

Double Dissociation between Motor and Visual Imagery in the Posterior Parietal Cortex

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Because motor imagery (MI) and visual imagery (VI) are influenced differently by factors such as biomechanical constraints or stimulus size, it is conceivable that they rely on separate processes, possibly involving distinct cortical networks, a view corroborated by neuroimaging and neuropsychological studies. In the posterior parietal cortex, it has been suggested that the superior parietal lobule (SPL) underlies VI, whereas MI relies on the supramarginalis gyrus (SMG). However, because several brain imaging studies have also shown an overlap of activations in SPL and SMG during VI or MI, the question arises as to which extent these 2 subregions really contribute to distinct imagery processes. To address this issue, we used repetitive transcranial magnetic stimulation to induce virtual lesions of either SMG or SPL in subjects performing a MI (hand drawing rotation) or a VI (letter rotation) task. Whatever hemisphere was stimulated, SMG lesions selectively altered MI, whereas SPL lesions only affected VI, demonstrating a double dissociation between MI and VI. Because these deficits were not influenced by the angular distance of the stimuli, we suggest that SMG and SPL are involved in the reenactment of the motor and visual representations, respectively, and not in mental rotation processes per se.

Keywords: mental rotation, sensorimotor theory, superior parietal lobule, supramarginalis gyrus, transcranial magnetic stimulation

Introduction

The idea that our conceptual system is grounded in sensorimotor representations has gained much interest in the past decade (Damasio and Tranel 1992; Barsalou et al. 2003; James and Gauthier 2003; Gallese and Lakoff 2005). According to this view, conceptual processing relies on mental imagery that allows the reenactment of perceptual or motor representations (Kan et al. 2003; Kosslyn et al. 2005).

However, mental imagery is probably not a unitary process as suggested by the finding that several factors may influence motor imagery (MI) and visual imagery (VI) in a different way. Indeed, MI can be affected by the actual body posture (Sirigu and Duhamel 2001; Shenton et al. 2004; de Lange et al. 2005; Stevens 2005), by biomechanical constraints (Parsons 1994; Johnson 2000b), and by the inertial properties of the body parts (Gentili et al. 2004); MI also conforms to the speed-accuracy trade-off predicted by Fitts' law (Sirigu et al. 1996; Stevens 2005). On the other hand, VI is influenced by visuospatial parameters, such as the relative size of the imagined objects (Kosslyn et al. 1978; Mellet et al. 1998; Stevens 2005). Consistently, with this apparent dichotomy, functional brain imaging studies have showed that the cortical networks involved in MI and VI are partly different: MI rather activates

frontoparietal regions, whereas VI relies on a parietooccipital network (Kosslyn et al. 1998; Booth et al. 2000; Vingerhoets et al. 2002; Zacks et al. 2002; de Lange et al. 2005). Along the same lines, several clinical studies have provided evidence for a functional dissociation between MI and VI (Tomasino, Rumiati, and Umiltà 2003; Zacks et al. 2003), also suggesting that both processes rely, at least partly, on distinct functional brain circuits.

In the posterior parietal cortex (PPC), however, whether different subregions are specifically involved in VI and MI remains debated because the conclusions of functional neuroimaging studies are contradictory (see Table 1). Indeed, some authors have suggested that the superior parietal lobule (SPL) is distinctively activated in VI (Jordan et al. 2002; Vingerhoets et al. 2002; Harris and Miniussi 2003), whereas others have shown that VI also recruits the supramarginalis gyrus (SMG) (Kosslyn et al. 1998; Zacks et al. 2002; Kawamichi et al. 2007). Similarly, brain imaging studies do not allow us to determine the respective contribution of SMG and SPL to MI performance (Kosslyn et al. 1998; Vingerhoets et al. 2002; Zacks et al. 2002; Creem-Regehr et al. 2007). The first goal of the present study was therefore to address this issue by using repetitive transcranial magnetic stimulation (rTMS) to induce virtual lesions of either the SMG or the SPL in subjects performing a mental rotation of hand drawings (MI task) or of letters (VI task). We predicted that, because SMG is usually regarded as a key area for movement representation, its lesion should specifically impair MI performance (Grezes and Decety 2001; Kuhtz-Buschbeck et al. 2003), whereas lesions of SPL, because of its potential contribution to visuospatial processes, should alter VI (Roland and Gulyas 1995; Carlesimo et al. 2001; Vanlierde et al. 2003). A double dissociation between VI and MI, that is, a selective impairment of VI after a virtual lesion of one of these parietal areas and an impairment of MI following a lesion of the other one, would demonstrate that these 2 types of mental imagery rely on anatomically distinct brain regions, ruling out an unspecific transcranial magnetic stimulation (TMS) effect or an effect due to a difference in task difficulty (Jahanshahi and Rothwell 2000; Walsh and Cowey 2000; Crawford et al. 2003; Robertson et al. 2003; Daprati and Sirigu 2006).

The second aim of the present study was to address the issue of the lateralization of mental imagery processes. As far as MI is concerned, most functional imaging studies have suggested a more pronounced contribution of the left than of the right PPC (Haaland et al. 2004; Johnson-Frey et al. 2005; Muhlau et al. 2005), a finding consistent with the well-known dominance of the left hemisphere in motor control (Sabate et al. 2004). For VI, the classical view is that visuospatial information is processed in the right PPC (Corballis 1997; Kosslyn et al.

Table 1

Comparison of MNI coordinates of left SMG, right SMG, left SPL, and right SPL in neuroimaging studies that investigated VI and/or MI by using mental rotation tasks

Study	Task	Left SMG			Right SMG			Left SPL			Right SPL		
		x	y	z	x	y	z	x	y	z	x	y	z
Creem-Regehr et al. (2007)	MI	-42	-40	54	44	-50	46	-36	-50	64	24	-68	64
Kosslyn et al. (1998) ^a	MI	-50	-32	40				-20	-72	44			
Vingerhoets et al. (2002)	MI							-25	-48	31	29	-50	50
Zacks et al. (2002) ^a	MI	-60	-55	33				-29	-61	44	32	-45	50
Alivisatos et Petrides (1997) ^a	VI	-40	-61	42							12	-74	52
Harris and Miniussi (2003) ^a	VI							-34	-68	50	34	-68	50
Jordan et al. (2002)	VI							-24	-72	48	24	-72	48
Kawamichi et al. (2007)	VI				56	-54	40	-22	-82	48	24	-80	52
Kosslyn et al. (1998) ^a	VI	-33	-45	41	35	-49	41	-15	-72	44	12	-69	49
Vingerhoets et al. (2002)	VI							-29	-58	53	17	-67	48
Zacks et al. (2002) ^a	VI	-60	-55	33				-29	-61	44	32	-45	50
	Mean	-48	-48	40.5	45	-51	42.3	-26	-64	47	24	-64	51.3
	SD	11.1	10.9	7.71	10.5	2.65	3.21	6.4	10.7	8.35	8.1	12.5	4.67
Present study	Mean	-56	-50	47	61	-46	42	-28	-72	56	30	-67	60

Note: Studies from 1997 were included, provided they mentioned SMG and/or SPL as a focus of activation and gave Talairach or MNI coordinates.

^aTalairach coordinates converted in MNI coordinates.

1998; Dong et al. 2000; Tomasino, Toraldo, and Rumiati 2003; Zacks et al. 2003) although some studies have suggested that the 2 hemispheres may equally contribute to the mental rotation of visual stimuli (Mellet et al. 1998; Jordan et al. 2001; Ferdeos and Sachdev 2006). In the present study, we addressed this question by comparing the effect of virtual lesions of left/right SMG or SPL on MI and VI performance.

Materials and Methods

Subjects

Twenty French-speaking males (mean age: 26.4 years), right handed according to the Edinburgh Handedness Inventory (Oldfield 1971), participated in this study. Their vision was normal, or corrected to normal, and none of them had a neurological history. Subjects gave their written informed consent and were screened for potential risks to TMS by means of the TMS Adult Safety Screen (Keel et al. 2001). All experimental procedures used were approved by the Ethics Committee of the Catholic University of Louvain.

The subjects' ability for mental imagery was assessed by the Vividness of Movement Imagery Questionnaire (VMIQ) (Isaac et al. 1986). The first part of this questionnaire aimed at assessing MI, and to do so, participants were asked to imagine themselves moving (mean score: $78 \pm 8\%$). VI was then assessed by asking the subjects to imagine an action performed by someone else (mean score: $75 \pm 4\%$) (Campos et al. 1998; Callow and Hardy 2004). Both conditions of the VMIQ did not differ statistically ($t < 1$) and all individual scores obtained exceed 70%, a normal score given the age of the studied group (Mulder et al. 2007).

Task Description

Experiments were performed in a dimly lit room. Subjects sat comfortably in an armchair, 60 cm in front of a computer screen; they wore earplugs to attenuate the TMS noise. Visual stimuli were either a hand drawing (MI task) or a letter (VI task); they were black line drawings on a white background, presented at the center of a computer screen using E-Prime (Psychological Software Tools, 2002, Pittsburgh, PA). Stimulus size did not exceed 5 degrees of visual angle. Each trial began with the presentation of a central cross for 200 ms and, after a 500-ms delay, the stimulus was presented for 500 ms followed by a blank screen (see Fig. 1A).

In the MI task, the subjects had to decide whether the drawing corresponded either to a right or a left hand (Parsons et al. 1995) and they had to give their response verbally by saying either "gauche" (left) or "droite" (right). In the VI task, the subjects had to decide whether the letter was shown in its canonical form or not, and to answer "oui"

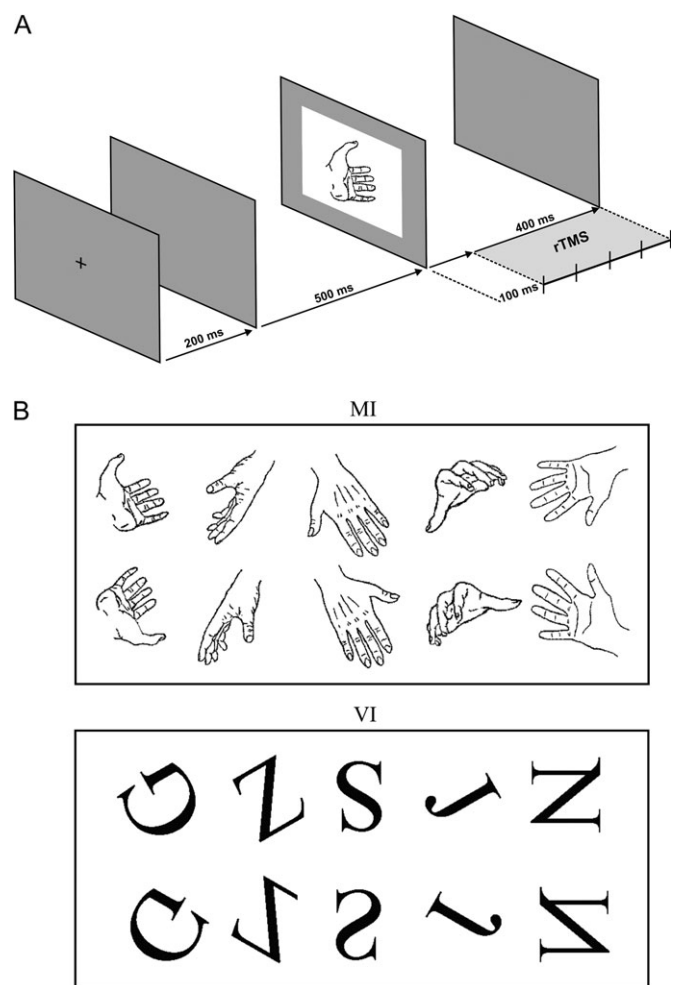


Figure 1. (A) Time course of stimulus presentation and of the magnetic stimulation for both MI and VI tasks. (B) Stimuli used for each task. Upper box: right and left hand posture. Lower box: canonical and mirror letters.

(yes) or "non" (no), respectively (see Fig. 1B). A microphone was used to record verbal responses and reaction times (RTs) were measured online by means of E-Prime.

In order to balance both MI and VI tasks in terms of RT (mean and standard deviation [SD]) and error rate, a pilot study was conducted, without TMS, with 6 different drawings of left and right hands and 10 letters presented either in a canonical or in a mirror form. This study was performed on 12 other male subjects (mean age: 24.5 years). Each stimulus (hand or letter) was presented in 12 different orientations varying from 0° to 330°, by step of 30°, from the vertical axis. Based on the mean and SD of RT and the error rate, 5 hand postures (a palm view, a back view, a side view, a thenar/hypothenar eminence view, and a front view of the finger tips) and 5 letters (J, N, S, Z, and G) were selected for the TMS experiment (see Fig. 1*B*); 6 angles of rotation were also selected, namely 30°, 90°, 150°, 210°, 270°, and 330°, from the vertical axis. In total, each task was performed on 60 stimuli (5 stimuli × 2 responses × 6 angles of rotation).

To confirm *a posteriori* that the selected stimuli actually gave rise to comparable performances in MI and VI tasks, we performed 3 separate *t*-tests on the control trials ("no-TMS" condition) gathered during the main experiment. Results showed that the 2 tasks were equivalent in terms of RT (mean RT: 1042 ms in MI, 1029 ms in VI, *t* < 1), RT variability (mean SD: 290 ms in MI, 297 ms in VI, *t* < 1), and error rate (3% in MI, 4.5% in VI, *t* < 1).

Experimental Design

The main experiment consisted of 12 blocks resulting from the combination of the 2 tasks (VI and MI), 2 sites (SPL and SMG), and 3 TMS conditions (right side, left side, and no-TMS). The no-TMS condition was included in order to assess the classical effect of stimulus ORIENTATION on RT (Parsons 1994). The MI and VI tasks were interleaved throughout the experiment but half of the subjects began with MI and the other half with VI. The 2 stimulation sites were investigated during 2 separate sessions, conducted on different days. For half of the subjects, the TMS was applied over SMG during the first session and over SPL during the second one; the reverse order was used for the other subjects. The 3 TMS conditions were also counter-balanced across subjects.

Each block included 60 trials equally distributed for the responses (i.e., "gauche" or "droite" for the HAND SIDE and "oui" or "non" for the canonical letter form) and for the rotation angles (30°, 90°, 150°, 210°, 270°, and 330°). Each block was composed in such a way that a given stimulus (i.e., 1 of the 5 hand drawings—HAND POSTURE—or the 5 letters—LETTER IDENTITY) or a given response never occurred more than 3 times in a row. Before the first TMS session, subjects performed 60 practice trials for each task.

Transcranial Magnetic Stimulation

rTMS (10 Hz, 5 pulses) was applied by means of a Rapid Magstim model 200 stimulator (Magstim Company, Whitland, UK) through a 35-mm inner diameter figure-of-eight coil. The TMS intensity was set arbitrarily at 65% of the maximal stimulator output because it has been shown that the excitability of the primary motor cortex is not always correlated with the excitability of other cortical areas (Stewart et al. 2001). rTMS trains were separated by at least 6 s. The coil was positioned over SPL or SMG (see below) and was held tangentially to the skull along a mediolateral line with the handle pointing laterally. rTMS was delivered 100 ms after the stimulus (hand drawing or letter) display. During the no-TMS condition, the coil was held at the same position on the scalp but no stimulation was applied.

Location of Stimulation Sites

For each subject, the coil position was precisely determined by performing an online coregistration of the stimulation sites onto individual anatomical magnetic resonance imaging (MRI) slices (Noirhomme et al. 2004). Before the TMS experiment, about 200 points distributed on the participants' scalp were digitized by means of a pen receiver whose position was determined relative to a forehead reference (Polhemus Isotrak II system, Kaiser Aerospace Inc., Colchester, VT). The registration process created a transformation matrix that minimized the mean square distance between these points and the segmented scalp surface extracted from each individual MRI.

Then, the figure-of-eight coil was placed over the target sites and 3 points were digitized at the intersection of the windings; the coil coordinates were then put in correspondence with the transformation matrix. A line, normal to the plane of the coil, was drawn from its center to the brain, indicating the stimulation point both on a segmented brain surface and on the MRI slices. This method allows the visualization of the target sites on individual brain images with a spatial accuracy close to the millimeter (Noirhomme et al. 2004).

To target SMG, the coil was positioned below the intraparietal sulcus (IPS), just in front of the Jensen sulcus in the mediocaudal part of SMG. To target SPL, the coil was placed above the medial part of the IPS, just at the level of the angular gyrus. Individual coordinates of the TMS sites were normalized with respect to the Montreal Neurological Institute (MNI) brain atlas (Andres et al. 2005; Davare et al. 2006, 2007; Collignon et al. 2008). The mean normalized MNI coordinates of the SMG and SPL sites corresponded, respectively, to Brodmann areas 40 and 7 (see Fig. 2) and were consistent with the coordinates of activation sites reported by functional imaging studies which have investigated MI and/or VI (see Table 1).

Electromyography

Subjects were required to keep both hands at rest for the duration of the experiment. However, in order to make sure that there was no background activity in the hand muscles during the experimental session, electromyography (EMG) activity was recorded from the first dorsal interosseous muscle (1DI) of each hand with surface electrodes. EMG signals were amplified (gain: 1k), high-pass filtered at 30 Hz (Neurolog, Digitimer Ltd, Welwyn Garden City, UK), and digitized online at 2 kHz using a personal computer with a CED 1401 interface (Cambridge Electronic Design, Cambridge, UK). For each trial, the EMG signal was acquired over a time window spanning a range of 200 ms before to 500 ms after the stimulus presentation. EMG traces were inspected visually in order to exclude trials where the EMG background noise was larger than 50 μ V (see Data Analysis).

Data Analysis

The following trials were discarded from analyses: error trials (MI task: 2.7%, VI task: 3.7%), trials with an RT falling outside the range of the individual mean $\pm$ 2 SD (MI task: 4.5%, VI task: 4.2%), trials in which the verbal response failed to be recorded properly (MI task: 0.43%, VI task: 0.44%), and trials in which the background EMG activity in the right or left 1DI exceeded 50 μ V (MI task: 2.6%, VI task: 2.9%). Analyses were performed on all remaining trials (MI task: 89.4%, VI task: 88.2%).

First, we performed 2 analyses of variance (ANOVAs) on the RTs collected in the no-TMS trials in order to ascertain that each task actually involved specific processes of mental rotation. The effect of biomechanical constraints in MI was investigated by the means of an ANOVA with HAND POSTURE (5 hand views), HAND SIDE (right or left) and ORIENTATION (6 degrees of angles) as within-subject factors. A second ANOVA, with LETTER IDENTITY (5 letters), LETTER FORM (canonical or mirror), and ORIENTATION as within-subject factors, was performed on the RTs collected in the no-TMS trials of the VI task to assess the effect of the angular distance during the mental rotation of letters.

Moreover, although the different conditions were exactly counter-balanced across subjects, we compared the no-TMS trials recorded on the day when TMS was applied over SMG with those recorded on the day when TMS was applied over SPL in order to rule out that the results could be partly explained by differences between task performance in the first and second day of testing.

The second part of the analysis aimed at testing the disruptive effects of TMS over SMG and SPL in each task. To do this, we performed an ANOVA on RTs with TASK (MI vs. VI), SITE (SMG vs. SPL), and TMS condition (left, right or no-TMS) as within-subject factors.

Finally, in order to test the hypotheses that the TMS effects were modulated by the ORIENTATION of each HAND POSTURE and that hemispheric lateralization interacted with the HAND SIDE (left or right) illustrated on the drawings, we performed an additional ANOVA on the RTs gathered during the MI task with SITE, TMS, ORIENTATION, HAND POSTURE, and HAND SIDE as within-subject factors. A similar ANOVA, but with LETTER IDENTITY and LETTER FORM instead of HAND POSTURE and HAND SIDE, was also performed on

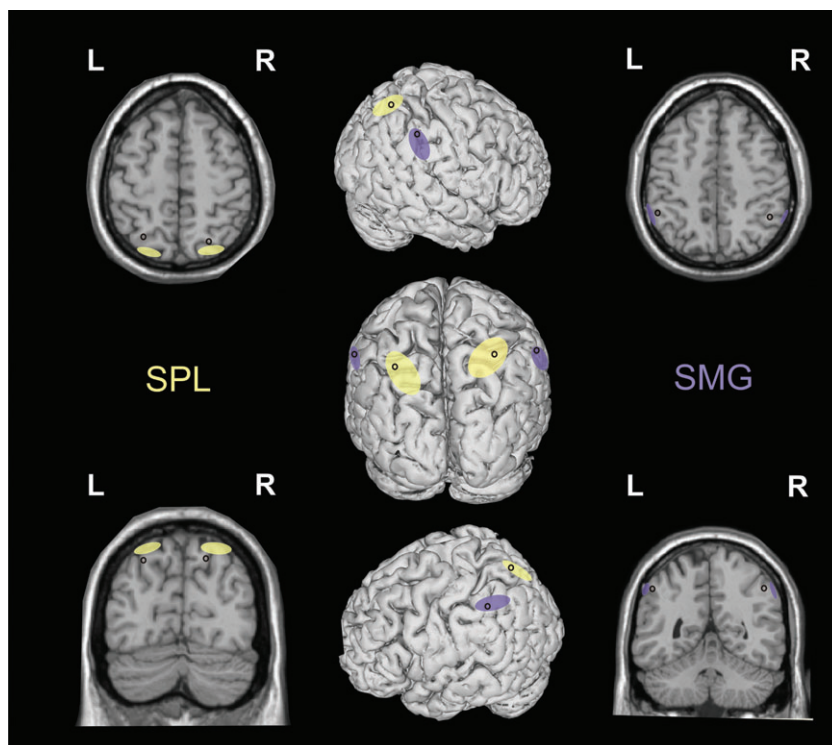


Figure 2. Coregistration of the TMS coil position used to target the right and left SMG (parma violet) and of the right and left SPL (yellow). Each ellipse is centered on the mean MNI coordinates (x, y, z , mean $\pm$ SD; $n = 16$) of right SMG ($61 \pm 6, -47 \pm 9, 42 \pm 10$ mm), left SMG ($-56 \pm 5, -51 \pm 13, 46 \pm 5$ mm), right SPL ($27 \pm 15, -71 \pm 12, 56 \pm 11$ mm), and left SPL ($-24 \pm 12, -76 \pm 11, 54 \pm 11$ mm). The ellipse surface shows the 95% confidence interval of the normalized coordinates calculated for each subject. Open circles represent the mean coordinates of the focus of activation in SMG and SPL during mental rotation as found in the literature (see Table 1 for detail).

the RTs of the VI task to study a possible left dominance when processing letters in their canonical form (response “oui”).

When appropriate, post hoc comparisons were performed using Tukey’s corrected t -tests ($\alpha = 0.05$).

Results

Behavioral Effects

Behavioral data indicated that subjects actually relied on mental rotation when performing the MI task. Indeed, an ANOVA with HAND POSTURE ($n = 5$), HAND SIDE (left or right), and ORIENTATION ($30^\circ, 90^\circ, 150^\circ, 210^\circ, 270^\circ$, and 330°) as within-subject factors showed a main effect of ORIENTATION on RTs in control (no-TMS) trials ($F_{20,120} = 2.001$; $P < 0.011$). Moreover, we found a double interaction between ORIENTATION and HAND POSTURE indicating that the influence of ORIENTATION was different for each HAND POSTURE ($F_{20,120} = 2.001$; $P < 0.011$). Finally, a 3-way interaction between ORIENTATION, HAND POSTURE, and HAND SIDE revealed that the mental rotation of hand drawings was influenced by biomechanical constraints, which were opposite for the left and right hand ($F_{20,380} = 8.577$, $P < 0.001$; see Fig. 3). For example, because hand flexion can be performed over a larger amplitude than its extension, the mental rotation of a drawing showing the side view of a right hand in the clockwise direction should be more difficult and, therefore, slower than in the anticlockwise direction; the opposite should hold true for left hand. As shown in Figure 3A, this prediction is corroborated by our results. Indeed, for a hand side view, the largest RTs were found for right hands presented at an angle of

150° ($F_{19,95} = 11.247$, $P < 0.001$; when compared with the 5 other angles, all Tukey’s t -tests were significant, $P < 0.002$) and for left hands presented at an angle of 210° ($F_{19,95} = 11.193$, $P < 0.001$; when compared with the 5 other angles, all Tukey’s t -tests were significant, $P < 0.001$) (see Fig. 3A). Opposite patterns of RTs for the left and right hands were systematically observed for the 4 other hand views and, except for the back view, they all followed the predictions based on biomechanics rules (see Fig. 3B–E).

As far as the VI task is concerned, an ANOVA with LETTER IDENTITY (J, N, S, Z, and G), LETTER FORM (canonical or mirror), and ORIENTATION ($30^\circ, 90^\circ, 150^\circ, 210^\circ, 270^\circ$, and 330°) as within-subject factors also revealed a significant effect of the ORIENTATION on RT ($F_{5,20} = 6.322$, $P < 0.001$), indicating faster responses when the letters were presented at an angle of 30° (mean RT + SD, 936 ± 258 ms) or 330° (928 ± 212 ms) than 90° (1039 ± 301 ms) or 270° (1053 ± 300 ms) and at an angle of 90° or 270° than 150° (1130 ± 289 ms, all Tukey’s t -tests $P < 0.008$; see Fig. 4). This effect was not different for the 5 letters indicating that the LETTER IDENTITY did not constraint the mental rotation (ORIENTATION by LETTER IDENTITY interaction, $F < 1$). No other significant interaction was found between the aforementioned variables (all $F < 1$).

Finally, the comparison between control trials performed during the 2 sessions failed to show any RT difference in both VI (1053 ± 325 ms and 1003 ± 232 ms for the SMG and SPL sessions, respectively; $t_{19} = 1.211$, $P > 0.241$) and MI tasks (1041 ± 275 ms and 1045 ± 220 ms for the SMG and SPL sessions, respectively; $t < 1$) indicating a similar task performance in the first and second day of testing. Moreover, within each testing day,

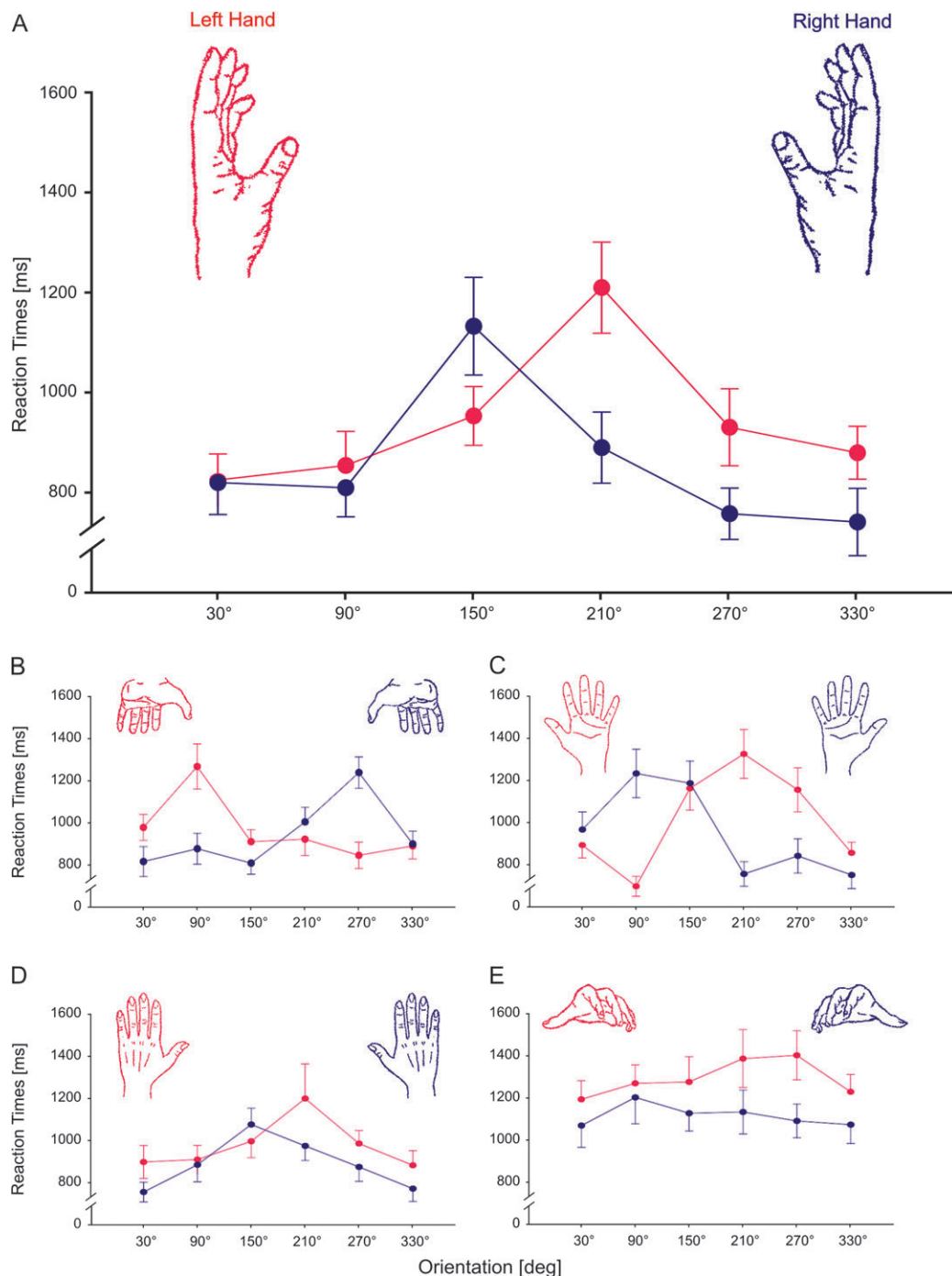


Figure 3. Mean RT and standard error (SE) gathered in the control, no-TMS, and trials of the MI, as a function of the ORIENTATION, for each HAND POSTURE of the left (red) and the right (blue) hand. (A) Side view (see Results for more details). (B) For the thenar/hypothenar eminence view, RTs were longer when right hands were presented at 270° ($F_{19,95} = 12.762$, $P < 0.001$; all Tukey's t -tests, $P < 0.006$) and when left hands were presented at 90° than at other angles ($F_{19,95} = 10.478$, $P < 0.001$; all Tukey's t -tests, $P < 0.05$). (C) For the palm view, RTs were longer when right hands were presented at 150° than 210°, 270°, and 330° ($F_{19,95} = 15.345$, $P < 0.001$; all Tukey's t -tests, $P < 0.04$) and when left hands were presented at 210°, 90°, or 330° ($F_{19,95} = 17.825$, $P < 0.001$; all Tukey's t -tests, $P < 0.05$). D. For the back view, RTs were longer when right hands were presented at orientation of 150° than 270° and 330° ($F_{19,95} = 7.242$, $P < 0.001$; all Tukey's t -tests, $P < 0.04$) and when left hands were presented at 210° than 30°, 90°, or 330° ($F_{19,95} = 2.886$, $P < 0.018$; all Tukey's t -tests, $P < 0.05$). (E) For the front view of the fingertips, no effect of the angular distance ($F < 1$) was observed.

the performance in the VI and MI tasks did not differ either, as shown by an absence of difference between the MI and VI control trials gathered in SMG sessions (MI: 1041 ± 275 ms, VI: 1053 ± 325 ms; $t < 1$) and SPL sessions (MI: 1045 ± 220 ms, VI: 1003 ± 232 ms; $t_{19} = 1.141$, $P > 0.268$) supporting the assumption that both tasks were of equal difficulty. (In order to ascertain the

absence of difference between the 2 tasks in control conditions, we used the Power Calculator software (<http://homepage.u-sask.ca/~jic956/work/MorePower.html>). The results of this power analysis showed that at least 6041 subjects should be added to have a chance to observe a significant difference ($\alpha < 0.05$) between the 2 sessions for the MI task with a power of 0.90

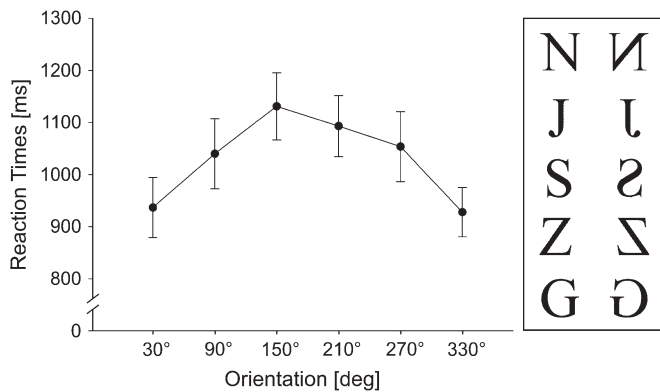


Figure 4. Mean RT and SE of the control, no-TMS, and trials in the VI task as a function of the letter ORIENTATION. Because no interaction was found between ORIENTATION and LETTER IDENTITY/FORM ($F < 1$), results from all letters were merged together.

($F = 0.853$; mean standard error [MSE] = 625) and 146 subjects for the V1 task ($F = 1.466$; MSE = 16 706). When considering the subject performance across the 2 sessions, the same analysis indicated that the 2 tasks would not differ in the SMG ($F = 0.597$; MSE = 24 196) and SPL session ($F = 1.302$; MSE = 13 648), unless a minimum of 3522 and 164 subjects were added, respectively.)

TMS Effects

As shown in Figure 5, we found a double dissociation between MI and VI subsequent to a virtual lesion of these 2 PPC areas. Indeed, the repeated-measures ANOVA with TASK, SITE, and TMS condition as within-subject factors showed a significant TASK $\times$ SITE $\times$ TMS interaction ($F_{2,38} = 13.564$; $P < 0.001$) and the decomposition of this ANOVA by the factor TASK showed a significant SITE $\times$ TMS interaction for both the MI ($F_{2,38} = 8.4251$; $P < 0.001$) and VI tasks ($F_{2,38} = 4.898$; $P < 0.012$). Post hoc analyses indicated that, in the MI task, a virtual lesion of either the left or right SMG led to a significant increase in RT (left SMG: 1148 ± 284 ms, $t_{19} = 6.095$, $P < 0.001$; right SMG: 1135 ± 286 ms, $t_{19} = 5.369$, $P < 0.002$) when compared with the control condition (no-TMS: 1041 ± 275 ms, see Fig. 5A); RT increases consequent to either a left or right SMG virtual lesion were indistinguishable ($t < 1$). TMS applied over SPL did not alter the performance in the MI task (left SPL: 1050 ± 198 ms; right SPL: 1031 ± 210 ms; no-TMS: 1045 ± 220 ms; all $t < 1$). In the VI task, RT increased significantly following a virtual lesion of the left SPL (1099 ± 269 ms) when compared with control trials (1003 ± 232 ms, $t = 5.674$, $P < 0.001$) and also following a right SPL condition (1073 ± 268 ms, $t_{19} = 4.12$, $P < 0.016$, see Fig. 5B); the RT increases following left and right SPL lesions were not statistically different ($t_{19} = 1.554$, $P > 0.1$). SMG virtual lesions had no effect on the RT in the VI task (left SMG: 1044 ± 294 ms; right SMG: 1047 ± 291 ms; no-TMS: 1053 ± 325 ms; all $t < 1$).

The 2 additional ANOVAs performed on the RTs gathered in the MI and VI tasks (SITE $\times$ TMS $\times$ ORIENTATION $\times$ HAND POSTURE/LETTER IDENTITY $\times$ HAND SIDE/LETTER FORM) confirmed the aforementioned results, that is, a specific contribution of SMG and SPL to MI and VI, respectively. Moreover, we found a main effect of the factor HAND SIDE in the MI task ($F_{1,19} = 26.986$, $P < 0.001$), indicating that RTs were shorter when the stimulus was a right hand (1039 ± 230 ms, mean $\pm$ SD) than a left hand (1110 ± 239 ms),

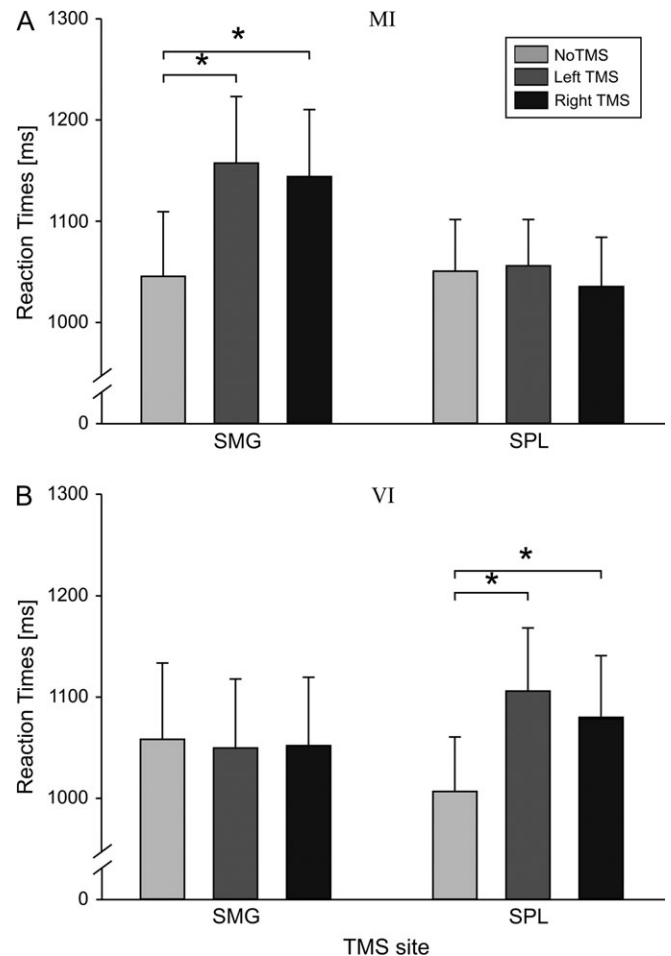


Figure 5. (A) Mean RTs and SE in the MI task, as a function of TMS condition and stimulation site. Asterisks indicate a significant difference between 2 conditions ($P < 0.05$). (B) Mean RTs and SE in the VI task, as a function of TMS condition and stimulation site. Asterisks indicate a significant difference between 2 conditions ($P < 0.05$).

as classically reported in the literature (e.g., Maruff et al. 1999). A main effect of the factor LETTER FORM was also found in the VI task ($F_{1,19} = 38.9232$, $P < 0.001$), indicating that RTs were shorter when the letter was in a canonical form (974 ± 221 ms) than when it was in a mirror form (1125 ± 294 ms). (The frequency of occurrence for the words “droite” and “gauche” in French was, respectively, 136 and 143 for 1 million [New et al., 2004]; <http://www.lexique.org>). This frequency was 375 for “oui” and 979 for “non.” In a control experiment ($n = 8$), we found no difference between the voice onset latency when reading aloud “droite” (415 ± 63 ms) or “gauche” (428 ± 69 ms; $t < 1$) or “oui” (395 ± 48 ms) and “non” (395 ± 46 ms; $t < 1$). Therefore, the main effect of HAND SIDE and LETTER FORM is likely to reflect the use of a particular strategy by participants rather than a difference between the linguistic characteristics of the response words.) However, we failed to find an interaction between HAND SIDE and TMS in the MI task and between LETTER FORM and TMS in the VI task (all $F < 1$). In other words, the interferential effect of the TMS on the left and right hemispheres was not influenced by the nature of the stimulus (left or right hand/canonical or mirror letter).

Finally, our results showed a main effect of the stimulus ORIENTATION in both MI ($F_{5,95} = 21.783$, $P < 0.001$) and VI

($F_{5,95} = 45.27$, $P < 0.001$) tasks indicating that RTs depended on the angular distance of the stimuli. Moreover, in the MI task, the main effect of ORIENTATION was integrated in a 3-way interaction with HAND POSTURE and HAND SIDE ($F_{20,380} = 19.773$, $P < 0.001$). As described in the previous section of the Results (see Fig. 3), this interaction demonstrates a specific influence of biomechanical constraints on the mental rotation of each hand posture.

In both the MI and VI tasks, the interaction between TMS condition and SITE was not influenced by the ORIENTATION (all $F < 1$) indicating that the disruptive effects of TMS were constant across all angles of rotation.

Discussion

The present study demonstrates a double dissociation in the PPC between processes underlying motor and visual mental imagery. Indeed, we found a specific impairment in the MI task following a virtual lesion of SMG, whereas only virtual lesions of SPL affected the VI task performance; this finding suggests that these 2 types of mental imagery rely on different PPC subregions. In addition, we found that the consequences of TMS applied over SMG or SPL were identical whatever the lesioned hemisphere, indicating an equivalent contribution of both hemispheres to mental imagery.

The present results indicate that SMG underlies mental representations of movements, whereas SPL is critically involved in the implementation of visuospatial representations. Importantly, the 2 tasks we used only differed by the nature of the stimuli to be rotated (either a hand drawing or a letter), and therefore, if virtual lesions of PPC were interfering with working memory processes, we should have found a comparable decrease in performance in both tasks. The finding of a double dissociation between the MI and VI tasks following a virtual lesion of 2 distinct parietal regions allows us to invalidate this prediction. Another possible flaw in our interpretation would be if SPL is actually involved in processing 2D stimuli—explaining why the VI task using letters was selectively impaired after an SPL lesion—whereas SMG preferentially underlies 3D stimuli processing, such as the hand pictures used in MI. Although the present study was not originally designed to address this issue, several arguments allow us to rule out that the distinct effects of SPL and SMG lesions on MI and VI were not determined by the 2D or 3D nature of the stimuli. Firstly, the MI task cannot be simply regarded as a rotation of 3D objects, as shown by the mirror pattern of RTs for the left and right hands and the influence of biomechanical constraints on the mental rotation performance. Indeed, this effect clearly indicates that the hand mental rotation was constrained by the body schema used in movement production. Consistently, previous studies have shown an increase in RT for mental rotation of stimuli corresponding to awkward body part positions (Parsons 1994; Petit et al. 2003; Fiorio et al. 2006). Second, it is sensible to assume a functional distinction between MI and mental imagery on 3D stimuli because it has been shown that some patients may have a profound impairment in MI but a preserved ability to perform mental rotation of 3D stimuli (Tomasino, Rumiati, and Umiltà 2003; Conson et al. 2008). Finally, the view that 2D and 3D stimuli may be underlain by distinct processes is challenged by the finding that processing 2D and 3D stimuli induces a similar pattern of activation in the PPC but spares SMG (Jordan et al. 2001). However, it is noteworthy that the

dissociation between 2D and 3D stimuli has received little attention in the literature and should be further investigated to definitely discard this alternative explanation for the present results.

Our finding of a distinct contribution of SMG to MI and of SPL to VI is consistent with the current view about the distribution of visuomotor and visuospatial processes in PPC (Simon et al. 2004). Indeed, SMG is known to intervene in hand and finger movement representations and in the control of complex actions (Krams et al. 1998; Grezes et al. 2003; Heuninckx et al. 2005; Hesse et al. 2006; Naito and Ehrsson 2006), whereas the contribution of SPL to the spatial processing of object location has been thoroughly demonstrated (Posner et al. 1984; van Eimeren et al. 2006; Sack et al. 2007; Kelley et al. 2008).

The neural dissociation between MI and VI evidenced in the present study is also consistent with earlier behavioral studies showing that different factors, such as biomechanical constraints or relative stimulus size, distinctively affected these 2 types of mental imagery (Kosslyn et al. 1978; Mellet et al. 1998; Sirigu and Duhamel 2001; Shenton et al. 2004; de Lange et al. 2005; Stevens 2005). Moreover, this dissociation within the PPC is also in agreement with the results of brain lesion studies showing a selective deficit in VI or in MI in some patients. For instance, in a recent study, Tomasino, Rumiati, and Umiltà (2003) presented the case of a patient with a left parietofrontal lesion, involving SMG but not SPL, who was selectively impaired in mental rotation of hand stimuli. In contrast, interfering with the normal functioning of SPL by means of electrical stimulation during a surgery has been shown to affect VI and not MI (Zacks et al. 2003).

However, the double dissociation we found between MI and VI is more difficult to reconcile with functional neuroimaging studies (see Table 1). Indeed, several studies have reported overlapping activation in both MI and VI. It is noteworthy, nonetheless, that only very few studies have directly contrasted activation gathered during VI and MI (Kosslyn et al. 1998; Vingerhoets et al. 2002; Zacks et al. 2002; de Lange et al. 2005), and therefore, the discrepancy between the results of neuroimaging studies may be explained by the lack of standardization in the VI and MI paradigms, and/or by the different methods used to analyze brain activation (Ehrsson et al. 2003; Goldenberg 2003). Finally, it is worth mentioning that whereas functional neuroimaging studies provide a picture of the whole network potentially involved in a given task, TMS allows us to identify the brain regions whose integrity is necessary to perform the task. Therefore, it is sensible to assume that, for example, SPL could be activated during mental rotation of hand drawings because it contributes to VI processes accompanying hand movement simulation. However, the absence of deficit in MI after a virtual lesion of this region suggests that the SPL contribution is not critical or is easily compensated by another brain region.

Of course, the finding of a double dissociation between MI and VI in the PPC does not exclude that other parietal regions are involved in common processes shared by the 2 types of mental imagery. Indeed, in a recent functional MRI study, de Lange et al. (2005) found an increased activation in the ventral area of the IPS (VIP) during both VI and MI and this activation was positively correlated with the degree of stimulus rotation. Because VIP neurons are able to process both visual and somatosensory information for motion analysis (Avillac et al.

2005), it is sensible to assume that the orientation-dependent activation of this region reflects an update of spatial coordinates during mental rotation of letters and hand drawings. In the present study, we failed to find such a correlation between the TMS-induced deficits in either MI or VI and stimulus rotation. Therefore, we propose that SPL and SMG are not directly involved in mental rotation per se. Indeed, these PPC regions could store and/or reactivate the motor and visual representations, whereas the mental rotation process could take place in another brain area, such as VIP. The dorsal part of the IPS could also be involved in mental rotation during MI because this region was found activated proportionally to the angular distance of hand drawings (de Lange et al. 2005).

The second issue addressed in the present study was the respective contribution of the right and left hemispheres to VI and MI, and more specifically, we aimed at testing the hypothesis that the integrity of 1 hemisphere is crucial only when performing MI with a stimulus representing the contralateral hand (Parsons et al. 1998). In the present study, we found that TMS had the same interhemispheric effects regardless of the lesioned hemisphere and, importantly, irrespective of the displayed hand (right or left). Therefore, it is very unlikely that each hemisphere is endowed with a representation of the 2 hands because such an organization predicts an absence of deficit after a unilateral virtual lesion of PPC, a prediction unsupported by our results. A more likely explanation is therefore that the participants used a strategy that consists of activating the representation of both hands to facilitate response selection, consistently with the view that, when faced with a forced choice, the 2 alternatives are evaluated and simulated before responding (Johnson 2000a, 2000b). If we assume that actions are represented in the contralateral hemisphere, TMS applied over either hemisphere should have disrupted the strategy used by the subjects whatever the displayed hand and a laterality judgment task, similar to that used in the present study, may not be appropriate to identify the respective contribution of each hemisphere to motor representations of each hemibody. To avoid such a drawback, possibly due to the use of different strategies (Tessari and Rumiati 2004; Tessari et al. 2007), future research should use MI tasks that allow to test each hand separately (Johnson 2000b; Sabate et al. 2004).

As far as VI is concerned, converging evidence supporting a right hemisphere dominance in this process comes from studies of stroke patients (Farah and Hammond 1988; Tomasino, Toraldo, and Rumiati 2003). Still, in the present experiment, we failed to confirm a right hemispheric dominance for VI because the deficits in this task were found identical whatever the side of SPL lesions; this indicates that the left hemisphere is also involved in visuospatial processing. It could be argued that the effect found after a left SPL lesion is due to the linguistic nature of the image to rotate. However, this hypothesis seems unlikely because bilateral involvement of the PPC in VI has also been reported in previous neuroimaging (Cohen et al. 1996; Jordan et al. 2001) and TMS studies (Feredoes and Sachdev 2006) using abstract form stimuli. Importantly, the finding that the VI deficits did not depend on the lesion side indicates that left and right hemispheres have a complementary role in VI. Supplementary investigations are necessary to determine precisely the specific contribution of these 2 regions.

In conclusion, the present study provides, for the first time, direct evidence that MI and VI involve different parietal

subregions. Whereas VI implicates visuospatial processes engaging SPL, SMG is thought to contain the motor representations critical for MI. Moreover, the present results allow us to hypothesize that these 2 parietal subregions act as “intermediary zones” in conceptual processing (Tranel et al. 1997, 2003; Damasio et al. 2001; Kan et al. 2003). These zones are thought to support the selection of the visual features and the action-related properties necessary for the simulation of specific visual and motor experiences. Although further investigations are needed to decipher the role of sensorimotor simulation in conceptual processing, the present results support the view that such simulation is grounded in modality specific systems.

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Notes

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