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Motor imagery of complex everyday movements. An fMRI study

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The present study aimed to investigate the functional neuroanatomical correlates of motor imagery (MI) of complex everyday movements (also called everyday tasks or functional tasks). 15 participants imagined two different types of everyday movements, movements confined to the upper extremities (UE; e.g., eating a meal) and movements involving the whole body (WB; e.g., swimming), during fMRI scanning. Results showed that both movement types activated the lateral and medial premotor cortices bilaterally, the left parietal cortex, and the right basal ganglia. Direct comparison of WB and UE movements further revealed a homuncular organization in the primary sensorimotor cortices (SMC), with UE movements represented in inferior parts of the SMC and WB movements in superior and medial parts. These results demonstrate that MI of everyday movements drives a cortical network comparable to the one described for more simple movements such as finger opposition. The findings further are in accordance with the suggestion that motor imagery-based mental practice is effective because it activates a comparable cortical network as overt training. Since most people are familiar with everyday movements and therefore a practice of the movement prior to scanning is not necessarily required, the current paradigm seems particularly appealing for clinical research and application focusing on patients with low or no residual motor abilities.

Introduction

Motor imagery (MI) is defined as internal rehearsal of a movement without any overt physical movement (Crammond, 1997; Jeannerod, 1994). As such, MI is the fundamental basis of motor imagery-based mental practice (MP), which is defined as the repeated imagination of movements by using MI. A key finding of research in this area is that MP can result in improvements of motor performance, despite the absence of any overt movement (Driskell et al., 1994; Feltz and Landers, 1983). Accordingly, MP is frequently employed by athletes and sportsmen to accompany standard training procedures. Recognizing the potential of MP, this method has recently gained interest by clinical researchers and practitioners as a potential rehabilitation technique to improve motor performance in patients with movement disorders (Crosbie et al., 2004; Dickstein et al., 2004; Dijkerman et al., 2004; Jackson et al., 2001, 2004; Johnson-Frey, 2004; Kimberley et al., 2006; Malouin et al., 2004; Sharma et al., 2006; Stevens and Stoykov, 2003).

To optimize rehabilitation and training strategies based on mental practice, an understanding of the functional neuroanatomical correlates of motor imagery would be highly beneficial (cf., Lacourse et al., 2004). However, a key characteristic of MP in training situations is that complex sequences of everyday movements are imagined, while previous evidence is restricted mainly to very basic and simple movements, such as finger/foot flexion extension or finger opposition. Taking the research on simple movements as a starting point, it has been shown that the imagery of a movement activates largely the same cortical motor areas as compared to the preparation (Jeannerod, 1994; Kosslyn et al., 2001) or even overt performance (Lotze et al., 1999; Porro et al., 1996) of that movement. Thus, from a functional neuroanatomical point of view, MI can be conceptualized as an "active" performance of the movements imagined, in the way that – although no overt movement is performed – the activity induced in the associated brain areas resembles the activity during active performance (Johnson et al., 2002). Thus, this theory suggests equivalent activations in MP and active performance, and consequently predicts functional changes in motor system organization for MP comparable to the changes described for overt training (Hlustik et al., 2004; Karni et al., 1995; Lacourse et al., 2004). Such functional changes may provide an explanation for the performance increments gained by MP. However, although this mechanism is quite appealing to account for the effectiveness of MP in improving motor performance in patients and athletes, it has not been verified yet. Such a verification would have to rely on movements which are actually used in the application of MP, i.e., everyday movements (also called everyday tasks or functional tasks). Because MP consists of repetitive application of motor imagery, the suggested mechanism can only be valid if motor imagery of everyday movements is shown to rely on the cortical motor system.

Based on studies using simple movements, it could be hypothesized that everyday movements will recruit large parts of the motor system. In particular, premotor cortices should be activated as these have been reported to be involved in MI by virtually all previous studies. However, contrary to these findings a previous study investigating everyday movements reported

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virtually no activation of lateral or medial premotor cortices during MI of stance, walking, and running (Jahn et al., 2004). This initial evidence on MI of everyday movements casts severe doubts on the proposed mechanism of MP efficacy and the development of theoretical considerations driving MP-based interventions.

Thus, the first aim of this study was to show that MI of everyday movements relies on the cortical (pre)motor system. Based on previous evidence derived from simple movements and on more theoretical accounts of MI (Jeannerod, 1994), we expected MI of everyday movements to activate mainly lateral and medial premotor cortices. However, if the finding of Jahn et al. (2004) holds true for all everyday movements, lateral premotor cortices may not be involved in MI of the currently used movements as well.

The complexity of everyday movements imposes a number of challenges for their investigation. For example, in MI studies on simple finger movements participants typically practice the task prior to scanning to ensure a comparable level of movement familiarity across participants. For everyday movements, such as swimming, this is not feasible and a comparable level of familiarity can therefore not be ensured. In the present experiment, we dealt with this problem by including a wide variety of different everyday movements, following the rationale that this should balance the effects of familiarity and hence ensure that a roughly comparable level of familiarity is achieved across movements and participants.

We further reasoned that a wide variety of movements would enhance the ecological validity of the current approach, not in the least because MP training employs a range of different movements. We therefore presumed that the current data were more likely to resemble the real-world application of MP if a wide variety of movements was employed and, therefore, result in knowledge which actually has the potential to facilitate the optimization of rehabilitation and training methods.

The advantages of using a variety of movements are countered by new methodological hurdles. Most critical here is the question of whether different everyday movements result in a comparable activation pattern or in very different ones. In other words, the specificity of the cortical activation patterns of different everyday movements is unknown. On the one hand, it is plausible to assume that most everyday movements involve so many different muscles that the cortical areas involved in MI overlap considerably (cf., also Schieber and Hibbard, 1993). In that case, specificity can be assumed to be low, and consequently the pooling of different movements may have no effect on the detection and identification of cortical areas related to MI. On the other hand, cortical activation during MI of different movements has been shown to map onto the homuncular organization in the sensorimotor system (Ehrsson et al., 2003; Stippich et al., 2002). This suggests that such different movements as swimming and eating a meal may activate very specific and distinct cortical areas. In that case, pooling such movements is likely to decrease statistical power considerably and may even prevent identification of MI-related cortical areas.

Based on these considerations, a further aim of the present study was to characterize the activation specificity of everyday movements. This question is not only of theoretical interest, but also of practical relevance because rather similar activation patterns would allow future studies to pool different movements, while different patterns suggest that different movements should be treated separately. To answer this question, we included two MI conditions which differed with respect to the limbs involved in the imagined movements, and tested whether these two conditions show differential cortical activation patterns. In essence, we employed movements confined to the upper extremities (e.g., eating a meal) and movements involving the whole body (e.g., swimming).

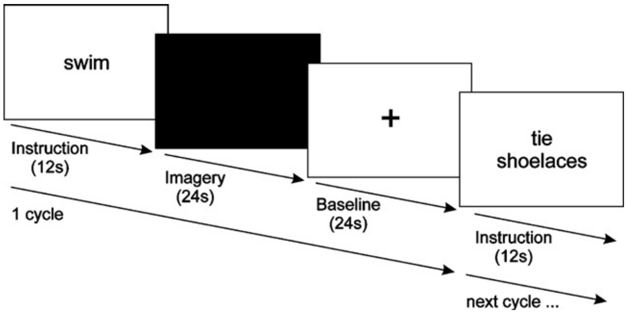

Fig. 1. Timecourse of one imagery cycle lasting 1 min. The experiment consisted of 14 such cycles with imagery of whole body (WB) and upper extremity (UE) movements presented alternatingly.

Methods

Participants

15 Neurologically healthy participants (9 male) took part in the experiment. The age ranged between 19 and 56 (average 28) years, and all participants were right handed (mean score 91, range 73–100) as assessed with the Edinburgh Inventory (Oldfield, 1971). Prior to scanning, all participants gave written informed consent according to the guidelines of the University of Surrey ethical review board. Participants received £10 for participation.

Task and procedure

While lying in the fMRI scanner, participants viewed a projection screen via a mirror. We employed three conditions, a resting baseline (BASE), motor imagery of upper extremity movements (UE), and motor imagery of whole body movements (WB).

The experiment was based on an fMRI block design and consisted of 14 cycles, each lasting 1 min. Each cycle embodied an instruction and preparation period (12 s), an imagination period (UE or WB, 24 s), and a resting baseline period (BASE, 24 s) (Fig. 1). The two imagery conditions, UE and WB, were presented alternatingly, resulting in seven repetitions of each MI condition and an experimental run time of 14 min.

A cycle started with the instruction and preparation period, during which the movement to be imagined next was presented on a screen using black letters on a white background. Prior to scanning participants received detailed instructions to use this period to prepare the imagination by setting up an action plan. Next, the screen turned black and the imagination period began. During this period, participants had to close their eyes and perform the imagination[1].

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[1] This procedure may have introduced a confound in the present data since participants had to open their eyes only during the baseline period, but not during imagination. However, this confound would most likely result in higher activation in some areas, e.g., the visual cortex, during Baseline as compared to Imagery, but not vice versa. Indeed, the comparison of Baseline > Imagery revealed only cortical activation in the visual areas of the occipital lobes. Therefore, the difference between eye-opened and eye-closed may have led to missing Imagery related activation in the visual cortex, but – most importantly – cannot account for any Imagery related activation.

Participants were cued to open the eyes again by the screen turning white, which, due to the intense change in luminance, was easy to recognize through the closed eye lids. Afterwards the resting baseline period was presented, during which participants had to fixate a cross on the screen. After this baseline period, the next cycle started by presenting the instruction and preparation period.

The instruction given to the participants strongly emphasized the use of a kinesthetic first person perspective during imagination, i.e., participants were asked to imagine performing the movement by themselves, instead of imagining watching themselves or others performing the movement (Stinear et al., 2006). Additionally, we emphasized that the imagination should be "action loaded", i.e., they should perform the imagined movement with high frequency and engage intensely. Participants were instructed to imagine during the whole imagination period and, if a movement finished earlier, to start over with the same movement until the imagination period finished.

The movements of the UE condition were (1) Eat a meal with knife and fork, (2) Cut your fingernails with scissors, (3) Write on a piece of paper using a pen, (4) Shuffle and deal playing cards, (5) Tie shoelaces, (6) Brush/comb your hair, and (7) Button a shirt/blouse. The WB movements were (1) Swim, (2) Lift heavy boxes from floor to table, (3) Run (for bus, for sport), (4) Dance (ballroom or disco/club), (5) Throw and kick balls, (6) Dig a hole using a spade, and (7) Hoover/use a vacuum cleaner. Three of the twelve participants had to imagine partly different WB and UE movements[2].

To ensure that the vividness of the imagery was comparable between UE and WB, twelve of the 15 participants were asked to fill out a short questionnaire directly after the MRI scanning, in which we asked for each movement, how good the imagination was during the experiment. Participants responded using a scale ranging from 1 ("bad/hard to imagine") to 7 ("perfect/very vivid and lively imagination").

To ensure a roughly comparable familiarity with the movements across participants, the questionnaire also asked how often the movements have been performed in everyday live. Participants responded using an ordinal scale with the following items: every few years/1; yearly/2; every few months/3; monthly/4; every few weeks/5; weekly/6; every few days/7; daily/8; more than once a day/9.

MRI procedure

Imaging was carried out at the Royal Holloway University London, UK, using a 3 T scanner (Trio, Siemens, Erlangen, Germany) equipped with an array head coil. Participants were supine on the scanner bed, and cushions were used to reduce head motion. Additionally, the build-in movement correction of the scanner was enabled. 36 axial slices (192 × 192 mm FOV, 64 × 64 matrix, 4 mm thickness, no gap, interleaved slice acquisition) were acquired using a BOLD-sensitive EPI sequence (TR 2 s, TE 30 ms, 90° flip angle). One functional run with 420 volumes was administered, with each volume sampling all 36 slices. In the same session, high-resolution whole brain images were acquired from each participant using a T1-weighted MPRAGE sequence (1 × 1 × 1 mm voxel size).

Data analysis

Preprocessing

The data were analyzed using the SPM2 software package (http://www.fil.ion.ucl.ac.uk/spm/software/spm2/). In a first step, the origin of the anatomical and functional images was manually set to the anterior commissure and all images were reoriented. To correct for movements, all functional volumes were spatially realigned to the first functional volume. In the same processing step ("Realign and Unwarp" in SPM2), signal changes due to head motion and magnetic field inhomogeneities were corrected (Andersson et al., 2001). Next, the normalization was performed. For this, first the anatomical and functional images were co-registered, then the anatomical image was normalized into a standard stereotaxic space using the T1 template provided by the Montreal Neurological Institute (MNI) delivered with SPM, and finally the transformation parameters derived from this transformation were applied to the functional images. Functional data were spatially smoothed using a Gaussian kernel with a FWHM of 8 mm.

Statistics

Statistical analysis was based on a voxelwise least squares estimation using the general linear model for serially autocorrelated observations (Friston et al., 1995a,b). All conditions were modeled using the standard hemodynamic response function implemented in SPM2. Low-frequency signal drifts were controlled for by applying a temporal highpass filter with a cutoff frequency of 1/240 Hz. Individual contrast maps were calculated for the comparisons IMAGERY vs. BASE (i.e., (UE+ WB)/2 vs. BASE), UE vs. BASE, WB vs. BASE, and UE vs. WB.

For the second-level analysis, a one-sample t test based on the individual contrast images was calculated for each comparison (random effect group analysis, $N=15$). The resulting statistical parametric t maps were thresholded at $t(14)>3.79$ ($p<0.001$, uncorrected) and a spatial extend threshold of 45 contiguous voxel (360 mm^3) was applied. Error probabilities (p values) corrected for multiple comparisons are reported on the cluster level.

To test in detail for a homuncular organization of WB and UE movements we conducted a region-of-interest (ROI) analysis. Using the stereotaxic atlas by Talairach and Tournoux (1988) we tracked the course of the central sulcus and determined one voxel in the centre of the central sulcus on each of the 18 slices given in the atlas[3]. Then we extracted the beta-values of the contrast UE–WB, derived from the second-level group statistics, from each of the above defined voxel along the central sulci. We predicted that if both movements activate their homuncular homologues, there should be a clear trend in the beta-values along the course of the

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[2] For WB, these were (1) Play tennis, (2) Play golf, (3) Play the drums, (4) Drive a car in heavy rush hour traffic or in a race, (5) Fight (e.g., karate or judo), (6) Ski (downhill racing), (7) Cleanse yourself under the shower with soap. For UE, these were (1) Eat a meal with knife and fork, (2) Cut your fingernails with scissors, (3) Cut hair of somebody else, (4) Build a small model of a car with glue, (5) Play the piano or flute, (6) Write a letter using a pen, and (7) Play jackstraws/pick-up sticks. Although some of these movements seem not ideal (e.g., in "play the drums" participants may have ignored using the legs so that it is more an upper extremity movements, and "Drive a car in heavy rush hour traffic or in a race" may involve higher visuo-spatial imagery), this seemed to not have affected the final results. In particular, a second-level group analysis omitting these three participants revealed the same cortical activation patterns for the comparisons Imagery > BASE, WB > UE, and UE > WB, except for decreased statistical power.

[3] Because the atlas of Talairach and Tournoux (1988) depicts only one hemisphere, the voxels of the left and right hemispheres were identical except for an inverted x coordinate.

central sulcus. To test for such a trend, we calculated a linear regression with a predictor variable encoding the coordinates $z=50$ mm (medial), $z=55$ mm (lateral), and $z=32$ mm (lateral) and the individual beta-values at these coordinates as the dependent variable. These z-coordinates were chosen to roughly resemble three parts of the central sulcus, the medial part, the superior lateral, and the inferior lateral part. For showing a trend in beta-values along these coordinates this regression approach is more parsimonious than testing the coordinates individually using t tests.

Results

Quality of imagination and familiarity

The vividness ratings for both types of movement imagery were virtually identical (scale 1 [worst] to 7 [best]; median UE: 6, WB: 6, Wilcoxon Signed Ranks Test $z=-0.577$, $p=0.564$). Individual values ranged between 4 and 7 for both movement types, which showed that no participant felt to be poor in imagery (cf., Ross et al.,

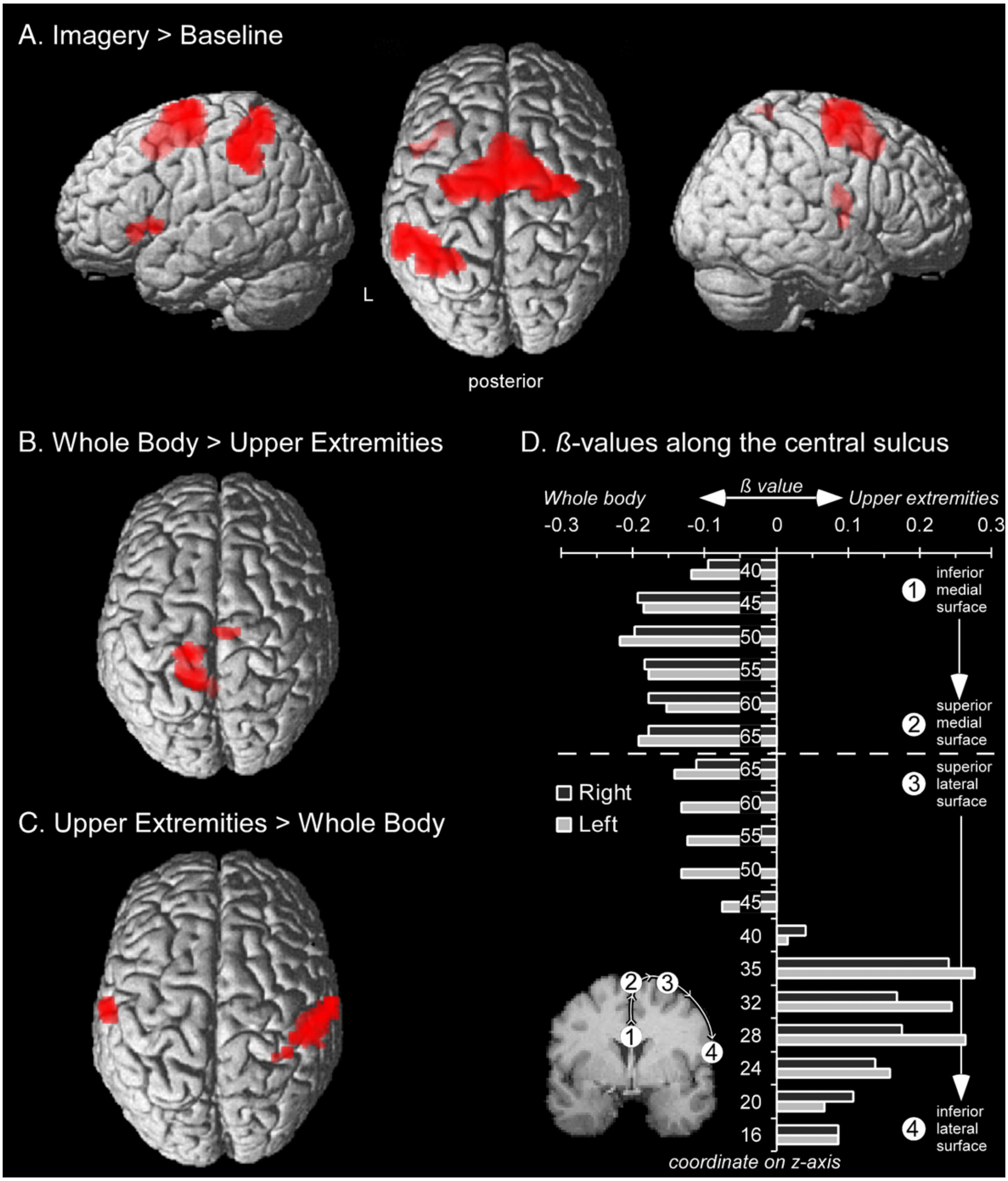

Fig. 2. fMRI group results ($N=15$). Statistical parametric maps (SPMs) of the combined imagery conditions > the resting baseline condition, i.e., [(WB+UE)/2−BASE] (A), of the comparison whole body movements > upper extremity movements, i.e., WB > UE (B), and the reverse comparison UE > WB (C). For illustration, all SPMs are thresholded at $p<0.001$ (uncorrected for multiple comparisons), extend threshold 45 voxel. Panel D depicts the results of the region of interest analysis. Shown are the beta-values of the group-level statistical evaluation for the comparison (UE > WB) along the central sulci of both hemispheres. The z coordinate refers to the inferior–superior axis (Talairach and Tournoux, 1988).

2003). The quality of the imagination of the individual movements showed that all movements were imagined in a high quality (range of medians UE: 5.5–7; range WB: 6–7).

With respect to familiarity, only two participants noted that they have never performed one of the movements ever before in their life. The median amount of performance across all movements and participants was "weekly"/6. Individual medians for the 12 participants were 3, 4, 4, 5, 5, 5, 5.5, 5.5, 6, 6.5, 7, and 7. Thus, 9 of the 12 participants had a median indicating quite regular performance of the movements to be imagined (every few weeks to every few days). This shows that the familiarity was roughly comparable across participants.

Imagery vs. BASE

In a first step, we identified the cortical areas associated with MI of everyday movements in general by subtracting the resting baseline condition from the average of both imagery conditions ((UE+WB)/2−BASE). This comparison confirmed a network of cortical areas well known to be involved in motor imagery (Fig. 2A, Table 1). Most importantly, we found activations in lateral and medial premotor cortices. More specifically, we observed an extended activation in the medial frontal gyrus (Brodmann's area (BA) 6), which covered the supplementary motor area (SMA) and the preSMA (Picard and Strick, 1996). Additionally, the precentral gyri of both hemispheres (BA 6) were activated in the region of the "hand knob", i.e., the omega-shaped curvature of the precentral gyrus and central sulcus associated with hand coordination in the primary motor cortex (Yousry et al., 1997). However, as can be seen in Table 1, only the right hemispheric activation was detected as a local peak, while the left hemispheric activation did not separate sufficiently from other nearby peaks to form a separate local peak (marked with [a]; this pattern is discussed in detail in the next paragraph). A further activation was apparent in the area of the left frontal operculum and insula which, however, reached significance only uncorrected for multiple comparisons. These frontal activations were accompanied by activations of parietal and subcortical areas. Parietal activation was present only in the left hemisphere and extended from the superior into the inferior parietal lobe (BA 7/40). Finally, we observed a subcortical activation covering areas of the right basal ganglia, namely putamen, pallidum, and caudate nucleus. Taken together, these results show that MI of everyday movements relies on cortical networks previously described to be involved in motor preparation and overt motor performance, as well as in MI of more simple movements.

The separate comparisons WB>BASE and UE>BASE revealed the same basic activation pattern (Tables 2 and 3). Noteworthy is that initially it may appear as if the lateral premotor cortex shows a lateralization, since local activation peaks are reported for the left precentral gyrus in WB>BASE, but for the right in UE>BASE. However, a closer inspection of the data revealed that the activation is bilateral in both comparisons, but that the algorithm detecting local peaks (SPM2; minimum distance between peaks 8 mm) just misses the respective peaks in the other hemisphere. To clarify this, Tables 1, 2, and 3 always show the data for both precentral gyri, with peaks marked with [a] referring to the data at that voxel although it is not identified as peak. As can be seen from Tables 1, 2, and 3, both precentral gyri are highly activated, with only minor differences in the respective *t* values.

MI of upper extremity movements vs. MI of whole body movements

To test whether the different types of everyday movements, i.e., UE and WB, share commonalities with respect to their activation pattern, we first calculated the comparison of each condition with the baseline condition (UE–BASE and WB–BASE). As can be seen in Tables 2 and 3, both conditions activated a largely overlapping network of cortical areas. Highly comparable activation foci were present not only in lateral and medial premotor cortices, but as well in parietal and subcortical regions.

To test directly for differences between MI of UE and WB movements, we calculated the comparison of both conditions (UE vs. WB). Cortical areas more strongly activated by WB than by UE movements (comparison WB–UE) were mainly located on the

Table 1

Stereotaxic coordinates (Talairach and Tournoux, 1988), anatomical locations, and *T* scores of (local) peak activations for the comparisons Imagery> BASE [(UE+WB)/2−BASE]

ID	Anatomical area	BA	Coordinate			Voxel		Cluster		
			x	*y*	*z*	MPM	*T*	MPM	Volume	*p* (corr)
1	R medial sup frontal G (preSMA)	6	6	6	49	6	7.86	6	3346	0.000
2	*L medial sup frontal G (preSMA)*	*6*	*−4*	*10*	*47*	*6*	*7.08*			
3	*R precentral G (lateral PMC)*	*6*	*32*	*−7*	*50*	*6*	*6.82*			
4	*L precentral G/S[a](lateral PMC)*	*6*	*−26*	*−7*	*63*	*6*	*5.78*			
5	L sup parietal lobe	7/40	−42	−45	61		11.78		951	0.000
6	*L sup parietal lobe*	*7*	*−30*	*−47*	*67*		*8.39*			
7	*L inf parietal lobe*	*40*	*−63*	*−43*	*39*		*7.41*			
8	R caudate nucleus		18	−3	19		6.6		212	0.032
9	*R putamen/pallidum*		*22*	*−4*	*4*		*6.04*			
10	L Insula/frontal operculum		−36	23	−5		5.49		165	$0.075^{n.s.}$
11	*L Insula/frontal operculum*		*−48*	*12*	*−1*		*4.56*			

ID refers to a specific anatomic location and is kept constant across Tables 1 Tables 2 Tables 3 for convenient comparison of activation patterns. Local activation peaks in italic. [a]This is not a local activation peak (see text for details). Brodmann's areas determined by atlas of Talairach and Tournoux (column BA) and by maximum probability maps based on the SPM Anatomy toolbox (Eickhoff et al., 2005) (columns MPM). Thresholded at $p<0.001$ (extent 45 voxel, 360 mm^3). *p* Values corrected for multiple comparisons reported on cluster level (n.s., non-significant as $p>0.05$; *p* value of 0.000 means $p<0.001$).

Note. Volume specified in voxel (2×2×2 mm). Abbreviations: BA=Brodmann's area, L/R=left/right hemispheric activation, respectively, inf=inferior, sup=superior, S=sulcus, G=gyrus, preSMA=pre-supplementary motor area, PMC=premotor cortex.

Table 2

Stereotaxic coordinates (Talairach and Tournoux, 1988), anatomical locations, T scores of (local) peak activations, and volume and corrected p values on the cluster level for the comparison WB—BASE

ID	Anatomical area	BA	Coordinate			Voxel		Cluster		
			x	y	z	MPM	T	MPM	Volume	p (corr)
1	R medial sup frontal G (preSMA)	6	10	5	51	6	8.42	6	3574	0.000
	L medial sup frontal G (SMA)	*6*	*−6*	*−7*	*59*	*6*	*6.91*			
3	*R precentral G^a (lateral PMC)*	*6*	32	*−7*	*50*	*6*	*6.26*			
4	*L precentral G/S (lateral PMC)*	*6*	*−26*	*−7*	*63*	*6*	*6.7*			
5	L sup parietal lobe	7/40	−42	−49	60		8.85	1/2/hIP2	754	0.000
6	*L sup parietal lobe*	*7*	*−28*	*−47*	*67*	*1*	*6.84*			
	L inf parietal lobe	*40*	*−46*	*−40*	*54*	*hIP2*	*6.43*			
9	R putamen/pallidum		22	−4	4		6.58		260	0.01
8	*R caudate nucleus*		20	*−3*	*17*		*5.9*			
10	L Insula/frontal operculum		−36	23	−3		5.49		226	0.018
	L Insula/frontal operculum		*−40*	*14*	*5*		*5.39*			
11	*L Insula/frontal operculum*		*−48*	*12*	*−1*		*4.31*			

For details see Table 1.

Note. Compared to Table 1, activation peaks with the ID 2 and 7 are not present. If no ID is given, this activation is not present in Table 1. ^{a}This is not a local activation peak (see text for details). hIP2 = human intraparietal area 2.

medial surface (BA 4), extending into the SMA, with a small activation focus along the left lateral central sulcus, which was located just superior to the hand area (BA 3/4/6) (Fig. 2B, Table 4). This activation extended into the left postcentral gyrus and the intraparietal sulcus (BA 4/5/7). Finally, there were two activation foci not significant if corrected for multiple comparisons, the first in the posterior cingulate gyrus (BA 29/30), and the second in the medial frontal gyrus (SMA, BA 4/6).

Opposed to this, cortical areas more strongly activated by UE than by WB movements (comparison UE–WB) were confined to the lateral surface of the hemispheres (Fig. 2C, Table 5). Firstly, we observed a right hemispheric activation of the inferior central sulcus, extending into the postcentral gyrus (BA 1/2/3/4). In the left hemisphere, a similar but more circumscribed activation was evident (BA 1/2/3/4), which just failed to reach statistical significance when corrected for multiple comparisons ($p = 0.099$). These activations were located slightly inferior to the hand motor area and may cover not only primary sensorimotor regions, but secondary sensory areas (SII) as well (Stephan et al., 1995). Furthermore, the right postcentral gyrus, extending into the intraparietal sulcus (BA 1/2/5/7/40), was activated, though non-significant, when corrected for multiple comparisons. Taken together, MI of WB movements activated predominantly medial and superior lateral motor cortices, while MI of UE movements activated predominantly inferior lateral motor cortices.

ROI analysis

If both movements activate their homuncular homologues, there should be a clear trend in the beta-values along the course of the central sulcus. Indeed, in the medial/superior part of the central sulcus WB showed stronger activation, while the pattern was

Table 3

Stereotaxic coordinates (Talairach and Tournoux, 1988), anatomical locations, T scores of (local) peak activations, and volume and corrected p values on the cluster level for the comparison UE—BASE

ID	Anatomical area	BA	Coordinate			Voxel		Cluster		
			x	y	z	MPM	T	MPM	Volume	p (corr)
2	L medial sup frontal G (preSMA)	6	−4	*10*	47	6	7.42	6	2509	0.000
	R medial sup frontal G (preSMA)	*6*	*12*	*3*	*66*	*6*	*7.13*			
3	*R precentral G (lateral PMC)*	*6*	32	*−7*	*50*	*6*	*6.66*			
4	*L precentral G/S^a (lateral PMC)*	*6*	*−26*	*−7*	*63*	*6*	*4.78*			
5	L sup parietal lobe	7/40	−42	−45	61		11.97	1/2/hIP2	924	0.000
6	*L sup parietal lobe*	*7*	*−32*	*−47*	*67*		*9.08*			
7	*L inf parietal lobe*	*40*	*−63*	*−43*	*39*		*7.22*			
	R inf parietal lobe	40	59	−36	50		5.14		48	0.702$^{\text{n.s.}}$
	R postcentral S	*2/40*	63	*−29*	*46*		*4.35*			
	R postcentral G	1/2/3	51	−23	40	1/2	4.91	1/2	90	0.347$^{\text{n.s.}}$
8	R caudate nucleus		20	−5	19		6.25		144	0.129$^{\text{n.s.}}$
9	*R putamen/pallidum*		20	*−2*	*4*		*5.61*			
10	L Insula/frontal operculum		−36	23	−6		5.08		50	0.682$^{\text{n.s.}}$

For details see Table 1.

Note. Compared to Table 1, activation peaks with the ID 1 and 11 are not present. If no ID is given, this activation is not present in Table 1. ^{a}This is not a local activation peak (see text for details).

Table 4
Stereotaxic coordinates (Talairach and Tournoux, 1988), anatomical locations, T scores of (local) peak activations, and volume and corrected p values on the cluster level for the comparison WB—UE

Anatomical area	BA	Coordinate			Voxel		Cluster		
		x	y	z	MPM	T	MPM	Volume	p (corr)
L paracentral lobule	4	−12	−30	53	4p	6.56	3/4	509	0.000
L central S (lateral)	*4*	*−18*	*−30*	*60*	*3b/4a/6*	*5.53*			
L postcentral G/IPS	*5/7*	*−16*	*−43*	*63*	*4p*	*5.52*			
L posterior cingulate G	29/30	−8	−48	10		5.5		164	$0.083^{\text{n.s.}}$
R medial frontal G (SMA)	6	4	−19	54	4a/6	4.42	4a/6	69	$0.491^{\text{n.s.}}$

For details see Table 1.
Note. IPS = intraparietal sulcus, SMA = supplementary motor area.

reversed in the inferior part, i.e. UE showed stronger activation (Fig. 2D). This finding was confirmed by calculating two linear regressions, one for each hemisphere, which yielded highly significant effects of the predictors encoding the z coordinate (standardized β=0.461 (0.423); $t_{(14)}$=3.408 (3.063); p<0.01 (0.01) for the right (left) hemisphere, respectively).

Discussion

Our first aim was to characterize the functional neuroanatomical correlates of MI of everyday movements. We showed that the imagination of everyday movements involving the upper extremities and the whole body recruited a cortical network consisting of the bilateral lateral and medial premotor cortices, the left inferior and superior parietal cortices, and the right basal ganglia. This finding is consistent with previous reports on MI of simple movements and, thus, shows the generalizability of simple to complex everyday movements. The second aim was to identify the specificity of the cortical activation patterns of everyday movements. We showed that the two different movement types, WB and UE, result in differentiated activation patterns along the sensorimotor cortex, which correspond to the homuncular organization of that area. Most other cortical areas showed no differences between the movement types.

MI of everyday movements (Imagery vs. BASE)

MI of everyday movements activated a network of cortical areas which is highly consistent with previous reports of MI of simple movements. Most importantly, lateral and medial premotor cortices were activated, i.e., activations were found in the ‘hand knob’ region (Yousry et al., 1997) of the left and right precentral gyrus as well as the medial part of the superior frontal gyrus corresponding to the SMA and preSMA (Picard and Strick, 1996). We observed further activations in inferior and superior parietal cortices and the right basal ganglia, including caudate nucleus, pallidum and putamen. This pattern of activations is fully consistent with the findings obtained in the study of well-controllable movements, such as finger opposition and finger tapping (Boecker et al., 2002; Dechent et al., 2004; Hanakawa et al., 2003; Jahn et al., 2004; Kuhtz-Buschbeck et al., 2003; Lacourse et al., 2004; Lafleur et al., 2002; Stephan et al., 1995).

Accordingly, we conclude that MI of everyday movements activates a cortical network similar to the one described for simple finger/hand movements. This is not self-evident considering the results of Jahn et al. (2004). Opposed to the present and nearly all previous studies, Jahn et al. did not observe activation of lateral or medial premotor cortices during MI of stance, walking, and running (but see Malouin et al., 2003). The only exception was an activation of the right SMA during imagery of walking. Jahn et al. hypothesized that their movements did not result in spatially congruent activation patterns in premotor cortices across participants, so that the group statistics did not reveal any significant activations. In the present study, individual activation patterns were spatially extended and localized in a rather congruent pattern. Indeed, 14 of the 15 participants in our study showed activation (T>3.0, first level statistics) at the voxels of peak activation in the medial frontal gyrus ([6 6 49] and [−4 10 47]; cf., Table 1), and the remaining participant had activations in the proximity (distance <10 mm). In both precentral gyri, twelve of the 15 participants showed activation right at the voxels of peak activation ([32 −7 50] and [−26 −7 63]; cf., Table 1), and two/

Table 5
Stereotaxic coordinates (Talairach and Tournoux, 1988), anatomical locations, T scores of (local) peak activations, and volume and corrected p values on the cluster level for the comparison UE—WB

Anatomical area	BA	Coordinate			Voxel		Cluster		
		x	y	z	MPM	T	MPM	Volume	p (corr)
R central S/postcentral G	2/3/4	65	−14	30	1	6.9	1/2/3b/4	734	0.000
R central S/postcentral G	*3/4*	*53*	*−18*	*36*	*2/3b*	*5.63*			
R postcentral G	*1/2*	51	*−25*	*53*	*1/2*	*5.4*			
L central S/postcentral G	3/4	−61	−14	34	1	6.22	2/3b/4	154	$0.099^{\text{n.s.}}$
L central S/postcentral G	*1/3*	*−67*	*−14*	*27*	*4*	*5.28*			
R postcentral G/central S	5/7	40	−38	63	1	4.36	1/2	45	$0.727^{\text{n.s.}}$
R intraparietal S	*7/40*	32	*−40*	*50*	*2*	*4.34*			

For details see Table 1.

three participants showed activation in close proximity (distance <5 mm) in the right/left precentral gyrus, respectively[4]. Therefore, it appears likely that the use of a wide variety of movements has led to spatially more extended cortical activations and smaller individual variability so that premotor activation was evident at the group level.

The discrepancy between our and Jahn et al.'s (2004) results may further be due to their baseline condition, since it comprised the imagination of lying, which may have induced baseline premotor activation. Our study used a resting baseline, in which premotor activation is less likely to occur. Furthermore, the data of Malouin et al. (2003) suggest that the involvement of premotor areas increases with the complexity of the movements to be imagined. Because we used more complex and less automatic movements the signal-to-noise ratio is likely to be higher so that systematic differences in the baseline-to-imagery contrast become apparent. Taken together, our data suggest that MI of everyday movements relies on premotor cortices, and that the results by Jahn et al. may have been caused by the specific selection of movements or methods employed.

The convergence of the results gained by simple movements and everyday movements supports current theoretical accounts of the mechanisms of MI (Jeannerod, 1994). Although the mechanisms of MI have been investigated mainly in simple movements, there was a tendency to generalize the findings to a broader level subsuming all kinds of movements. In other words, it has essentially been assumed that MI of more complex movements would be similar to the MI of more simple movements. Our study supports this implicit generalization by providing empirical underpinning for this claim and, thus, is an important step towards a deeper understanding of movement control.

Everyday movements typically aim to achieve a particular goal and therefore depend on the use of, interaction with, or manipulation of objects. One may therefore argue that the activations seen in the present study not only represent the motor component of the task, but also the imagery of their multimodal associations. Such "co-imagery" may well have occurred but appears to contribute little to the general findings. For instance, taste and odor imagery should be strongest in the UE action of eating a meal, but absent for WB movements. However, the comparison UE and WB movements showed no indication of activations in the regions known to be involved in the imagery of odor and taste (Djordjevic et al., 2005; Kikuchi et al., 2005; Yoo et al., 2003). Furthermore, although tactile imagery is rather prevalent in MI due to the nature of kinesthetic imagery (cf., Yoo et al., 2003), there was no activation in somatosensory areas in the comparison Imagery>BASE. Activation in somatosensory cortices was only observed in the comparison UE>WB, which may be related to a more vivid tactile imagery in UE movements. Taken together, motor imagery, but not other modes of imagery, is the most likely source of the observed activation pattern.

Commonality and specificity of cortical activation patterns (UE vs. WB)

The implications of the analysis of both MI types are twofold: firstly, because both types of movements engage lateral and medial premotor cortices as well as parietal and subcortical areas in a comparable fashion, very different movements may be pooled together in one condition without profound loss in specificity of cortical activation patterns, if these areas are in the focus of interest. Secondly, as activation patterns in sensorimotor cortices followed the homuncular organization, movements involving very different sets of muscles need to be analyzed separately if the focus of interest concerns aspects of sensorimotor processing.

A close inspection of Fig. 2D reveals that the hand area is not differently activated for UE and WB movements. This is probably caused by an overlap in limb use as not only UE but also some WB movements involved the upper extremities. This may also explain, why in the direct comparison the UE movements seem to activate rather inferior parts of the motor cortex, which are likely to be involved in movements of tongue, finger, neck, and face (e.g., Stippich et al., 2002), but not of hand and arm. At the same time, WB movements activated the other extreme of the homuncular representation, i.e., areas described for toe, leg, and feet movements (e.g., Stippich et al., 2002), but not intermediate parts such as hip and trunk. In the light of these findings, we propose that the absence of hand area activation in the UE–WB comparison is due to its activation in both conditions.

Implications for mental practice

Our data support the suggestion that MP may improve motor performance by activating the cortical areas involved in motor preparation and overt performance (Johnson et al., 2002; Johnson-Frey, 2004). However, it is critical to note that due to the nature of our everyday movements, this conclusion is drawn on the basis of existing knowledge on motor system organization (e.g., Roland, 1984), rather than the direct comparison of imagery and overt performance.

A more detailed account for the mechanism of MP was recently suggested by Jackson et al. (2001). Based on earlier findings (e.g., Jacobson, 1930; Paivio, 1985; Sackett, 1934), he suggested that the beneficial outcomes of MP are due to learning in at least two different processes, declarative knowledge and nonconscious processes. Regarding declarative knowledge, MP may improve motor performance by rehearsing the cognitive components of a movement, i.e., by strengthening the symbolic representations (Jackson et al., 2001; Sackett, 1934). Accordingly, Jackson et al. proposed these mechanisms to be prevalent during the initial stages of skill acquisition, i.e., mainly during MP of untrained movements, so that it seems rather unlikely that this component was present during the MI of the highly trained movements in our study. Our MRI results support this conclusion since declarative learning is likely to involve the working memory system in dorsolateral prefrontal cortices (Halsband and Lange, 2006) and these cortices did not show any activation during imagery[5].

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[4] One might suspect that the three participants who had to imagine different movements were the ones who showed activation at different locations. However, this was not the case. Except for one participant showing only activation in the close proximity (<5 mm) and not exactly at the peak activation of the group comparison, all three participants had activations exactly at the location of the group-level peaks. This supports the notion that the broader movement category is of more importance than the detailed particular movement.

[5] However, this suggestion must be taken with caution, since MP may actually involve partly different processes as compared to MI (Ravey, 1998) and, furthermore, this interpretation is based on a null result, which is problematic from a methodological point of view (Kluger and Tikochinsky, 2001).

Regarding nonconscious processes, MP may improve motor performance by improving implicit components of the motor performance, such as the force or dynamics of the movement (Gandevia, 1999; Yágüez et al., 1998; Yue and Cole, 1992), and it is assumed that this system is prevalent during MP of highly trained movements (Jackson et al., 2001). In line with this idea, MI in the current study resulted in activation of areas typically associated with nonconscious or implicit motor processes, such as the premotor cortices and the basal ganglia (Halsband and Lange, 2006). In particular, lateral and medial premotor cortices are assumed to play a vital role in implicit motor learning and may eventually be part of a larger network, including the basal ganglia, which realizes the storage and retrieval of motor programs (Halsband and Lange, 2006; Hikosaka et al., 2002). In other words, the presently observed premotor areas represent a central component of the skill acquisition network, so that an involvement of these areas in MI may well explain the efficacy of motor imagery-based MP. Thus, with respect to Jackson et al.'s (2001) model, the current data tentatively suggest that MP based on everyday movements may more strongly rely on implicit than on declarative processes.

While the involvement of premotor cortices is clear-cut, the role of the primary sensorimotor cortex (SMC) is less clear. No SMC activation was found in the comparison of IMAGERY vs. BASE, WB vs. BASE, and UE vs. BASE. However, the SMC showed activation when WB and UE were contrasted directly. We suggest that this pattern is due to a rather small and subtle effect of MI on SMC activation. The observation that the SMC is not activated in the comparisons of WB and UE vs. BASE, respectively, suggests that this effect may be either differential, i.e., that the medial part of the SMC which is activated by WB movements, is slightly de-activated by UE movements, and vice versa, or that there is some SMC activation during the BASE condition (e.g., induced by slight lolling). However, we think that the latter is rather unlikely, since we did not observe any overt movement of the participants. Generally, the SMC involvement in MI is unclear and much debated (e.g., Dechent et al., 2004). Our data contribute to this discussion by showing that SMC activity is at least modulated by MI of different types of everyday movements.

A recurring critique in most MI studies, including our own, is that SMC activation can principally be explained by muscle activity as well (but see e.g. Galdo-Álvarez and Carrillo-de-la-Peña, 2004; Lotze et al., 1999). During MRI scanning, we visually controlled for overt movement on a random basis, but low and hence invisible muscle activity would probably remain undetected. This interpretation cannot be ruled out, however, it is important to note that the methods used in our study make potential muscle effects at least less likely. For instance, in some previous studies using complex finger sequences, imagery and overt movement were performed alternatingly (e.g., Wexler et al., 1997). In such a case there may be a strategic advantage for the participant to slightly move the fingers during MI, e.g., as a reminder cue for the sequence. In addition, the change from overt movement to imagery may make participants more prone to slight muscle activity. In the present study, neither argument applies, since the movements were well trained and highly familiar, and because there was no overt movement condition. In addition, physical constraints may make it rather unlikely to show even tendencies to execute the movement, e.g., running while lying supine in the scanner. We therefore suggest that the SMC activation is more likely related to MI than to muscle activity. Further research employing better control of (subthreshold) muscle activity is clearly needed to clarify the role of the SMC in MI of everyday movements.[6]

The present finding has relevant implications for the study of MI in the context of applied research questions, such as rehabilitation of patients or training of athletes. Activation patterns of MI of complex everyday movement in our study basically mirrored the patterns seen with simple, typically better controlled hand movements in numerous experiments. In essence, this provides the empirical basis for the assumption that paradigms based on simple movements provide valid and meaningful insights into the control of everyday motor behavior.

In contrast to a number of studies on MP efficacy, we employed highly familiar movements. We chose this procedure, since athletes actually use MP to improve their highly trained motor skills. Studying MI of highly familiar movements therefore appeared more appropriate, as it is closer to the real world situation. Secondly, we were interested in tasks that could not be practiced prior to scanning, so familiarity with the movements was essential, to ascertain a vivid kinesthetic, first-person perspective imagination. Thirdly, MP has also been shown to be effective for trained movements (Cumming and Hall, 2002; Driskell et al., 1994; Feltz and Landers, 1983; Pascual-Leone et al., 1995; Ungerleider, 1985). Finally, a further aim of the study was to provide a basis for future clinical research. As described in the next paragraph, practice periods may not be feasible in the clinical domain.

Clinical implications

The present findings are highly relevant for clinical research in several respects. Firstly, and most importantly, they demonstrate that activities of the daily life can be used to investigate the functional neuroanatomical correlates of MI. The advantage of using such movements or activities is that everybody is familiar with them and, therefore, is able to generate a vivid and lively first-person imagination without any prior training. This is especially crucial for the investigation of cohorts who cannot train new movements, e.g., because they do not have sufficient residual movement abilities after a neurological disease or cortical damage (Grotta et al., 2004; Johnson-Frey, 2004; Kimberley et al., 2006; Sharma et al., 2006; Weiss et al., 1994). Secondly, we were able to show that, except for the SMC, very different everyday movements drive a robust movement-related cortical network that is not specifically modulated by the kind of movement that is imagined, which implies that a wide variety of movements can be used in one experiment. From a clinical perspective, this is particularly important as it provides the necessary methodological latitude to accommodate the multitude of constraints patient studies are often faced with. However, as we also found that the activation of the SMC is homuncularly organized, care in selecting a specific sample of movements is advised if the SMC is of interest, as pooling movements of different types may profoundly decrease statistical power.

MP has recently been recognized as a potential treatment in motor rehabilitation (e.g., Pomeroy et al., 2005; Sharma et al., 2006). The rationale behind this approach is that MP may benefit recovery

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[6] The optimal way to exclude even subthreshold muscle activity, i.e., application of an electromyogram (EMG) during MRI scanning, was not available to us due to lack of equipment. In addition, the MRI study was conducted and participants were recruited at Royal Holloway University of London, so that there was no option to employ EMG at least outside the MRI.

by activating the residual cortical motor system for the (imagined) performance of meaningful actions (Kimberley et al., 2006; Sharma et al., 2006). Such functionally relevant and specific activation of the motor system is different to the unspecific activation changes observed after brain damage (e.g., Ward et al., 2003a,b). The latter may be caused by physiological changes such as hyperexcitability facilitating neuronal reorganization or by the mere higher effort required by patients to perform the motor task (Ward and Frackowiak, 2006). In contrast, performing a given task or movement – even if done only in imagination – requires the motor system to engage in a highly specific way aimed to reach the action goal. Such activation is likely to result in functionally relevant changes of the motor system, such as fine-tuning or strengthening of neural pathways (Doyon and Benali, 2005; Halsband and Lange, 2006; Jackson et al., 2001; Kimberley et al., 2006; Sharma et al., 2006). From a treatment perspective, the premotor activations found in the present study are particularly encouraging, because the activated areas correspond to those regions involved in recovery related reorganization (Halsband and Lange, 2006; Jackson et al., 2001; Ward, 2004; Ward and Frackowiak, 2006).

Ecological validity, clinical application, and experimental control

Basic research that takes the demands of ecological validity or clinical constraints into account, frequently faces the problem of properly controlling variables that may influence the outcome. On the one hand, a maximum of control over the experimental paradigm and the participant's behavior and strategies is methodological gold standard. But on the other hand, such highly controlled situations often seem arbitrary and complex so that they are not optimal for clinical research or may lack ecological validity. In the current experiment, we tried to balance these two needs in the best possible way. For instance, the use of everyday movements is beneficial from an applied point of view but prevents the control of familiarity. Although we were able to account for this by using a variety of movements, other variables such as the intensity and frequency of imagery were not as well controlled. However, one solution to uncontrolled variables is to consider the possible consequences of potential biases.

In general, lack of experimental control can have three different consequences. The first and most desirable possibility is that the uncontrolled variable is a random factor that does not distort the results in a condition specific fashion. The second possibility is that the lack of control results in a type-I error. This is likely if an unrepresentative sample is investigated (selection bias), in our study for instance if participants showed unusually high imagination intensities and frequencies. However, this seems rather unlikely, as the cortical areas of main interest, i.e., the motor system, were activated in virtually every participant. If unusually high imagination intensities or frequencies were to account for this finding, most participants had to show above population mean intensity and frequency. For a random sample of 15 participants which spanned a considerable range of age and occupation, this would be a highly implausible selection bias. The third and final possibility is that the lack of control results in a type-II error. This may happen, since lack of control is likely to increase the variance between participants, which in turn decreases statistical power. Although we cannot exclude this possibility for the current data, it is noteworthy that the cortical motor system, which was in the focus of the current study, is activated by MI. Therefore, such undetected areas related to MI can only be located in areas which are beyond the scope of this paper.

Taking these considerations together, it appears that the weak experimental control of some variables is unlikely to alter the final interpretation of our data. This shows that uncontrolled variables, although highly undesired, do not necessarily prevent firm and valid inferences. Accordingly, we think that for some research questions it is legitimate to knowingly abandon some carefully chosen experimental control for other advantages, such as ecological validity and clinical feasibility.

Conclusion

MI of everyday movements activated lateral and medial premotor and parietal cortices, thereby providing empirical data to support the claim that the findings for MI of simple, pre-trained movements can be generalized to more complex real-world situations. Different movement types, i.e., whole-body and upper extremity movements, showed a homuncular organization in sensorimotor cortices, while they resulted in the same activation in cortical areas related to more abstract information processing, i.e., premotor, prefrontal, and parietal areas. However, to exclude some alternative interpretations of the current data and to extend our findings, further research is clearly required. Taken together, this finding provides initial empirical evidence for the idea that MP effectively improves motor skills by the same mechanism as overt practice, i.e., the repetitive activation of the cortical areas encoding this movement.

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