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 (fMRI) 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.

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 et al., 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 loss of the mental formula and semantics of actions. At the basis of ideational apraxia there would be 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 e 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 seconds, TE = 30 ms, flip angle = 90°, voxel dimensions 1.88 x 1.88 x 5.00 mm. 128x128x24) 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 minutes and 20 seconds, and was preceded by 30 seconds 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 seconds interspersed with 1 second 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 seconds). 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 x 8 x 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 hand 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 1-5 and Figures 1, 2 and 3 provide detail on the analyses of each hand separately, in addition to the conjunction analyses.

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

- Insert Figure 1 and Table 1 around here -

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 Figure 1b and Table 2c).

- Insert Table 2 around here -

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 Figure 1c and Table 3c).

- Insert Table 3 around here -

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 Figure 2 and Table 4c).

- Insert Table 4 around here -

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 Figure 3 and Table 5c).

-Insert Table 5 around here -

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 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 et al., 2015), visuo-perceptual processing (Coubard et al., 2014) and visual mental imagery (Gardini et al., 2005; Gardini et al., 2006).

Recent evidence (Pellegrino et al., 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 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 distributed 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 structure, 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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Conflict of interest statements

All authors declare that they have no conflict of interest.

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Figures captions

Figure 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.

Figure 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).

Figure 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).

Table 1. Pre-specified movement versus rest. 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 ($p < 0.05$).

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	16692	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

Note: Separate clusters are distinguished by blank rows in the table.

Table 2. Choice of movement versus rest. 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 ($p < 0.05$).

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	18633	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

Note: Separate clusters are distinguished by blank rows in the table.

Table 3. Movement ideation versus rest. 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 ($p < 0.05$).

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	18986	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

Note: Separate clusters are distinguished by blank rows in the table.

Table 4. Choice of movement versus pre-specified movement. 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 ($p < 0.05$).

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	13168	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
Inferior frontal gyrus (BA 47)	R			2.19	48	33	-5

Note: Separate clusters are distinguished by blank rows in the table.
* p-values at uncorrected cluster level

Table 5. Movement ideation versus choice of movement. 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 ($p < 0.05$).

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
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

Note: Separate clusters are distinguished by blank rows in the table.

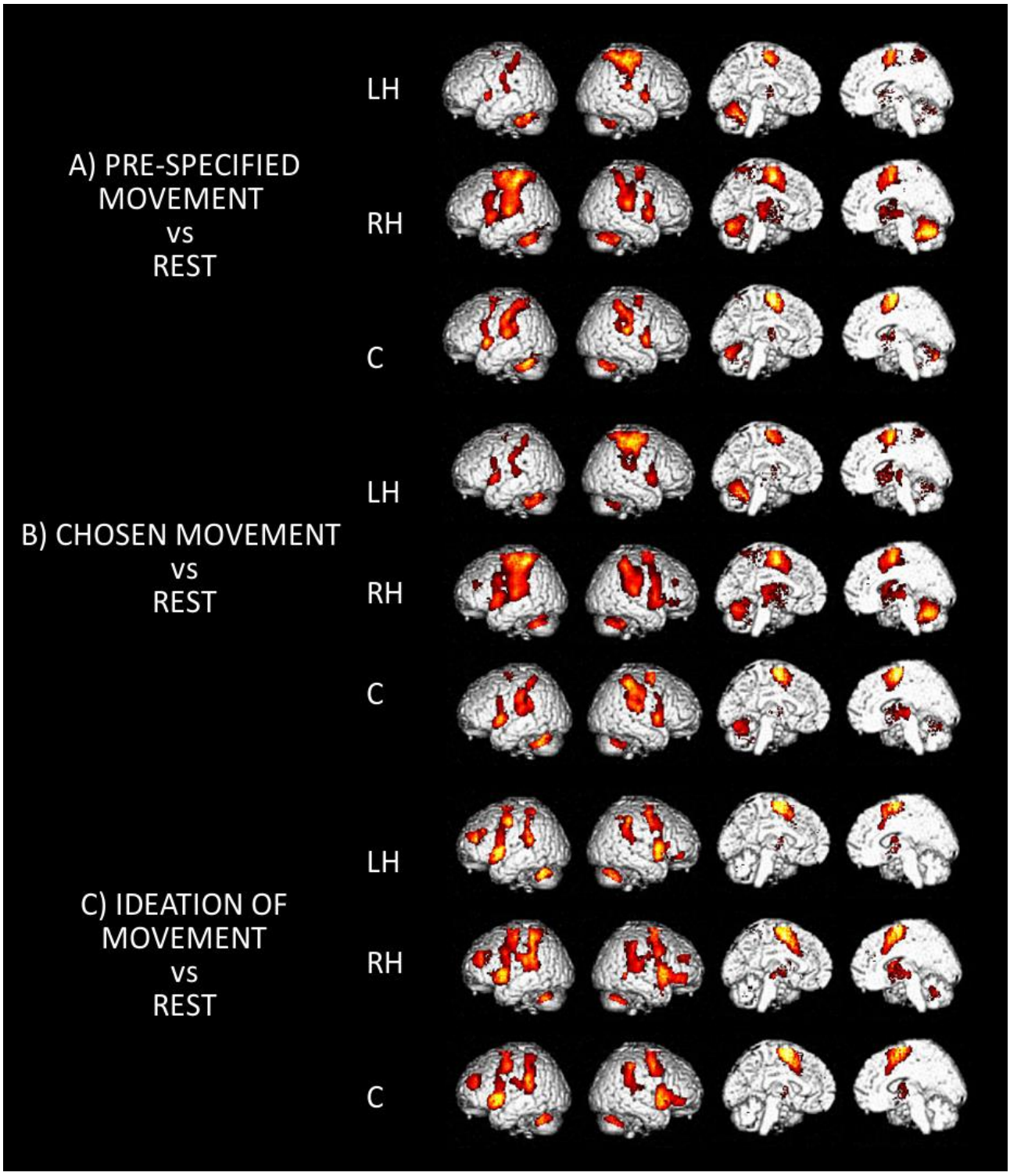
A) PRE-SPECIFIED MOVEMENT vs REST
LH
RH
C
B) CHOSEN MOVEMENT vs REST
LH
RH
C
C) IDEATION OF MOVEMENT vs REST
LH
RH
C

Figure 1

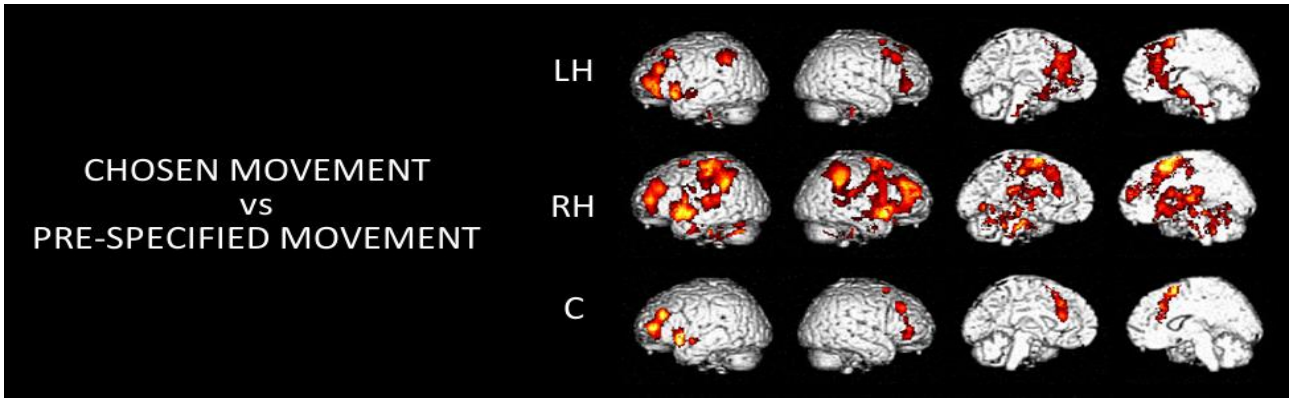

Figure 2

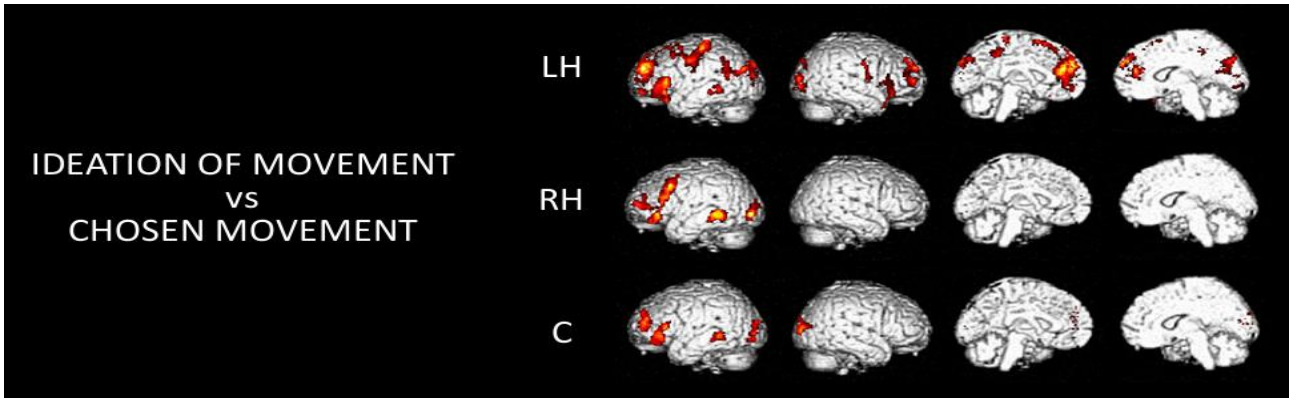

Figure 3