involved in motor execution, including parts of the SMA, the dorsal premotor cortex, the posterior parietal cortex, the cerebellum and M1 in certain conditions (Lui et al. 2008; Gao et al. 2011; Raffin et al. 2012), showing the potential role of motor imagery in motor rehabilitation (Sharma et al. 2006). Recent functional neuroimaging studies, using region of interest analyses, however, have shown a specific pattern associated with motor execution and imagery (Raffin et al. 2012). The former would activate more the primary somatosensory cortex, the primary motor cortex and the anterior lobe of the cerebellum, whereas the latter would involve the parietal and occipital lobes, and the posterior lobe of the cerebellum, which demonstrates a clear neurophysiological distinction between movement execution and imagery. Further analysis using dynamic causal modelling showed that motor imagery and motor execution have opposite effects on the activation of the SMA-M1 cortical network. In an fMRI study, Bajaj et al. (2015) found that after treatment following a stroke, patients activated the same pattern during motor imagery and motor execution, but the SMA had a suppressive influence on M1 during motor imagery, whereas the influence of the SMA on M1 was unrestricted during motor execution.

In a few reports, the terms motor imagery and motor ideation have been used to indicate the same process (Olsson and Nyberg 2010), even if they refer to distinct cognitive functions. Motor imagery and motor ideation are different in nature, the first signifying an image-like representation and the second a verbal and abstract one. Based on cognitive models of information coding, Paivio (1971) (see also Mammarella et al. 2004) proposed a dual coding theory of mental processing. Two different sub-systems exist: a verbal one, responsible for the encoding and processing of verbal material, and a non-verbal one, responsible for encoding non-verbal input, like images. The two representational systems would be independent. From the beginning the two kinds of representation would be different: the logogens are the basic units of verbal stimuli, while the imagens indicate the basic units for the imagery material. The basic units refer to different systems in long-term memory. Representational connections directly activate the verbal or non-verbal representations. Referential connections between the two processes are activated when one type of information (verbal or image based) activates the other system. In this case there is a double encoding. In the present study we refer to Paivio's model to conceptualize the ideation of movement in an abstract format.

Delineating an exact border between imagery and abstract thinking can be difficult because mental images are created almost continually in our minds, and represent a basic element of thinking (Singer and Antrobus 1972). Helping to draw a distinction between motor ideation and motor imagery, and further illustrating the hierarchical organisation of the motor system, clinical studies have described patients with ideational apraxia—a disorder of voluntary movement caused by a specific impairment of motor planning, in the absence of any perceptual, strength or motor coordination disorders—who as a result of brain damage are unable to represent a movement mentally, for example how to light a candle (De Renzi and Lucchelli 1988), because the corresponding motor programme has been damaged. For these reasons patients with ideational apraxia suffer from incapacity to represent an action in its entirety and sequence. The correct motor programme necessary to finalize an action is altered and the goal of the motor act cannot be reached due to the loss of the mental formula and semantics of actions. At the basis of ideational apraxia there would be an amnesia for the use of objects, such as a disorder in recalling semantic memory of attributes relating to object use. In conclusion, ideational apraxia might not constitute a higher-order programming deficit of movement per se, but a combination of executive, language, and memory deficits or a diffuse reduction of cognitive resources (Gross and Grossman 2008). Different lesion sites have been indicated as responsible for ideational apraxia, showing an involvement of mainly left temporo-parieto-occipital regions (Hécaen 1972; Bolognini et al. 2015) even if patients with ideational apraxia have also been reported following frontal lesions, or basal ganglia damage (De Renzi and Lucchelli 1988; Manuel et al. 2013; Huey et al. 2009). Patients with ideational apraxia can retain mental imagery abilities (Tomasino et al. 2003). On the other hand there are patients who show mental imagery deficits (e.g. patients with posterior cortical neurodegeneration) who do not experience ideational apraxia (Gardini et al. 2011). The evidence from such dissociation supports, in addition to the evidence from experimental psychology, the independence of ideational and imagery processes and their relative neural substrates.

Only a few studies have focused on the neural correlates of motor ideation, such as the process of mentally representing a sequence of movement, but without actually performing it. Ingvar and Philipson (1977) investigated the changes of regional cerebral blood flow during three different situations: at rest, during motor ideation (attempts to conceive rhythmic clenching movements of the right hand), and during actual movements of the right hand. Motor ideation produced an increase of the mean flow in fronto-temporal structures, a pattern which was different from that observed during actual hand movements when a blood flow increase in the rolandic regions was seen. These results suggested that the neural centres for motor ideation and actual hand movement were located in different parts of the brain. In line with Ingvar and Philipson (1977), we investigated the neural substrates of motor ideation during the attempts to conceive movements of the index finger.

In this paper, action ideation (conceiving a movement) is considered to be at the top of the motor hierarchy, followed by choosing and performing an action, and performing a pre-defined action (without the requirement for decision making) is considered to be at the bottom of the hierarchy.

Bernstein (1996) referred to an internal structure at the highest level of the motor hierarchy, which could be considered as the neural centre of motor ideation. The preliminary attempt to investigate the neuroimaging substrates of motor ideation described above showed that this process involves specifically frontal and temporal regions (Ingvar and Philipson 1977). In terms of choosing a movement, PET studies have shown involvement of the dorso-lateral pre-frontal cortex (DLPFC) during the performance of willed actions (Frith 1991) and in particular the influence of the left DLPFC in the selection of actions (Schluter et al. 2001). Functional magnetic resonance imaging (fMRI) studies have also revealed the involvement of the pre-SMA (supplementary motor area) in the early stage of movement preparation, which precedes the onset of voluntary movements (Cunnington et al. 2002).

Given the limited literature on motor ideation, the mapping of this component of movement in the brain remains unclear and the neural networks that are engaged in this higher-order cognitive process have not been identified. In our study a hierarchical structure of experimental conditions was set up in the attempt to extrapolate the neural structures involved in motor ideation without contamination from the motor component. To our knowledge this is the first study attempting to investigate the neural substrates of motor ideation generated through a verbal representation, comparing the pattern of activation with that of motor choice and pre-specified motor execution.

The experimental conditions have been fixed following the progression from a low level where the effector takes place (execution of pre-specified movement), to the highest level of motor ideation without motor execution.

We hypothesized that motor ideation would require greater frontal involvement (deputed to higher-order executive motor control) than would be recruited in motor execution. Motor choice would engage both motor areas and structures deputed to motor control and selection. Motor execution would activate a set of structures belonging to the motor execution network and including fronto-parietal and cerebellar regions.

Materials and Methods

Participants

Twenty right-handed volunteers underwent fMRI after written consent. After quality control check, image data from five volunteers had to be discarded because of contamination due to movement artefacts. The final sample, therefore, included fifteen right-handed volunteers (five males, ten females; mean age 28.5, SD 3.42; mean education 19, SD 3.28 years). The present study received ethical approval from the University of Modena and Modena Province Ethics Committee, Italy and was carried out in accordance with the Code of Ethics of the World Medical Association (Declarations of Helsinki of 1975) for experiments involving humans. Informed consent was obtained from all volunteers included in the study.

Procedure

Echo planar single shot T2* weighted images (TR $= 2.5$ s, TE $= 30$ ms, flip angle $= 90°$, voxel dimensions $1.88 \times 1.88 \times 5.00$ mm. $128 \times 128 \times 24$) were acquired on a 3T

Philips Intera MRI system with SENSE Head Coil. One hundred and seventy-six volumes of 24 contiguous slices were acquired in each run ($n = 4$). Each run lasted 7 min and 20 s, and was preceded by 30 s of dummy scans to allow the scanner to reach equilibrium. A block design fMRI paradigm of hierarchically organized movement conditions, from execution to higher order motor ideation, was implemented using the E-Prime software and delivered using the integrated IFIS visual presentation system. The paradigm involved four conditions: 1. "Rest" condition; 2. "Motor execution"—perform a pre-specified movement (move index finger up or down) selected by the examiner; 3. "Choice"—move index finger up or down at the choice of the participant; 4. "Ideate"—think about making a movement of the index finger up or down at the choice of the participant. The instructions were: 'please move your right index finger as indicated' for pre-specified movement condition, 'please move your right index finger up or down when indicated' for chosen movement; and 'please think about moving your right index finger up or down when indicated' for movement ideation.

During the condition of movement ideation, participants were specifically requested to ideate the movement, by mentally choosing and representing it abstractly (but without imagining it visually and without actually executing it). The process of ideation would therefore include, for example, identifying the goal of the movement, selecting the movement, the motor planning of the movement and the theoretical representation of the movement.

Participants underwent behavioural training in performing all experimental conditions prior to MRI scanning. A post-fMRI experiment check was carried out and an informal questionnaire was administered to participants in order to observe how they performed the tasks, in particular the ideation one. Participants' reports showed that they had no difficulties in following the instructions and to ideate (Think) the movement.

Four runs were obtained, two involving the right hand and two the left hand. Hand order was counterbalanced across participants. Each condition was repeated four times in each run (16 in total across the experiment; a total of eight for each hand). The time-periods containing the instructions were not modelled in the analysis. The movement/movement ideation required was paced via on-screen single word cues (rest, move up or move down, choose, and ideate), which remained on-screen for 1.5 s interspersed with 1 s blank screens (10 trials in each condition). There were therefore 40 trials per condition per run. All durations modelled for each condition were the same (10 TRs = 25 s). Participants had to respond as quickly as possible following the appearance of the on-screen cues. Movements of other fingers were restrained by participants wearing a customized polystyrene cast on each hand, which allowed them to move their index finger either up or down but impeded movements of the remaining fingers. Practice trials were given outside the scanner environment so that participants could familiarize themselves with the experimental paradigm.

Neuroimaging data were analysed using the SPM5 (Wellcome Trust Centre for Neuroimaging, London, UK) software package. For each subject, all functional volumes were realigned to the first volume acquired, slice time corrected, normalized to the MNI (Montreal Neurological Institute) template, and smoothed with a $8 \times 8 \times 8$ mm FWHM Gaussian kernel. The six motion parameters obtained during image realignment were included as nuisance regressors to account for possible residual movement-related signal changes. For each hand, the following contrasts were examined: pre-specified movement versus rest, voluntary movement versus rest, movement ideation versus rest, voluntary movement versus pre-specified movement, movement ideation versus voluntary movement. At the second level, conjunction analyses of activations maps obtained from each individual contrast for the right and left hands were carried out to find out the areas commonly activated by either hands in each experimental condition. A conjunction is the joint refutation of multiple null hypotheses, in this instance, of no activation in any subject. Using a conjunction analysis (SPM-"Conjunction Null"), allows one to infer that every subject studied activated the observed regions and that at least a certain proportion of the population would have shown this effect (Friston et al. 1999).

Because we were interested in observing brain activations during each experimental condition independently from the hand side, we reported all statistical contrasts computed in the results section (including those referring to Left/Right hand), and we discuss only results referring to the conjunction analyses.

Unless otherwise stated, the significance level was set using an uncorrected voxel threshold of $p < 0.001$. To account for multiple comparisons, only those clusters that survived FWE correction (based on Gaussian Random Field Theory) with a cluster-level threshold of $p < 0.05$ were reported as significant.

Results

We report here the foci of activation detected during the tasks, which were commonly activated by movements in both hands, as revealed by conjunction analyses. Tables 1, 2, 3, 4, 5 and Figs. 1, 2 and 3 provide details on the analyses of each hand separately, in addition to the conjunction analyses.

Table 1 Pre-specified movement versus rest

Brain area—Brodmann area (BA)	Left/right	Number of voxels in cluster	Cluster-level *p* value (corrected)	Z value at local maximum	Talairach coordinates		
					x	y	z
(a) Pre-specified movement versus rest—left hand							
Cerebellum	L	2317	0.000	5.87	−18	−54	−23
Postcentral gyrus (BA 2)	R	6455	0.000	5.50	40	−25	44
Precentral gyrus (BA 4)	R			5.44	34	−20	62
Precentral gyrus (BA 44)	R	377	0.002	4.87	48	0	7
Inferior frontal gyrus (BA 44)	R			3.65	55	5	16
Cerebellum	R	533	0.000	4.77	32	−48	−30
Putamen	L	767	0.000	4.51	−22	−5	9
Superior temporal gyrus (BA 22)	L			4.11	−48	0	4
Putamen	R	726	0.000	4.41	28	−21	−2
Inferior parietal lobule (BA 40)	L	510	0.000	3.92	−38	−35	48
Postcentral gyrus (BA 5)	L			3.70	−38	−40	61
Postcentral gyrus (BA 40)	L	350	0.003	3.85	−55	−25	14
Postcentral gyrus (BA 2)	L			3.77	−61	−18	27
(b) Pre-specified movement versus rest—right hand							
Cerebellum	R	5633	0.000	6.24	30	−58	−27
Postcentral gyrus (BA 40)	L	16,692	0.000	6.15	−38	−32	53
Medial frontal gyrus (BA 6)	L			5.66	−14	−1	52
Transverse temporal gyrus (BA 41)	L			5.65	−53	−25	10
Postcentral gyrus (BA 40)	R	2977	0.000	5.31	61	−24	18
Postcentral gyrus (BA 1)	R			4.42	65	−16	28
Inferior parietal lobule (BA 40)	R			4.28	42	−33	48
Precentral gyrus (BA 6)	R	2834	0.000	5.01	59	5	27
Superior temporal gyrus (BA 22)	R			4.69	51	6	0
Putamen	R			4.44	26	−4	8
(c) Pre-specified movement versus rest—conjunction							
Cerebellum	L	1371	0.000	5.18	−24	−63	−22
Medial frontal gyrus (BA 6)	L	4489	0.000	5.09	−4	−3	57
Medial frontal gyrus (BA 6)	R			5.04	2	1	52
Cingulate gyrus (BA 24)	L			5.01	−16	−3	50
Cerebellum	R	1385	0.000	5.08	30	−58	−26
Cerebellum	L			4.98	−2	−71	−13
Superior temporal gyrus (BA 22)	R	1349	0.000	5.04	50	4	5
Putamen	R			4.51	26	−5	9
Superior temporal gyrus (BA 41)	L	2633	0.000	5.03	−55	−25	12
Postcentral gyrus (BA 40)	L			4.47	−38	−34	51
Postcentral gyrus (BA 2)	L			4.43	−57	−18	29
Inferior parietal lobule (BA 40)	R	2144	0.000	4.92	42	−31	44
Postcentral gyrus (BA 40)	R			4.76	59	−22	18
Precentral gyrus (BA 6)	R			4.42	63	−16	39

Significant activations for (a) the left hand, (b) right hand, and (c) the conjunction (left hand and right hand). Combined height threshold $p < 0.001$, and clusters with p value correction applied ($p < 0.05$)

Pre-specified movement execution versus rest was accompanied by bilateral activations in the cerebellum, perirolandic areas peaking in the postcentral gyri (BA 40 and 2 on the left; BA 40 on the right), medial frontal gyri (BA 6), superior temporal gyri (BA 41 and 24 on the left; BA 22 on the right), left cingulate (BA 24), right precentral

Table 2 Choice of movement versus rest

Brain area—Brodmann area (BA)	Left/right	Number of voxels in cluster	Cluster-level *p* value (corrected)	Z value at local maximum	Talairach coordinates x y z		
(a) Choice of movement versus rest—left hand							
Cerebellum	L	2417	0.000	6.36	−14	−54	−23
Postcentral gyrus (BA 2)	R	7304	0.000	6.10	40	−25	44
Precentral gyrus (BA 4)	R			5.45	38	−17	58
Middle frontal gyrus (BA 6)	R			5.26	28	−4	46
Putamen	L	1258	0.000	4.81	−26	0	9
Insula (BA 13)	L			4.69	−36	−3	17
Cerebellum	R	481	0.000	4.79	34	−48	−31
Putamen	R	1792	0.000	4.66	24	−6	6
Claustrum	R			4.39	32	−4	−5
Superior temporal gyrus (BA 22)	R			4.29	50	2	4
Inferior frontal gyrus (BA 44)	L	179	0.030	4.09	−59	9	18
Postcentral gyrus (BA 2)	L	1054	0.000	4.00	−61	−18	29
Transverse temporal gyrus (BA 41)	L			3.99	−51	−25	10
Postcentral gyrus (BA 40)	R	212	0.014	3.73	63	−28	18
Inferior parietal lobule (BA 40)	R			3.61	61	−36	24
Thalamus	R	160	0.046	3.65	16	−21	5
Red Nucleus	R			3.39	8	−22	−7
(b) Choice of movement versus rest—right hand							
Postcentral gyrus (BA 3)	L	18,633	0.000	6.30	−36	−32	53
Medial frontal gyrus (BA 6)	L			6.12	−2	−3	55
Precentral gyrus (BA 4)	L			6.02	−32	−22	56
Cerebellum	R	4867	0.000	5.84	32	−48	−30
Superior temporal gyrus (BA 42)	R	3780	0.000	5.17	61	−25	14
Inferior parietal lobule (BA 40)	R			4.89	42	−38	52
Insula (BA 13)	R	4365	0.000	5.17	46	4	3
Inferior frontal gyrus (BA 9)	R			4.74	61	7	27
Middle frontal gyrus (BA 10)	R	151	0.049	3.71	36	36	22
Middle frontal gyrus (BA 10)	L	174	0.028	3.58	−36	38	17
(c) Choice of movement versus rest—conjunction							
Cerebellum	L	1799	0.000	6.50	−24	−61	−22
Medial frontal gyrus (BA 6)	L	3612	0.000	5.97	−4	−3	57
Medial frontal gyrus (BA 6)	R			5.74	6	−1	52
Middle frontal gyrus (BA 6)	R			5.59	30	−3	50
Superior temporal gyrus (BA 22)	R	2273	0.000	5.53	50	2	4
Putamen	R			5.06	28	−2	6
Inferior frontal gyrus (BA 44)	R			4.50	59	8	14
Inferior parietal lobule (BA 40)	R	3619	0.000	5.39	38	−35	44
Precentral gyrus (BA 6)	R			4.63	59	−12	37
Cerebellum	R	598	0.000	5.20	34	−50	−29
Superior temporal gyrus (BA 22)	L	1556	0.000	4.85	−50	4	2
Putamen	L			4.75	−32	−2	2
Inferior frontal gyrus (BA 44)	L			4.53	−59	7	16
Transverse temporal gyrus (BA 41)	L	2090	0.000	4.63	−53	−25	10
Postcentral gyrus (BA 2)	L			4.42	−57	−18	29
Inferior parietal lobule (BA 40)	L			4.42	−44	−28	33

Significant activations for (a) the left hand, (b) right hand, and (c) the conjunction (left hand and right hand). Combined height threshold $p < 0.001$, and clusters with p-value correction applied ($p < 0.05$)

Table 3 Movement ideation versus rest

Brain area—Brodmann area (BA)	Left/right	Number of voxels in cluster	Cluster-level *p* value (corrected)	Z value at local maximum	Talairach coordinates		
					x	y	z
(a) Movement ideation versus rest—left hand							
Cerebellum	L	791	0.000	4.98	−46	−62	−27
Cerebellum	R	708	0.000	4.96	36	−56	−27
Medial frontal gyrus (BA 6)	L	5688	0.000	4.75	−4	−5	59
Middle frontal gyrus (BA 6)	L			4.75	−20	−9	56
Precentral gyrus (BA 6)	R			4.57	57	0	42
Middle frontal gyrus (BA 10)	L	782	0.000	4.74	−30	38	17
Middle frontal gyrus (BA 9)	L			4.12	−40	31	28
Precentral gyrus (BA 4)	L	2755	0.000	4.69	−50	−4	44
Claustrum	L			4.41	−36	−2	0
Precentral gyrus (BA 6)	L			4.36	−61	5	16
Superior temporal gyrus (BA 42)	R	954	0.000	4.62	67	−30	18
Inferior parietal lobule (BA 40)	R			4.00	42	−35	42
Superior temporal gyrus (BA 13)	L	1102	0.000	4.22	−55	−40	19
Inferior parietal lobule (BA 40)	L			3.95	−61	−35	29
Postcentral gyrus (BA 2)	L			3.88	−42	−36	61
(b) Movement ideation versus rest—right hand							
Medial frontal gyrus (BA 6)	L	18,986	0.000	5.24	−4	1	52
Superior frontal gyrus (BA 6)	R			5.06	8	5	64
Claustrum	L			4.95	−36	2	−2
Cerebellum	L	615	0.000	4.82	−46	−58	−29
Cerebellum	R	890	0.000	4.61	34	−56	−31
Inferior parietal lobule (BA 40)	R	1570	0.000	4.55	65	−39	30
Superior temporal gyrus (BA 42)	R			4.27	65	−32	20
Medial frontal gyrus (BA 9)	R	389	0.001	3.61	26	38	22
Middle frontal gyrus (BA 10)	R			3.55	36	38	22
Superior frontal gyrus (BA 10)	R			3.53	30	48	22
(c) Movement ideation versus rest—conjunction							
Medial frontal gyrus (BA 6)	L	8129	0.000	5.79	−2	−1	57
Superior frontal gyrus (BA 6)	R			5.58	8	5	64
Superior frontal gyrus (BA 6)	L			5.47	−6	8	49
Cerebellum	L	709	0.000	5.19	−46	−58	−29
Superior temporal gyrus (BA 22)	R	3091	0.000	5.04	51	6	5
Precentral gyrus (BA 44)	R			4.97	59	8	11
Inferior parietal lobule (BA 40)	L	1509	0.000	4.78	−61	−35	29
Superior temporal gyrus (BA 22)	L			4.77	−59	−38	20
Postcentral gyrus (BA 40)	L			3.78	−59	−22	20
Cerebellum	R	591	0.000	4.69	36	−58	−29
Superior temporal gyrus (BA 42)	R	1161	0.000	4.60	65	−32	20
Inferior parietal lobule (BA 40)	R			4.54	65	−39	31
Superior frontal gyrus (BA 10)	L	744	0.000	4.48	−36	48	23
Middle frontal gyrus (BA 10)	L			3.72	−28	42	26
Inferior parietal lobule (BA 40)	L	466	0.001	4.30	−38	−35	46

Significant activations for (a) the left hand, (b) right hand, and (c) the conjunction (left hand and right hand). Combined height threshold $p < 0.001$, and clusters with p-value correction applied ($p < 0.05$)

Table 4 Choice of movement versus pre-specified movement

Brain area—Brodmann area (BA)	Left/right	Number of voxels in cluster	Cluster-level *p* value (corrected)	Z value at local maximum	Talairach coordinates x y z		
(a) Choice of movement versus pre-specified movement—left hand							
Middle frontal gyrus (BA 11)	L	5764	0.000	4.80	−26	39	−4
Middle frontal gyrus (BA 47)	L			3.80	−36	37	−4
Inferior frontal gyrus (BA 10)	L			3.27	−38	49	3
Superior temporal gyrus (BA 38)	L	989	0.007*	3.87	−44	15	−11
Insula (BA 13)	L			2.79	−38	12	1
Medial globus pallidus	R	1550	0.001*	3.47	10	−6	−10
Middle frontal gyrus (BA 8)	R			2.95	42	29	39
Lateral globus pallidus	R			2.82	18	0	−5
Inferior parietal lobule (BA 40)	L	618	0.028*	3.11	−57	−42	44
Inferior frontal gyrus (BA 10)	R	499	0.045*	2.80	36	43	0
Middle frontal gyrus (BA 10)	R			2.20	38	38	15
Middle frontal gyrus (BA 11)	R			2.18	24	40	−12
(b) Choice of movement versus pre-specified movement—right hand							
Cerebellum	R	2514	0.009	4.02	22	−50	−31
Cerebellum	L			3.78	−12	−42	−23
Lingual gyrus (BA 19)	L			3.44	−6	−66	2
Superior frontal gyrus (BA 6)	R	13,168	0.000	3.93	20	12	47
Superior frontal gyrus (BA 10)	R			3.91	24	47	16
Superior temporal gyrus (BA 38)	R			3.88	38	3	−14
Superior temporal gyrus (BA 38)	L	2470	0.010	3.82	−46	0	−8
Insula	L			3.48	−38	12	−2
Caudate	R	1029	0.005*	3.77	16	17	−3
Inferior frontal gyrus (BA 47)	R			3.30	22	21	−13
Putamen	R			3.15	16	11	−9
Uncus (BA 20)	L	904	0.008*	3.76	−36	−17	−28
Brainstem (Pons)	L			3.18	−4	−23	−26
Parahippocampal gyrus (BA 36)	L			3.09	−28	−19	−28
Superior temporal gyrus (BA 22)	L	4578	0.000	3.63	−46	−35	4
Postcentral gyrus (BA 3)	L			3.44	−38	−21	47
Inferior parietal lobule (BA 40)	L			3.15	−57	−42	46
Thalamus	R	1906	0.044	3.47	20	−21	7
Posterior cingulate (BA 23)	R			3.44	6	−26	22
Thalamus	L			3.08	−4	−5	17
Middle frontal gyrus (BA 10)	L	1581	0.001*	3.01	−34	47	9
(c) Choice of movement versus pre-specified movement—conjunction							
Superior temporal gyrus (BA 38)	L	739	0.027*	3.20	−46	11	−12
Insula (BA 13)	L			2.92	−38	12	1
Middle temporal gyrus (BA 21)	L			2.72	−48	−2	−10
Inferior frontal gyrus (BA 10)	L	1070	0.010*	3.11	−38	47	5
Superior frontal gyrus (BA 9)	L			2.75	−42	38	28
Middle frontal gyrus (BA 9)	L			2.74	−34	34	24
Anterior cingulate gyrus (BA 24)	L	983	0.013*	2.89	−2	26	17
Superior frontal gyrus (BA 6)	R			2.88	12	18	53
Middle frontal gyrus (BA 9)	R	585	0.045*	2.33	38	31	33
Middle frontal gyrus (BA 10)	R			2.21	36	38	18

Table 4 continued

Brain area—Brodmann area (BA)	Left/right	Number of voxels in cluster	Cluster-level *p* value (corrected)	Z value at local maximum	Talairach coordinates x y z		
Inferior frontal gyrus (BA 47)	R			2.19	48	33	−5

Significant activations for (a) the left hand, (b) right hand, and (c) the conjunction (left hand and right hand). Combined height threshold $p < 0.05$, and cluster p-value correction applied ($p < 0.05$)

* *p* values at uncorrected cluster level

gyrus (BA 6), inferior parietal lobule (BA 40) and putamen (See Fig. 1a; Table 1c).

In the comparison between movement choice and rest, significant activation could be seen in the left postcentral gyrus (BA 2) and the transverse temporal gyrus (BA 41), the right middle frontal gyrus (BA 6) and precentral gyrus (BA 6), and in the inferior frontal gyrus (BA 44), medial prefrontal gyrus (BA 6), superior temporal gyrus (BA 22), inferior parietal lobule (BA 40), putamen and cerebellum bilaterally (See Fig. 1b; Table 2c).

Comparing movement ideation to rest, revealed significant differences within the left middle frontal gyrus (BA 10), superior frontal gyrus (BA 10), medial frontal gyrus (BA 6) and postcentral gyrus (BA 40), the right precentral gyrus (BA 44) and superior temporal gyrus (BA 42), and in the superior frontal gyrus (BA 6), superior temporal gyrus (BA 22), inferior parietal lobule (BA 40) and cerebellum bilaterally (See Fig. 1c; Table 3c).

The comparison between the execution of a movement of choice and the execution of a pre-specified movement showed no significant findings at the set threshold. When a more liberal combined threshold of height threshold $p < 0.05$ and cluster threshold $p < 0.05$ was chosen, the areas which were more active during the execution of a movement of choice than during the execution of a pre-specified movement were the superior (BA 38) and middle temporal (BA 21) gyri, insula and anterior mid-cingulate (BA 24) in the left hemisphere, and bilateral inferior (BA 10 on the left; BA 47 on the right), middle (BA 9 on the left; BA 9 and 10 on the right) and superior (BA 9 on the left; BA 6 on the right) frontal gyri (See Fig. 2; Table 4c).

The comparison between motor ideation and execution of a movement of choice conditions showed areas of significant activation in the left hemisphere in fronto-temporal regions, namely in the inferior (BA 47 and 45), middle (BA 47 and 10), and superior (BA 9) frontal gyri and middle temporal gyrus (BA 21). The right precuneus (BA 31) and bilateral middle occipital gyrus (BA 18 and 19 on the left; BA 19 on the right) were also active (See Fig. 3; Table 5c).

Discussion

This functional neuroimaging study showed that motor processes investigated in this study, i.e. execution of a pre-specified movement or of a movement of choice and motor ideation, require the recruitment of specific cortical networks.

The execution of a pre-specified action by both hands involved a bilaterally distributed network of cortical and sub-cortical structures engaged in motor control (Rizzolatti and Luppino 2001; Dum and Strick 2002), including, as expected, medial frontal gyrus (including the premotor and supplementary motor areas, parietal regions, cingulate cortex, cerebellum and putamen.

The neural regions commonly activated by both hands during the voluntary chosen movement (compared to a pre-specified movement) included mainly left fronto-temporal and insular regions and the anterior mid-cingulate cortex (BA 24). Our data thus support the hypothesis that the cingulate cortex is involved in appropriate movement selection (Schulz et al. 2011). Significant BOLD increases were detected in supplementary motor area and lateral premotor areas (BA 6) in both the pre-specified and movement choice conditions. These regions are reciprocally connected with the primary motor cortex (Toma and Nakai 2002), receive input from the somatosensory parietal regions and cortico-cortical projections between the premotor and parietal cortices have been found in the literature (Toma and Nakai 2002; Matelli and Luppino 2001; Borra et al. 2008; Matsumoto et al. 2012; Koch and Rothwell 2009).

Higher levels of activity were observed in the motor ideation condition compared with the chosen movement condition in fronto-temporal regions, namely in inferior, middle, and superior frontal gyri and middle temporal gyrus. Furthermore, the right precuneus and bilateral middle occipital gyrus were also activated. These results suggested that motor ideation activated a fronto-temporo-occipital network, more lateralized to the left hemisphere. This network involved left associative prefrontal and inferior frontal regions which are involved in several

Table 5 Movement ideation versus choice of movement

Brain area—Brodmann area (BA)	Left/right	Number of voxels in cluster	Cluster-level *p* value (corrected)	Z value at local maximum	Talairach coordinates x y z		
(a) Movement ideation versus choice of movement—left hand							
Superior frontal gyrus (BA 10)	L	3553	0.000	5.64	−24	52	23
Medial frontal gyrus (BA 9)	L			5.11	−18	42	22
Superior frontal gyrus (BA 9)	L			4.90	−14	51	18
Precentral gyrus (BA 4)	L	1377	0.000	5.18	−46	−12	39
Precentral gyrus (BA 6)	L			4.58	−46	−4	37
Inferior frontal gyrus (BA 45)	L	1126	0.000	5.07	−53	24	10
Inferior frontal gyrus (BA 47)	L			4.32	−24	22	−20
Middle frontal gyrus (BA 6)	L	321	0.000	4.91	−20	20	54
Superior frontal gyrus (BA 6)	L			4.04	−10	11	60
Angular gyrus (BA 39)	L	369	0.000	4.67	−44	−74	30
Superior temporal gyrus (BA 22)	L			3.72	−46	−53	19
Middle temporal gyrus (BA 39)	L			3.65	−46	−63	25
Precuneus (BA 31)	R	514	0.000	4.39	24	−73	22
Cuneus (BA 7)	R			4.08	18	−74	33
Precuneus (BA 7)	R			3.85	24	−66	31
Middle frontal gyrus (BA 10)	L	157	0.012	4.38	−20	54	−9
Middle frontal gyrus (BA 11)	L			3.82	−26	42	−7
Precentral gyrus (BA 6)	R	179	0.006	4.18	63	−1	13
Superior temporal gyrus (BA 38)	R	326	0.000	4.13	44	18	−28
Inferior frontal gyrus (BA 45)	R			4.04	59	25	4
Inferior frontal gyrus (BA 47)	R			3.98	55	27	−8
Middle temporal gyrus (BA 21)	L	220	0.002	4.04	−53	−33	−5
Middle temporal gyrus (BA 22)	L			3.78	−55	−45	1
Inferior parietal lobule (BA 40)	L	199	0.003	3.88	−57	−44	43
Supramarginal gyrus (BA 40)	L			3.70	−63	−47	24
Middle occipital gyrus (BA 19)	R	410	0.000	3.88	34	−89	15
Middle occipital gyrus (BA 18)	R			3.58	42	−85	3
Precuneus (BA 7)	L	527	0.000	3.78	−12	−72	39
Cuneus (BA 19)	L			3.71	−10	−88	36
Cingulate gyrus (BA 31)	L	213	0.002	3.63	−14	−43	41
Paracentral lobule (BA 5)	L			3.54	−8	−38	52
(b) Movement ideation versus choice of movement—right hand							
Inferior frontal gyrus (BA 47)	L	1417	0.000	4.25	−48	29	−6
Middle frontal gyrus (BA 11)	L			4.09	−38	36	−14
Middle frontal gyrus (BA 9)	L			4.03	−42	19	32
Middle occipital gyrus (BA 19)	L	364	0.000	4.17	−46	−83	6
Middle occipital gyrus (BA 18)	L			3.96	−30	−83	2
Middle temporal gyrus (BA 21)	L	509	0.000	4.16	−57	−39	−1
Middle temporal gyrus (BA 22)	L			4.09	−57	−46	4
(c) Movement ideation versus choice of movement—conjunction							
Inferior frontal gyrus (BA 47)	L	543	0.000	4.42	−48	29	−6
Inferior frontal gyrus (BA 45)	L			4.07	−51	24	12
Middle frontal gyrus (BA 47)	L			3.84	−42	37	−7
Superior frontal gyrus (BA 9)	L	542	0.000	4.32	−24	54	29
Middle frontal gyrus (BA 10)	L			4.28	−26	50	20
Middle occipital gyrus (BA 19)	R	308	0.003	3.95	34	−91	16

Table 5 continued

Brain area—Brodmann area (BA)	Left/right	Number of voxels in cluster	Cluster-level p value (corrected)	Z value at local maximum	Talairach coordinates x	y	z
Precuneus (BA 31)	R			3.63	24	−75	15
Middle temporal gyrus (BA 21)	L	218	0.016	3.94	−67	−41	0
Middle occipital gyrus (BA 18)	L	282	0.004	3.89	−28	−85	6
Middle occipital gyrus (BA 19)	L			3.67	−46	−83	6

Significant activations for (a) the left hand, (b) right hand, and (c) the conjunction (left hand and right hand). Combined height threshold $p < 0.001$, and clusters with p-value correction applied ($p < 0.05$)

cognitive processes, such as abstract thinking (Shamay-Tsoory et al. 2011), cognitive control and motivation (Matsuda and Nittono 2015), motor control and planning (Hanakawa 2011; Tanji and Hoshi 2008), emotional control and regulation (Morawetz et al. 2015). Recent neuroimaging evidence suggests that prefrontal regions constitute a common neurofunctional substrate responsible for self-control mechanisms in emotion, behaviours and motor functions (Tabibnia et al. 2014). Motor ideation activated also middle temporal areas involved in semantic memory processes (Simmons and Martin 2009). These results suggest that during motor ideation these areas contribute to the retrieval of semantic information regarding the sequences and attributes of gestures. Moreover, parieto-occipital regions have been found active in motor ideation. These areas are deputed to spatial representation (Pellegrino and Làdavas 2015), visuo-perceptual processing (Coubard et al. 2014) and visual mental imagery (Gardini et al. 2005, 2006).

Recent evidence (Pellegrino and Làdavas 2015) suggests that the brain constructs multiple representations of space, centred on different body parts (e.g., hand-centred), which arise through extensive multisensory interactions within a set of interconnected parietal and frontal regions. These peripersonal space representations guide motor behaviour.

In the direct contrast between movement ideation compared with movement choice, there were no changes in brain activity in motor areas responsible for motor execution, but we found the involvement of prefrontal cortical regions which are associated with motor control and planning (Hanakawa 2011; Tanji and Hoshi 2008). The involvement of the right parietal cortex and bilateral occipital regions during the motor ideation task suggests that even though participants were not required to image the movement but only to ideate its sequence in an abstract/verbal like modality, the visual counterpart of the movement was also automatically produced. This evidence seems to suggest that motor ideation relies not only on an abstract mental representation (deputed to the frontal cortical regions) but also on a visual mental representation (supported by parieto-occipital structures). Processes such as visuo-spatial working memory may be utilized, in which the prefrontal cortex would operate as the control structure, visual features would be processed in the occipital cortex, spatial coordinates would be represented in the parietal cortex and visual imagery supported by occipito-temporal structures (Zimmer 2008).

Previous studies have stated that the execution of a voluntary movement is preceded by the formation of a motor representation of the entire movement, including its plan and its results (Olsson and Nyberg 2010). These authors have also argued that motor representation can be detached from movement execution and can exist on its own as an independent mental process. In our study we appear to have segregated this preliminary phase of motor ideation disentangling the neural correlates of this mental process.

Our results are in agreement with those of Ingvar and Philipson (1977), who found a different pattern of regional cerebral blood flow during motor ideation (attempts to conceive rhythmic clenching movements of the right hand) when contrasted with the pattern of activation resulting from actual movements of the right hand. During motor ideation an increase of regional cerebral blood flow occurred in frontal and temporal structures, whereas during actual hand movements increases occurred in rolandic regions. Our neuroimaging results, from conjunction analyses of the brain activations obtained from both hands, directly support the notion that the frontal and temporal cortex underpins the voluntary processes which take place in motor behaviour (Fried et al. 2011).

Some methodological limitations were present in our study, such as the absence of a measure of the amplitude of the finger movements, intensity of movements, and kinematics. The polystyrene cast used within the study

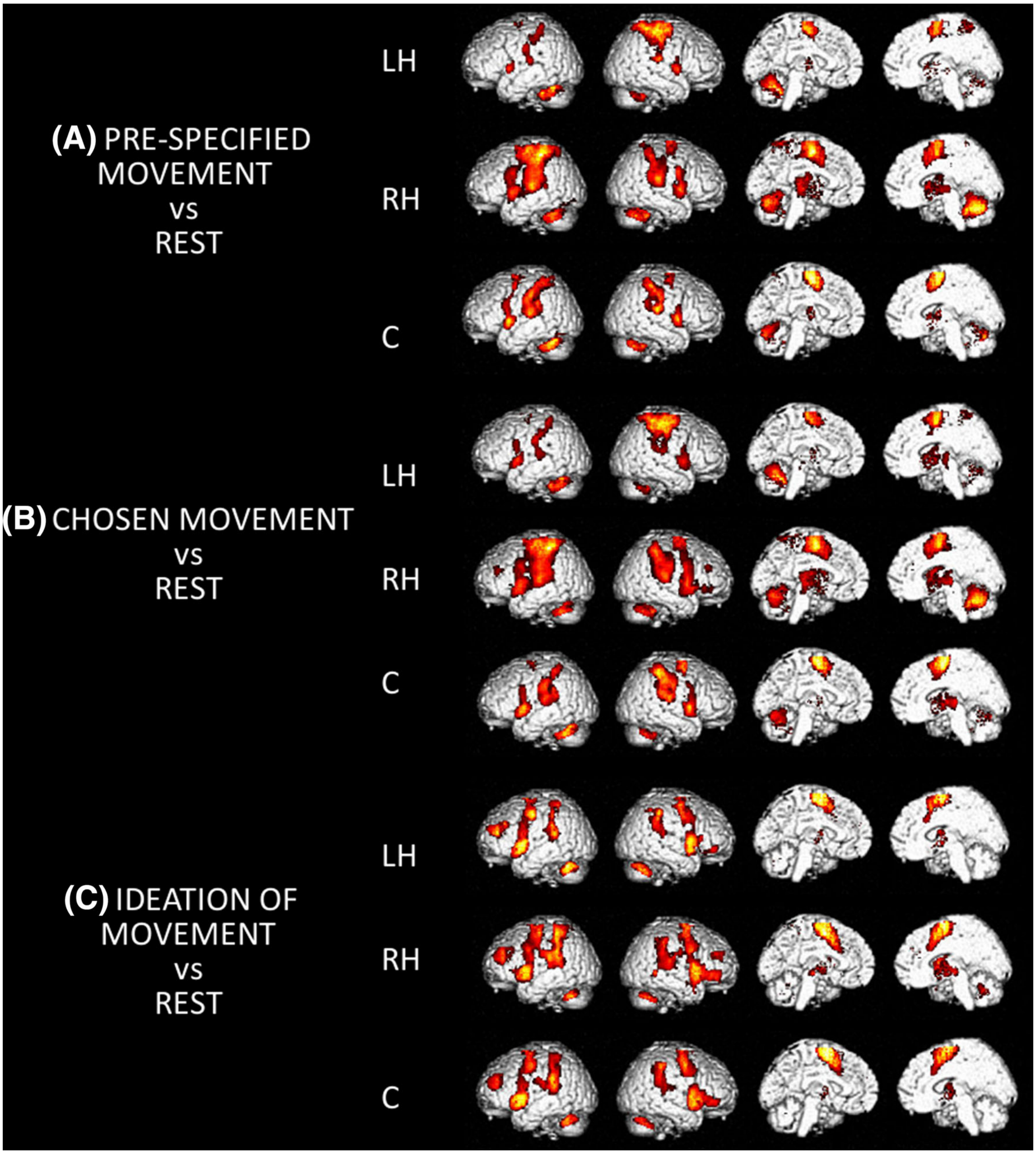

Fig. 1 Areas of significant activation for *a* pre-specified movement execution versus rest, *b* chosen movement versus rest, and *c* ideation of movement versus rest. LH—left hand, RH—right hand, C—conjunction (conjunction of left hand and right hand). A height threshold of $p < 0.001$ was applied, with only those clusters which survived cluster-level correction ($p < 0.05$) considered as significant

restricted movement amplitude and the movements/movement ideations were paced however. Furthermore, although leading to stronger activation, e.g., within the primary sensorimotor cortex (Waldvogel et al. 1999), factors such as amplitude would not necessarily translate into recruitment of the additional brain regions that were seen in the current experiment, such as the left PFC and the temporal gyrus in the comparison between chosen movement and pre-specified movement. Future studies may nonetheless consider refining the design by further controlling these movement related factors.

Conclusion

The present data confirm and extend evidence from previous functional neuroimaging studies (Rao et al. 1993; Grafton and Hamilton 2007) that described a widely dis-

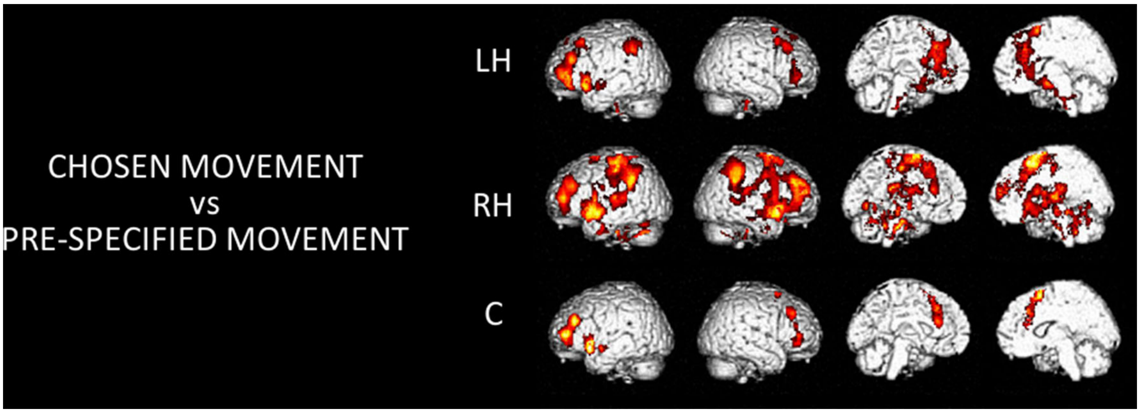

Fig. 2 Areas of significant activation for chosen movement versus pre-specified movement execution (height threshold $p < 0.05$, uncorrected clusters $p < 0.05$). LH—left hand, RH—right hand, C—conjunction (conjunction of left hand and right hand)

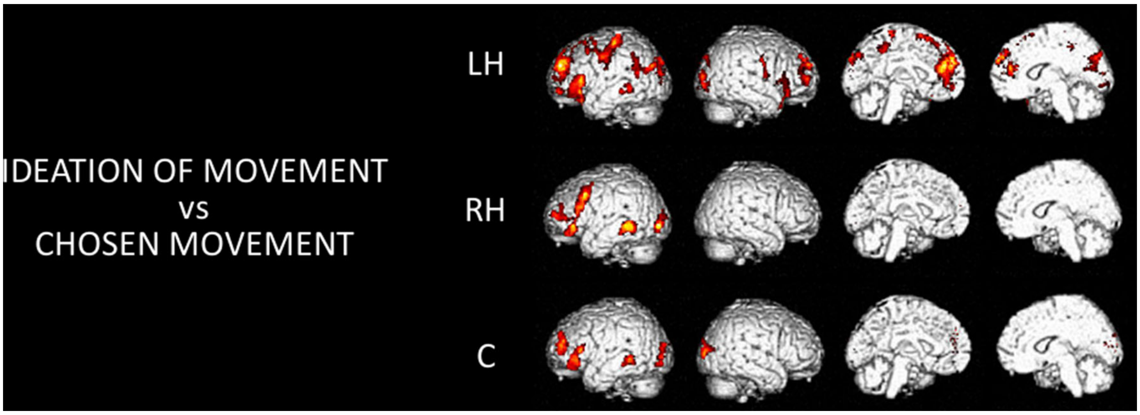

Fig. 3 Areas of significant activation for ideation of movement versus chosen movement (height threshold $p < 0.001$, cluster-level correction $p < 0.05$). LH—left hand, RH—right hand, C—conjunction (conjunction of left hand and right hand)

tributed organization of different motor functions. Specifically, it is suggested that the higher-order process of motor ideation operates through a neural network involving a left hemisphere array of structures, deputed to motor control and planning, semantic processes of movement and visual mental imagery.

These findings are in line with clinical studies, showing that cerebral lesions in middle frontal and parietal circuits can cause ideational apraxia (Hécaen 1972; Bolognini et al. 2015; De Renzi and Lucchelli 1988). Further investigations will be necessary to explore whether patients with movement disorders, such as patients with Parkinson's disease, would engage the same neural circuits during motor ideation.

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Compliance with Ethical Standards

Conflict of interest All authors declare that they have no conflict of interest.

References

Bajaj S, Butler AJ, Drake D, Dhamala M (2015) Brain effective connectivity during motor-imagery and execution following stroke and rehabilitation. Neuroimage 8:572–582

Bernstein NA (1996) On dexterity and its development. In: Latash ML, Turvey MT (eds) Dexterity and its development. Lawrence Erlbaum Associates, Mahwah

Bolognini N, Convento S, Banco E, Mattioli F, Tesio L, Vallar G (2015) Improving ideomotor limb apraxia by electrical stimulation of the left posterior parietal cortex. Brain 138:428–439

Borra E, Belmalih A, Calzavara R, Gerbella M, Murata A, Rozzi S, Luppino G (2008) Cortical connections of the macaque anterior intraparietal (AIP) area. Cereb Cortex 18:1094–1111

Breveglieri R, Galletti C, Dal Bò G, Hadjidimitrakis K, Fattori P (2014) Multiple aspects of neural activity during reaching preparation in the medial posterior parietal area V6A. J Cogn Neurosci 26:878–895

Coubard OA, Urbanski M, Bourlon C, Gaumet M (2014) Educating the blind brain: a panorama of neural bases of vision and of training programs in organic neurovisual deficits. Front Integr Neurosci 8:89

Cunnington R, Windischberger C, Deecke L, Moser E (2002) The preparation and execution of self-initiated and externally-triggered movement: a study of event related fMRI. Neuroimage 15:373–385

De Renzi E, Lucchelli F (1988) Ideational apraxia. Brain 111:1173–1185

Drew T, Marigold DS (2015) Taking the next step: cortical contributions to the control of locomotion. Curr Opin Neurobiol 33:25–33

Dum RP, Strick PL (2002) Motor areas in the frontal lobe of the primate. Physiol Behav 77:677–682

Fried I, Mukamel R, Kreiman G (2011) Internally generated preactivation of single neurons in human medial frontal cortex predicts volition. Neuron 69:548–562

Friston KJ, Holmes AP, Price CJ, Büchel C, Worsley KJ (1999) Multisubject fMRI studies and conjunction analyses. Neuroimage 10:385–396

Frith C (1991) Positron emission tomography studies of the frontal lobe function relevance to psychiatric disease. Ciba Found Symp 163:181–191

Gao Q, Duan X, Chen H (2011) Evaluation of effective connectivity of motor areas during motor imagery and execution using conditional Granger causality. Neuroimage 54:1280–1288

Gardini S, De Beni R, Cornoldi C, Bromiley A, Venneri A (2005) Different neuronal pathways support the generation of general and specific mental images. Neuroimage 27:544–552

Gardini S, Cornoldi C, De Beni R, Venneri A (2006) Left mediotemporal structures mediate the retrieval of episodic autobiographical mental images. Neuroimage 30:645–655

Gardini S, Concari L, Pagliara S, Ghetti C, Venneri A, Caffarra P (2011) Visuo-spatial imagery impairment in posterior cortical atrophy: a cognitive and SPECT study. Behav Neurol 24: 123–132

Grafton ST, Hamilton AF (2007) Evidence for a distributed hierarchy of action representation in the brain. Hum Mov Sci 26:590–616

Gross RG, Grossman M (2008) Update on apraxia. Curr Neurol Neurosci Rep 8:490–496

Hanakawa T (2011) Rostral premotor cortex as a gateway between motor and cognitive networks. Neurosci Res 70:144–154

Hécaen H (1972) Introduction à la neuro-psychologie. Librairie Larousse, Paris

Huey ED, Pardini M, Cavanagh A, Wassermann EM, Kapogiannis D, Spina S, Ghetti B, Grafman J (2009) Association of ideomotor apraxia with frontal gray matter volume loss in corticobasal syndrome. Arch Neurol 66:1274–1280

Ingvar DH, Philipson L (1977) Distribution of cerebral blood flow in the dominant hemisphere during motor ideation and motor performance. Ann Neurol 3:230–237

Koch G, Rothwell JC (2009) TMS investigations into the task-dependent functional interplay between human posterior parietal and motor cortex. Behav Brain Res 202:147–152

Lui F, Buccino G, Duzzi D, Benuzzi F, Crisi G, Baraldi P, Nichelli P, Porro CA, Rizzolatti G (2008) Neural substrates for observing and imagining non object-directed actions. Soc Neurosci 3:261–275

Mammarella N, Cornoldi C, Pazzaglia F (2004) Psicologia dell'apprendimento multimediale. Il Mulino, Bologna

Manuel AL, Radman N, Mesot D, Chouiter L, Clarke S, Annoni JM, Spierer L (2013) Inter- and intrahemispheric dissociations in ideomotor apraxia: a large-scale lesion-symptom mapping study in subacute brain-damaged patients. Cereb Cortex 23:2781–2789

Matelli M, Luppino G (2001) Parietofrontal circuits for action and space perception in the macaque monkey. Neuroimage 14:S27–S32

Matsuda I, Nittono H (2015) The intention to conceal activates the right prefrontal cortex: an event-related potential study. NeuroReport 26:223–227

Matsumoto R, Nair DR, Ikeda A, Fumuro T, Lapresto E, Mikuni N, Bingaman W, Miyamoto S, Fukuyama H, Takahashi R, Najm I, Shibasaki H, Lüders HO (2012) Parieto-frontal network in humans studied by cortico-cortical evoked potential. Hum Brain Mapp 33:2856–2872

Morawetz C, Bode S, Baudewig J, Kirilina E, Heekeren HR (2015) Changes in effective connectivity between dorsal and ventral prefrontal regions moderate emotion regulation. Cereb Cortex. doi:10.1093/cercor/bhv005

Olsson CJ, Nyberg L (2010) Motor imagery: if you can't do it, you won't think it. Scand J Med Sci Sports 20:711–715

Paivio A (1971) Imagery and verbal processes. Holt, Rinehart, and Winston, New York

Pellegrino G, Làdavas E (2015) Peripersonal space in the brain. Neuropsychologia 66C:126–133

Raffin E, Mattout J, Reilly KT, Giraux P (2012) Disentangling motor execution from motor imagery with the phantom limb. Brain 135:582–595

Rao SM, Binder JR, Bandettini BS, Hammeke TA, Yetkin FZ, Jesmanowicz A, Lisk LM, Morris GL, Mueller WM, Estkowski LD et al (1993) Functional magnetic resonance imaging of complex human movements. Neurology 43:2311–2318

Rizzolatti G, Fogassi L (2014) The mirror mechanism: recent findings and perspectives. Philos Trans R Soc B 369:20130420

Rizzolatti G, Luppino G (2001) The cortical motor system. Neuron 31:889–901

Schluter ND, Krams M, Rushworth MFS, Passingham RE (2001) Cerebral dominance for action in the human brain: the selection of actions. Neuropsychologia 39:105–113

Schulz KP, Bédard AC, Czarnecki R, Fan J (2011) Preparatory activity and connectivity in dorsal anterior cingulate cortex for cognitive control. Neuroimage 57:242–250

Shamay-Tsoory SG, Adler N, Aharon-Peretz J, Perry D, Mayseless N (2011) The origins of originality: the neural bases of creative thinking and originality. Neuropsychologia 49:178–185

Sharma N, Pomeroy VM, Baron JC (2006) Motor imagery: a backdoor to the motor system after stroke? Stroke 37:1941–1952

Simmons WK, Martin A (2009) The anterior temporal lobes and the functional architecture of semantic memory. J Int Neuropsychol Soc 15:645–649

Singer JL, Antrobus JS (1972) Daydreamer, imaginal processes, and personality: a normative study. In: Sheehan PW (ed) The function and nature of imagery. Academic Press, New York, pp 175–202

Tabibnia G, Creswell JD, Kraynak T, Westbrook C, Julson E, Tindle HA (2014) Common prefrontal regions activate during self-control of craving, emotion, and motor impulses in smokers. Clin Psychol Sci 2:611–619

Tanji J, Hoshi E (2008) Role of the lateral prefrontal cortex in executive behavioral control. Physiol Rev 88:37–57

Toma K, Nakai T (2002) Functional MRI in human control studies and clinical applications. Magn Reson Med Sci 1:109–120

Tomasino B, Rumiati RI, Umiltà CA (2003) Selective deficit of motor imagery as tapped by a left-right decision of visually presented hands. Brain Cogn 53:376–380

Waldvogel D, van Gelderen P, Ishii K, Hallett M (1999) The effect of movement amplitude on activation infunctional magnetic resonance imaging studies. J Cereb Blood Flow Metab 19:1209–1212

Zimmer HD (2008) Visual and spatial working memory: from boxes to networks. Neurosci Biobehav Rev 32:1373–1395