

The embodied nature of motor imagery: the influence of posture and perspective

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Abstract It is assumed that imagining oneself from a first-person perspective (1PP) is more embodied than a third-person perspective (3PP). Therefore, 1PP imagery should lead to more activity in motor and motor-related structures, and the postural configuration of one's own body should be particularly relevant in 1PP simulation. The present study investigated whether proprioceptive information on hand position is integrated similarly in 1PP and 3PP imagery of hand movements. During functional magnetic resonance imaging (fMRI) scanning, 20 right-handed female college students watched video sequences of different hand movements with their right hand in a compatible versus incompatible posture and subsequently performed 1PP or 3PP imagery of the movement. Results showed stronger activation in left hemisphere motor and motor-related structures, especially the inferior parietal lobe, on 1PP compared with 3PP trials. Activation in the left inferior parietal lobe (parietal operculum, SII) and the insula was stronger in 1PP trials with compatible compared with incompatible posture. Thus, proprioceptive information on actual body posture is more relevant for 1PP imagery processes. Results support the embodied nature of 1PP imagery and indicate possible applications in athletic training or rehabilitation.

Keywords Motor imagery · Embodied cognition · Action simulation · Hand posture · fMRI

Introduction

We are all familiar with pictures of professional skiers preparing for a competition. We see them with a focused facial expression and their eyes shut, and we know that they are imagining key aspects of their pending motor performance. They do not engage in gross motor movement during imagery, but, interestingly, they prefer to adopt a posture resembling their body position during ski racing. During the last decade, such phenomena of embodied cognition have attracted renewed attention in cognitive neuroscience. The key-idea is that body-related experiences also shape processes such as perception or imagery that were formerly conceptualized as purely “cognitive” (Gallese 2003, 2005; Wilson 2002). As a result, motor imagery (MI) might not remain unaffected by postural signals, particularly when a cognitive simulation task refers to one's own body. In the example cited above, we can ask how body position and MI may form a coherent picture for the skier or, more generally, for any persons using MI as a technique for enhancing their motor skills.

Mentally rehearsing movements has become an important technique in applied sport and exercise psychology with both athletes and patients (Lotze and Halsband 2006; Murphy 1994). In this context, MI is defined as an internal rehearsal of movements from a first-person perspective without any overt physical movement (Crammond 1997; Decety and Jeannerod 1996; Hanakawa et al. 2008; Jeannerod 1994). Behavioral studies using MI have shown improvements in speed, accuracy, and strength of motor execution (Feltz and Landers 1983; Yáñez et al. 1998;

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Yue and Cole 1992), thus supporting the notion that MI is not just epiphenomenal but plays a functional role for cortical plasticity. During recent years, data have accumulated viewing MI as a profound body-based simulation process that uses the motor system as a substrate (Gallese 2005; Svensson et al. 2007). Several neuroimaging studies have demonstrated that roughly the same neural structures are involved in both motor execution and in MI (Decety et al. 1994; Deiber et al. 1992; Lotze et al. 1999; Porro et al. 1996; Stephan et al. 1995). Related studies have focused on involvement of core and broader motor areas (Munzert et al. 2008; Wolfensteller et al. 2007). Specifically, these neural structures are the supplementary motor area (SMA), the premotor cortex (PMC), and, in a growing number of studies, the primary motor cortex (M1), the inferior parietal lobule (IPL), the basal ganglia (BG), and the cerebellum.

Recent computational models have challenged the earlier conceptions of action control, and these have also been used to describe covert states of action such as MI. In these models, a “planner” (the inverse model) maps the information between the movement goal and the motor command, and a predictive forward-model estimates the anticipated sensory outcome (Miall and Wolpert 1996; Wolpert and Flanagan 2001). Although movement-related sensory feedback is lacking in MI, forward-model estimates still predict the sensory outcome in action simulation. This indicates that somatosensory processes need to be an integral part of MI. But what is so specific about MI?

Jeannerod (1994) has analyzed the differences between MI and visual imagery of motor actions. He describes MI as part of a broader phenomenon related to intending and preparing actions that can be understood as a first-person process involving kinesthetic and visual representations. Visual imagery, in contrast, refers to a third-person process involving a visual representation of an action. This distinction offers the opportunity to examine the neural substrates of differences in perspective and of the feeling of being the cause of an action in a simulation task. Ruby and Decety (2001) asked participants to simulate object-related hand movements from either a first-person perspective (1PP) or a third-person perspective (3PP). In contrast to 3PP simulation of action, during 1PP, only regions in the left hemisphere were activated. These included the IPL, the precentral gyrus, the superior frontal gyrus, the occipitotemporal junction, and the anterior insula. Probably, this reflects the distinction between 1PP and 3PP representation as well as the left hemisphere dominance for one’s own actions and action simulation (Vogeley and Fink 2003).

It has been argued that MI is a simulation of one’s own body movements using a pre-existing body-model and, hence, an instance of embodied cognition (Gallese 2003, 2005). Several studies have tested the embodied nature of movement simulation by observing the influence of actual

and imagined hand posture on MI (de Lange et al. 2006; Fourkas et al. 2006; Vargas et al. 2004). The compatibility of the hand position modulates the blood-oxygen-level-dependent (BOLD) signal in parietal structures as well as the excitability of the precentral gyrus, suggesting that such bodily states as the configuration of one’s own posture are relevant for MI.

The present study focused on the impact of body positions on neural activation in motor-related areas during movement imagery based on different imagery perspectives by investigating whether proprioceptive information on hand position is integrated into 1PP imagery and 3PP imagery of intransitive (i.e., without any object-manipulation) hand movements. During fMRI scanning, healthy participants viewed four video clips depicting two hand movements with durations of 6 and 9 s. Subsequently, they were asked to imagine the movements in 1PP or 3PP with their own hand in either a compatible or an incompatible posture. In the reported literature, it was suggested that 1PP imagery involves kinesthetic representations and evokes motor simulations of one’s own body. By contrast, 3PP imagery refers to a rather visual representation of an action (Jeannerod 1994). If these two imagery processes differ on a phenomenological level, they might also differ at a representational level as has been shown previously by Ruby and Decety (2001). A further implication refers to the current body and limb position. If 1PP imagery specifically refers to own body movements while 3PP imagery does not, the current position of the imager’s body should only influence neural activity during 1PP imagery (de Lange et al. 2006). Therefore, we hypothesized that the integration of proprioceptive information from the hand would be more relevant in 1PP than in 3PP imagery and it should elicit stronger neural activation in sensorimotor areas. If so, we argue that 1PP imagery is more *embodied* than 3PP imagery, because it uses a pre-existing body-model in the brain to a higher extent (Gallese 2003, 2005).

Materials and methods

Participants

Twenty, right-handed female students (mean age 22.3 years, SD = 2.6 years) with normal or corrected-to-normal vision participated in the study. Imagery ability was assessed with the Movement Imagery Questionnaire (Hall and Martin 1997). Average scores ranged from 1.6 to 2.6 ($M = 2.2$, $SD = 1.1$) on a scale from 1 (very easy to imagine) to 7 (very difficult to imagine), indicating that all participants were able to rehearse very vivid images of their actions. They reported no history of psychiatric or neurological disorders, and no history or current use of any psychoactive

medication. The study was approved by the ethical committee of the *Deutsche Gesellschaft für Psychologie* (DGPs), and all participants gave their informed consent in accordance with the Declaration of Helsinki.

Training session

Several days prior to the fMRI experiment, participants attended a training session in order to familiarize themselves with the different imagery modes and the experimental setting. After first filling out the Movement Imagery Questionnaire (Hall and Martin 1997), they were trained to imagine beating on a table with a fist and running their plane hand over a table in both 1PP and 3PP imagery. In 1PP imagery, participants were asked to imagine the movement kinesthetically as if they were performing it. In 3PP imagery, they were requested to imagine the movement visually just as if they were watching another person performing it. These training stimuli were the same as those in subsequent the fMRI experiment. Prior to every imagery trial, participants were instructed to place their hand in a position compatible to the imagined movement. They had to report the beginning and the end of each imagery phase by giving a sign with their left hand. This served as a direct feedback to the experimenter in order to control for imagery performance with a mental chronometry paradigm. Further, participants lay in a supine position to familiarize themselves with the fMRI scanner position. While performing imagery, surface EMG (Schuhfried, Mödling) was recorded over two target muscles of the right hand (*musculus extensor* and *musculus flexor digitorum superficialis* of the forearm) to ensure that participants refrained from contracting their hand muscles during imagery. The training session had a total duration of 180 min.

Stimulus material and task

The stimulus material in the experimental phase consisted of four 6- or 9-s video sequences of hand movements performed by a human model. Two of the sequences showed a fist beating a table; the other two, a plane hand running over a table. All videos were presented from a neutral perspective focusing on the right arm and hand. These stimuli were presented by a PC running Presentation software (Neurobehavioral Systems, Albany, USA) and projected onto a screen behind the scanner that could be viewed through a mirror attached to the head coil (visual field 188 mm in the horizontal and 168 mm in the vertical plane, rectangular aperture). Participants were scanned during four target conditions: 1PP compatible (1PP comp), 1PP incompatible (1PP incomp), 3PP compatible (3PP comp), 3PP incompatible (3PP incomp), and one rest (re) condition. Conditions were presented in a randomized order counterbalanced

across participants. Prior to presentation of a video sequence, participants were instructed to place their hand in either a compatible or an incompatible hand posture (fist, plane hand). Compatibility refers to the match between hand posture and content of imagery (i.e., imagining a fist beating on the table and positioning the hand on a horizontal plane was an incompatible trial). Each participant's right-hand posture was controlled through a video camera recording of hand and forearm. Subsequently, participants viewed a video sequence of a hand movement and were instructed which perspective they should adopt (1PP or 3PP). This was followed directly by an imagery phase in either 1PP or 3PP. Participants marked the beginning and the end of each imagery phase by pressing a key on a button box with their left hand. During imagery, participants kept their eyes closed and re-opened them only when imagery was over and the button was pressed. Eye closure and opening were also controlled with a video camera. After the imagery phase, participants rated how vivid their imagery had been on a 7-point scale by using their left hand to move the cursor on the rating scale and enter their rating. In a rest condition, participants also pressed a button at the beginning and closed their eyes.

Participants performed 60 trials (2 postures \times 2 video sequences \times 2 perspectives \times 6 replications + 12 \times resting phase) during a total scanning time of approximately 40 min. After the experiment, they were surveyed regarding their awareness of the effects of the postural manipulation on task performance.

Data acquisition and analysis

MRI data were collected on a 1.5-T whole-body scanner (Siemens Symphony, Erlangen, Germany) with a standard head coil. Structural image acquisition consisted of 160 T1-weighted sagittal images (MPRAGE, 1-mm slice thickness). For functional imaging, a total of 912 volumes were registered using a T2*-weighted gradient echo-planar imaging sequence (EPI) with 25 slices covering the whole brain (slice thickness 5 mm; 1 mm gap; TA = 100 ms; TR = 2.5 s; TE = 55 ms, flip angle 90°; field of view 192 mm \times 192 mm; matrix size 64 \times 64). The orientation of the axial slices was parallel to the AC–PC line. Trial onsets were jittered within a range of $\pm\frac{1}{2}$ TR.

Image processing was carried out using SPM2 (Wellcome Department of Imaging Neuroscience, London, UK) running in MATLAB 6.5.1 (Mathworks Inc. Sherborn, MA). Head motion in the scanner did not correlate substantially with the experimental conditions. Origin coordinates were adjusted to the anterior commissure (AC). Furthermore, slice time correction, realignment (sinc interpolation), and normalization to the standard space of the Montreal Neurological Institute brain (MNI brain) were performed.

Smoothing was executed with an isotropic three-dimensional Gaussian filter with full-width at half-maximum (FWHM) of 9 mm.

A first-level analysis was computed participant-wise using the general linear model. A boxcar function was convoluted with the hemodynamic response function. Boxcar function length covered the imagery interval of each condition as well as the rest period. Moreover, six movement parameters of the rigid-body transformation of the motion-correction procedure were introduced as covariates in the general linear model. The voxel-based time series were filtered by a low-pass filter (FWHM = 4 s) and a high-pass filter (time constant 256 s).

The four experimental conditions and the rest condition were entered into the model. Eight T-contrasts were calculated for each participant (1PP comp > re; 1PP incomp > re; 3PP comp > re; 3PP incomp > re; 1PP > 3PP; incomp > comp; 1PP comp > 1PP incomp; 3PP comp > 3PP incomp).

First-level contrasts were subjected to a second-level statistical analysis (random-effects analysis) to allow population inferences. Main and interaction effects were computed using one-sample *t* tests, including all participants for each of the contrasts. The statistical threshold was set at $P = 0.05$, corrected for multiple comparisons using the false discovery rate (FDR) criterion. *T* values of significant activations of the highest activated voxels were given for the MNI-coordinates and were assigned to anatomical regions. All regions were detected with the Automated Anatomical Labeling (AAL) software (Tzourio-Mazoyer et al. 2002) or, if already cytoarchitecturally mapped, with maps based on cytoarchitectural data with 50% probability (Eickhoff et al. 2005).

Furthermore, a small-volume correction was conducted for the contrasts comp versus incomp, incomp versus comp, 1PP comp versus 1PP incomp, 1PP incomp versus 1PP comp, 3PP comp versus 3PP incomp, and 3PP incomp versus 3PP comp. Regions of interest (ROI) were selected on the basis of previous findings reported in the literature (Lotze et al. 1999; Porro et al. 1996; Ruby and Decety 2001; Stephan et al. 1995). These were the inferior parietal cortex (parietal operculum, SII), the insula, the SMA, the M1, the SI, the inferior parietal lobe, and the basal ganglia. All regions of interest were defined cytoarchitecturally with maps based on cytoarchitectural data with 50% probability (Eickhoff et al. 2005). Masks for small-volume correction were created using FSL software (Smith et al. 2004). Significance was tested on voxel level ($\alpha = 0.05$, family-wise error (FWE)-corrected).

Behavioral data acquisition and analysis

Subjective ratings of each imagery trial were gathered while participants were in the scanner by using a visual

scale to indicate imagery vividness. Mean rating scores were calculated for each experimental condition (1PP comp, 1PP incomp, 3PP comp, 3PP incomp). A 2 (posture) \times 2 (perspective) repeated measures ANOVA was computed to examine the effects of perspective and hand posture on the participants' subjective ratings.

Durations of all imagery trials were collected as a manipulation check, and mean imagined durations were calculated. Data were analyzed with a 2 (posture) \times 2 (perspective) repeated measures ANOVA.

EMG data, collected in the training session, were averaged for each participant in each condition. The differences between the 1PP condition, the 3PP condition, and the rest condition were subjected to a 2 (posture) \times 3 (perspective: rest, 1PP, 3PP) \times 2 (right-hand target muscle) repeated measures ANOVA.

Results

Behavioral results: mental chronometry

Participants were able to perform the imagery task successfully in all conditions. Mean absolute durations for the imagery phases over all 48 trials are presented in Fig. 1. Results showed significant main effects for video duration, $F(1, 19) = 2560.32$, $P < 0.01$, $\eta^2 = 0.99$, and perspective, $F(1, 19) = 10.66$, $P < 0.01$, $\eta^2 = 0.36$, but no significant main effect for posture, $F(1, 19) = 1.41$, $P = 0.25$, $\eta^2 = 0.07$. A 2 (perspective) \times 2 (posture) \times 2 (video duration: 6 s, 9 s) repeated measures ANOVA revealed no significant interaction effects. These data confirmed compliance in imagining similar movement durations to video observation. Participants exhibited slightly longer imagery durations in 1PP than in 3PP imagery irrespective of hand posture (Fig. 1).

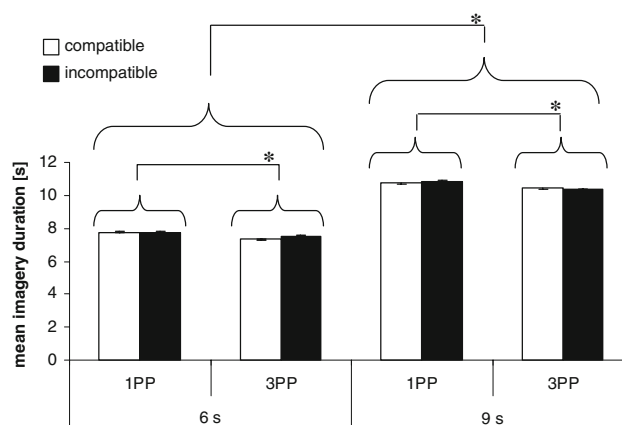


Fig. 1 Average imagery durations and standard errors of means for two imagery perspectives (1PP and 3PP) and two video durations (6 vs. 9 s)

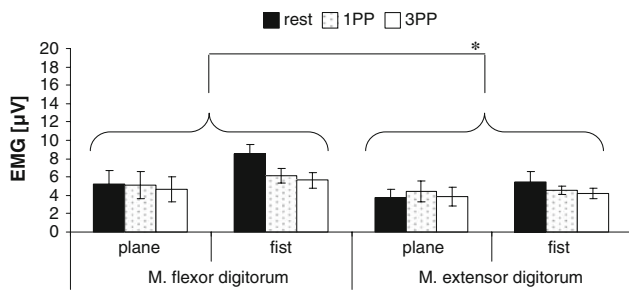


Fig. 2 Average EMG activation and standard errors of means for two muscles (M. flexor digitorum, M. extensor digitorum), two imagery conditions (1PP vs. 3PP) and rest, as well as two hand positions (plane vs. fist)

Behavioral results: EMG data

Figure 2 depicts the EMG data of all participants. In the plane hand position, baseline EMG was $5.20 \mu\text{V}$ ($\text{SD} = 6.68$) for the right *musculus flexor digitorum superficialis* and $3.72 \mu\text{V}$ ($\text{SD} = 4.08$) for the *musculus extensor digitorum*. In the fist position, baseline EMG was $8.48 \mu\text{V}$ ($\text{SD} 4.82$) for the *musculus flexor digitorum superficialis* and 5.48 ($\text{SD} 4.76$) for the *musculus extensor digitorum*.

A 3 (perspective) $\times 2$ (posture) $\times 2$ (muscle) repeated measures ANOVA for the EMG of both muscles showed only a significant main effect for muscle, $F(1, 19) = 6.29$, $P < 0.05$, $\eta^2 = 0.25$. There were no further main or interaction effects. Hence, there were no significant EMG differences between resting baseline and imagery irrespective of posture and perspective. Therefore, it was assumed that neural activation differences between experimental conditions were not due to muscle activity while imagining hand movements.

Ratings of imagery vividness

After each imagery trial, participants were asked to evaluate the quality of their imagery performance on a 7-point scale assessing imagery vividness. All participants showed high levels of imagery vividness in every imagery condition (1PP comp: $M = 5.92$; $\text{SD} = 0.61$; 1PP incomp: $M = 5.66$; $\text{SD} = 0.82$; 3PP comp: $M = 5.49$; $\text{SD} = 0.66$; 3PP incomp: $M = 5.45$; $\text{SD} = 0.70$). A 2 (perspective) $\times 2$ (posture) $\times 2$ (video duration) repeated measures ANOVA revealed a significant main effect for perspective, $F(1, 19) = 13.15$, $P < 0.01$, $\eta^2 = 0.41$, but no main effect for posture, $F(1, 19) = 3.23$, $P = 0.09$, $\eta^2 = 0.15$, and no interaction effects for the different conditions. This indicated that participants judged 1PP imagery trials more vividly—possibly due to the lack of MI experience prior to the experiment. The gain in expertise, especially in MI, due to the training session might have led to the slightly more positive rating of 1PP imagery trials.

fMRI data: imagery

There were significant activation increases in regions previously shown to be involved in motor imagery. Brain areas activated by imagery were the SMA, the PMC, the precentral gyrus, the lingual gyrus, the posterior cingulate cortex, the superior temporal lobe, the supramarginal gyrus, the precuneus, and the putamen bilaterally (corrected, $q[\text{FDR}] < 0.05$). These results were highly consistent with a number of studies demonstrating the involvement of motor areas in body-associated imagery (Ruby and Decety 2001; Lotze et al. 1999; Porro et al. 1996) and served as a validation of participants' imagery performance. All results are summarized in Table 1.

fMRI data: perspective effects

Compared with 3PP, 1PP imagery was associated with higher activation in the inferior parietal lobe, the SMA, the vPMC, the putamen, the cuneus, and the postcentral gyrus in the left hemisphere. In the right hemisphere, the precuneus, the insula, and the cerebellum showed stronger activation (corrected, $q[\text{FDR}] < 0.05$) (Fig. 3). These results are reported in Table 1. The opposite contrast, 3PP versus 1PP, revealed no significant activation differences.

fMRI data: posture effect

A ROI analysis revealed that a compatible hand position was associated with stronger activations in the precentral gyrus and the inferior parietal lobe (parietal operculum, SII) of the left hemisphere, as well as in the insula, the SMA, the cerebellum, and the superior temporal lobe of the right hemisphere ($P < 0.05$, FWE-corrected) compared with an incompatible hand position (Table 2). Contrasting imagery trials with an incompatible and a compatible hand position revealed no significant activation differences.

fMRI data: interaction between posture and perspective

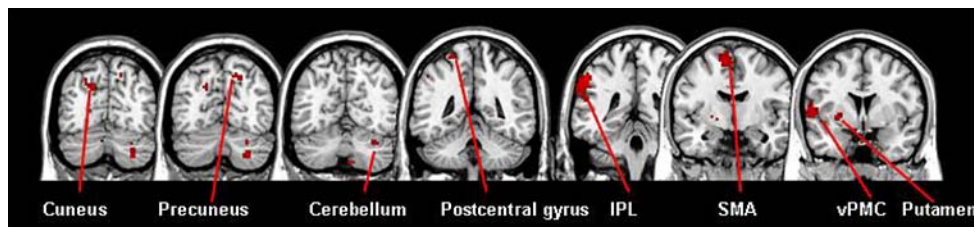
As the main focus of this study was on the neural effects of the compatibility of hand posture while participants performed 1PP and 3PP imagery, the contrasts 1PP comp versus 1PP incomp and 3PP comp versus 3PP incomp were particularly relevant. A ROI analysis showed that a compatible hand posture compared with an incompatible hand posture during 1PP imagery was associated with stronger activation in the insula of the left hemisphere, the inferior parietal lobe (parietal operculum, SII) of both hemispheres, and the putamen of the right hemisphere ($P < 0.05$, FWE-corrected) (Fig. 4).

These results are summarized in Table 2. No activation differences were found for the comparison between compatible and incompatible hand posture during 3PP.

Table 1 Brain regions identified by contrasting the 1PP and 3PP imagery to rest; brain regions identified contrasting 1PP to 3PP imagery

	Left/right	Coordinates of max. <i>T</i> value			<i>T</i> value
Imagery versus rest					
SMA	l	0	3	66	8.61
Putamen	l	-21	3	3	8.14
SMA/PMC	l	-48	-12	51	7.7
vPMC	r	60	12	12	6.53
SMA/PMC	r	54	0	42	6.1
Lingual gyrus	l	-33	-51	0	6.08
Putamen	r	21	3	9	5.33
Posterior cingulate cortex	l	-18	-39	18	5.25
Precentral gyrus	l	-39	-6	30	4.49
Superior temporal gyrus	l	-51	-36	21	4.42
Supramarginal gyrus	l	-45	-39	27	3.99
Precuneus	r	30	-48	9	4.29
1PP versus 3PP					
Inferior parietal lobe	l	-57	-39	42	6.68
Cerebellum	r	6	-63	-51	6.09
SMA	l	-9	-6	60	5.78
vPMC	l	-57	3	6	5.6
Putamen	l	-27	3	0	5.23
Cuneus	l	-18	-72	33	5.01
Postcentral gyrus	l	-21	-45	66	4.7
Precuneus	r	18	-69	42	4.59
Insula	r	30	-21	24	4.19

MNI coordinates, cluster size
>5, $q[\text{FDR}] < 0.05$

**Fig. 3** Significantly activated voxels ($P = 0.05$, FDR-corrected) of the comparison 1PP > 3PP

Discussion

Using fMRI, the aim of the present study was to determine whether the integration of proprioceptive information is especially relevant in first-person perspective (1PP) imagery. The results support the notion that a compatible hand posture in 1PP imagery influences neural activity in the inferior parietal lobe (parietal operculum, SII) and in the insula. Neural activation during the 3PP imagery process remains unaffected by hand position. A further finding is that different perspectives adopted by participants during imagery influence neural activation patterns. Here, we find a left hemispheric dominance for 1PP imagery.

Both findings provide evidence for the embodied nature of imagining hand movements. First, they highlight that

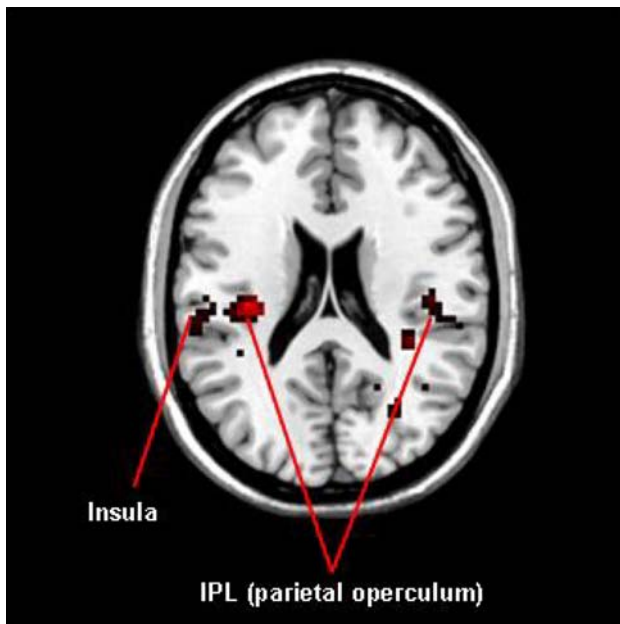
movement simulation does not remain unaffected by body sources, especially when the cognitive simulation task refers to one's own body. Second, 1PP imagery conditions lead to stronger activation in motor and motor-related areas of the left hemisphere, using a pre-existing body-model in the brain. The integration of bodily position information in imagery and the stronger activation of motor areas provide additional empirical support for the embodied nature of cognition. The following sections will discuss the main findings in more detail.

Simulation of hand movements

The analysis of both imagery conditions (1PP and 3PP) contrasted with rest shows an activation of motor and

Table 2 Brain regions identified by contrasting compatible and incompatible imagery conditions; brain regions identified by contrasting IPP compatible and IPP incompatible imagery conditions

	Left/right	Coordinates of max. <i>T</i> value			<i>T</i> value	Mask size
Compatible versus incompatible						
Precentral gyrus	l	−36	−30	63	3.79	108 voxels
Precentral gyrus	l	−51	−9	33	3.62	55 voxels
Inferior parietal lobe (parietal operculum)	l	−42	−27	21	6.25	349 voxels
Insula	r	36	−18	3	4.49	158 voxels
SMA	r	3	−6	63	3.52	83 voxels
Cerebellum	r	6	−51	−42	6.03	3132 voxels
Superior temporal lobe	r	51	−18	−6	3.83	106 voxels
IPP compatible versus IPP incompatible						
Inferior parietal lobe (parietal operculum)	l	−36	−21	21	6.07	349 voxels
Inferior parietal lobe (parietal operculum)	r	45	−21	24	4.24	341 voxels
Insula	l	−36	−18	6	3.81	149 voxels
Putamen	r	33	−18	−3	4.05	229 voxels

**Fig. 4** Significantly activated voxels ($P = 0.01$, uncorrected) of the within-group comparison IPP comp > IPP incomp

motor-related structures. This activation pattern is in line with previous neuroimaging studies comparing the activation patterns of not only MI and movement execution but also MI and visual imagery (3PP imagery) of movements (Deiber et al. 1992; Gerardin et al. 2000; Lotze et al. 1999; Solodkin et al. 2004; Stephan et al. 1995). The overlapping activation pattern is interpreted as indicating a functional equivalence between mental simulation and the execution of actions.

In this study, the analysis of the imagery conditions compared with rest serves as a validation of the partici-

pants' imagery performance. Because we find the well-known activation pattern of motor and motor-related areas, we assume that the participants actually have simulated the instructed movements. Taking our EMG results into consideration, which reveal no differences between resting and the imagery conditions, it can be concluded that the cerebral activation differences between experimental conditions are not due to muscle activity while imagining hand movements. It should be underlined that participants had practiced generating vivid images without eliciting any movement outcomes prior to the scanning session.

Left hemisphere dominance during simulation of hand movements in IPP

We show that particularly IPP imagery conditions lead to stronger activation in motor and motor-related areas of the left hemisphere, that is, the left inferior parietal lobe, the left SMA, and the left vPMC, together with the right cerebellum. This replicates the finding that two imagery modes need to be distinguished depending on which perspective is taken (Ruby and Decety 2001). The discrimination between 1PP and 3PP imagery offers a model with which to examine the neural distinction between perspectives and between one's own and other's actions. One common finding of neuroimaging experiments over the last decade has been that the same neural network is involved not only in the preparation and simulation of self-generated actions but also in the observation of actions performed by others, that is, either 1PP- or 3PP-related processes. This network includes the premotor cortex, the primary motor cortex, and posterior parietal regions (Hamilton et al. 2006; see, for a review, Jeannerod 2006). It is assumed that this overlap defines the

neural substrate of understanding others' actions and intentions. However, this overlap is not complete, which might be relevant for differentiating self-generated actions from those of others (Ruby and Decety 2001; Ramnani and Miall 2004; Saxe et al. 2006; Schütz-Bosbach et al. 2006). However, the neural basis of the process accounting for the differentiation between self and other as well as between the different perspectives has yet to be determined unequivocally.

Ruby and Decety (2001) asked participants to imagine either themselves manipulating an object or the experimenter manipulating an object. Their results showed a dramatic increase in activation in the right inferior parietal lobule at the junction with the temporal cortex when participants imagined the experimenter manipulating an object. Additionally, the inverted comparison revealed a stronger activation of the inferior parietal cortex, the posterior insula, and the postcentral gyrus in the left hemisphere. Obviously, humans require differential physiological substrates to avoid confusion of 1PP and 3PP processes. Accordingly, other studies have demonstrated the importance of the left hemisphere in tasks that require self-processing (Brady et al. 2004; Turk et al. 2002). It has been suggested that the self versus other discrimination during a mental task relies on a vivid representation of oneself based on an amplified activation in motor and sensorimotor structures. Recent studies using other approaches also support this suggestion. Saxe et al. (2006) compared brain activation while viewing images of body parts from a 1PP (egocentric) and a 3PP (allocentric). The response of the primary sensory cortex was suppressed when participants saw images from an allocentric perspective (3PP). Similarly, Maeda et al. (2002) found greater MEP facilitation for 1PP views of grasping actions. Therefore, it seems that motor and sensorimotor structures are heavily involved in the process of differentiating between oneself and others. The taken perspective influences neural activity in these systems, leading to the assumption of a quantitative agent-specific representation in these structures. In general, both recent research and the present study support the notion that our motor system makes an important contribution to self-related processes, even in an imagery task.

The relevance of proprioceptive information for 1PP imagery

As 1PP imagery is considered to be a simulation of oneself and one's own body movements, the integration of bodily signals might be specific for this process and reflect a prerequisite for experiencing oneself. Processing proprioceptive signals is proposed to be one of the relevant components that constitute sources of bodily awareness (Tsakiris et al. 2006). Proprioception in 1PP simulation

processes was initially demonstrated in behavioral studies revealing that incompatible postural signals affect implicit and explicit imagery (Funk et al. 2005; Ionta et al. 2007; Parsons 1994; Sirigu and Duhamel 2001). With regard to the underlying neuronal processes, some studies have demonstrated that imagined and actual body position influence the activity in neural structures during own body simulation processes (Arzy et al. 2006; de Lange et al. 2006, Fourkas et al. 2006; Vargas et al. 2004). These results suggest that the plastic and dynamic representation of the properties of the body, derived from multiple sensory inputs (Schwoebel and Coslett 2005), is involved in solving such a mental task. Our results show increased activation in the left inferior parietal cortex (parietal operculum, SII) as well as in the insula when participants imagine hand movements in 1PP while holding their hand in a compatible hand position. In contrast, no compatibility effects are found in the 3PP imagery condition. This indicates that the modulation of neural activity by arm posture is specific for 1PP imagery and suggests that bodily, that is, proprioceptive information is integrated when simulating oneself.

Generally, the parieto-insular region is associated with the integration of multisensory inputs (Giummarra et al. 2008; Ventre-Dominey et al. 2003). In particular, the parietal operculum, a prominent part of the inferior parietal lobe, is related to higher order somatosensory functions and the integration of somatosensory information and other sensory modalities (Caselli 1993; Cipolloni and Pandya 1999; Servos et al. 2001). It receives somatosensory, polysensory, and visual information coming from the primary somatosensory cortices and from polysensory areas in the parietal lobe. Furthermore, its reciprocal connections to the insula (Augustine 1996) support the notion that the parietal operculum forms the neural correlate for the integration of sensory body information. The insula is designated as a multisensory and motor association area and maintains multiple connections to sensory and motor-relevant areas. Especially, its posterior portion is associated with the multisensory integration processes that contribute to the experience of body ownership (Tsakiris et al. 2007).

The roles of the parietal operculum in action simulation or prediction have been emphasized in several fMRI studies. For example, Carlsson et al. (2000) claimed that this region even responds to a mere expectation of a sensory stimulus. Hence, activation in this area within the IPL might indicate its involvement in embodied simulation processes (Gallese 2003, 2005; Rizzolatti and Craighero 2004; Keysers et al. 2004). Furthermore, activation of the parietal operculum is also considered to reflect reafferent proprioceptive signals (Iacoboni et al. 1999). In this regard, a modulation of parietal opercular activity might occur due to predicting the sensory consequences of a movement. Indeed, it was shown that activity in the bilateral parietal

operculum (SII) was higher during externally produced tactile stimulation of the palm than during self-produced tactile stimulation (Blakemore et al. 1998). Besides prediction processes, these data underpin the notion that the parietal operculum is also associated with attributing actions to oneself (Decety et al. 2002; Sirigu et al. 1999).

In the present study, a compatible limb position leads particularly to a higher activation of the mentioned parieto-insular region. Thus, the congruency between hand position and the imagined movement might be viewed as facilitation due to higher amounts of sensory input coming from the periphery (Shimura and Kasai 2002). This has been shown directly in TMS studies demonstrating higher excitability of the precentral gyrus when hand position matches the imagined movement (Fourkas et al. 2006; Vargas et al. 2004). On a cellular level, Stein (1992) has shown that neurons in the posterior parietal cortex discharge more strongly when sensory information is reafferent, meaning that it is determined by forward-predicted estimation of the limb from a self-generated movement via the efference copy. This finding fits nicely with the notion that activation of the parietal operculum (SII) is associated with reafferent information processing (Iacoboni et al. 1999).

The present data support the notion that 1PP imagery is a prediction based on a forward-model process. Depending on the actual hand posture, the afferent input provides a signal that is either compatible or incompatible with the predicted sensory outcome. The higher activation in the parieto-insular region in the compatible condition can then be explained through a facilitating mechanism when the feedback matches the prediction, i.e., is reafferent. Similar to Sirigu and Duhamel (2001), the effect of postural compatibility occurs only for the 1PP condition, indicating that visual 3PP imagery utilizes a more visual representation of the movement. Hence, parietal structures such as the parietal operculum are less involved in 3PP imagery, because one's own body representations are of less importance for this mental process. Within 3PP imagery, no specific motor plan is generated as a function of the current configuration of the limbs. Altogether, these results suggest that the plastic and dynamic representation of the body, derived from multiple sensory inputs interacting with motor systems in the genesis of actions (Schwoebel et al. 2002; Schwoebel and Coslett, 2005), is involved in 1PP but not 3PP imagery. This strongly underpins the embodied nature of 1PP imagery.

Conclusion

Using an explicit imagery task involving intransitive hand movements, we have been able to show that 1PP leads to a stronger activation of motor and motor-related areas than

3PP imagery. Our data support the embodied nature of 1PP imagery in which body representations are involved. Stronger activation of the insula and the inferior parietal cortex (parietal operculum, SII) reveals that bodily information is integrated into the image of one's own body movement, but not in a movement that is not attributed to the own body. This suggests that self-experience is composed of efferent and reafferent information not only in real action execution situations but also in MI.

Turning to the embedding of imagery in an applied context such as athletic training or the rehabilitation of Parkinson's disease or stroke patients, we consider that there are strong indications for using 1PP imagery. The 1PP imagery process draws on the motor system and somatosensory integration processes that contribute to motor skill (re-)learning.

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