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Complete List of Authors:	Andres, Michael; Université catholique de Louvain, Psychological Sciences Research Institute; Université catholique de Louvain, Institute of Neuroscience Pelgrims, Barbara; Université catholique de Louvain, Institute of Neuroscience Olivier, Etienne; Université catholique de Louvain, Institute of Neuroscience Vannuscorps, Gilles; Université catholique de Louvain, Psychological Sciences Research Institute; Unvirsité catholique de Louvain, Institute of Neuroscience; Harvard University, Department of Psychology
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Role of the left supramarginal gyrus in computing the appropriate position of fingers for functional object use: A neuronavigated TMS study

Michael Andres[1,2], Barbara Pelgrims[1], Etienne Olivier[1], Gilles Vannuscorps[1,2,3]

[1] Institute of Neuroscience, Université catholique de Louvain, Belgium

[2] Psychological Sciences Research Institute, Université catholique de Louvain, Belgium

[3] Department of Psychology, Harvard University, USA

Corresponding author :

Michael Andres, PhD
Institute of Neuroscience
Université catholique de Louvain
Avenue Mounier, 53
COSY- B1.53.04
1200 Brussels
Belgium

michael.andres@uclouvain.be

Abstract

In everyday actions, the hand posture adopted to grasp manipulable objects, such as a pen or a screwdriver, must accommodate their functional use. Neuroimaging studies showed that forming a hand posture appropriate for object use involves a left-lateralized network including the supramarginal gyrus (SMG), the anterior intraparietal area (AIP) and the ventral premotor cortex (PMv). However, because previous works premised their conclusions on tasks requiring action execution, it has remained difficult to discriminate between the areas specifying the hand posture and those implementing the motor program required to perform the action. To address this issue, we asked healthy participants to make judgements about pictures of manipulable objects while repetitive transcranial magnetic stimulation (rTMS) was applied over the left SMG, AIP, PMv or, as a control, the Vertex. The participants were asked to name the part of the image (lower vs. upper part) where a given finger (*e.g.*, thumb) was expected to contact the object during its normal utilization or where a given attribute of the same object (*e.g.*, wooden handle) was located. The two tasks were strictly identical in terms of visual display, working memory demands, and response requirements. Results showed that rTMS over SMG slowed down judgements about finger positioning but not judgements about object attributes. Both types of judgements remained unaffected when rTMS was applied over AIP or PMv. This finding demonstrates that, within the parieto-frontal network dedicated to object use, left SMG is involved in defining the appropriate position of fingers onto the object.

Keywords : dorsal stream, parietal, transcranial magnetic stimulation, tool use

1. Introduction

Our ability to use objects in a fast and efficient way presupposes the existence of mechanisms that determine the adequate hand configuration for using them effectively. It is widely agreed that the control of hand-object interactions relies on a left-lateralized network including the supramarginal gyrus (SMG), the anterior intraparietal area (AIP) and the ventral premotor cortex (PMv) (Brandi, Wohlschlager, Sorg, & Hermsdorfer, 2014; Johnson-Frey, Newman-Norlund, & Grafton, 2005; Kroliczak & Frey, 2009). If the view that these brain areas cooperate to allow object use is undisputed, their exact contribution is still unclear. This study aims to test the causal implication of these areas in the process of selecting the appropriate hand configuration for object use.

Up to now, the identification of the brain areas involved in selecting the appropriate hand configuration for object use has remained problematic because previous research on this issue has mostly relied on tasks requiring an action execution, making it difficult to discriminate between the areas specifying hand configuration and those implementing the motor program to perform the appropriate action (Brandi, Wohlschlager, Sorg, & Hermsdorfer, 2014; Johnson-Frey, Newman-Norlund, & Grafton, 2005; Kroliczak & Frey, 2009). In order to address this issue, some studies have investigated the role of the dorsal visual stream in hand-object interactions by asking participants to infer the hand configuration required to use objects presented on images. An fMRI study showed that hand configuration judgements increased activation in left SMG as well as in several areas along the intraparietal and precentral sulci, slightly superior and posterior to AIP and PMv (Canessa et al., 2007). This study suggests that a large parieto-frontal network is involved in selecting the appropriate hand configuration for object use, but brain imaging results are not immune to the possibility that the task automatically activates areas serving other purposes, such as action preparation, even in the absence of hand movement. Other brain imaging studies have tried to separate the processes involved in defining hand configuration from those involved in motor execution by using mental imagery or action judgement tasks, but the results do not suffice to establish the causal implication of the activated regions because fMRI data are of correlative nature (Binkofski et al., 1999; Decety et al., 1994; Grafton et al., 1996; Grezes & Decety, 2001;

Imazu et al., 2007; Moll et al., 2000; Vingerhoets et al., 2010; Vingherhoets et al., 2013). In theory, lesional studies should provide more convincing evidence by showing that the integrity of a given region is necessary to select the appropriate hand shape for object use. A brain lesion mapping study showed that AIP lesions are responsible for the inability of patients to adjust grip aperture to the size of objects (Binkofski et al., 1998). Other data indicate that left inferior parietal lesions, encompassing left SMG, are associated with difficulties in making judgments that require to access knowledge of the hand posture required to use objects (Buxbaum, Veramonti, & Schwartz, 2000; Buxbaum & Saffran, 2002; Buxbaum, Kyle & Menon, 2005; Kalenine, Buxbaum, & Coslett, 2010). This observation was replicated by using repetitive transcranial magnetic stimulation (rTMS) in healthy participants: left SMG disruption affected judgements about the hand configuration associated to object use but not judgements about the functional interaction between two objects (Pelgrims, Olivier, & Andres, 2011) or their context of use (Andres, Pelgrims, & Olivier, 2013). However, another lesional mapping study revealed an association between inferior frontal lesions, encompassing PMv, and deficits in judging the correctness of an observed hand or finger configuration related to object use (Pazzaglia, Smania, Corato, & Aglioti, 2008). More importantly, the hand configuration judgements used in previous studies do not allow us to decide whether the involvement of SMG is driven by motor or non-motor attributes of the objects (Andres et al., 2013; Pelgrims et al., 2011). Judging whether two objects are used with the same hand configuration requires a refined analysis of their visual characteristics. This raises the possibility that the contribution of SMG was not to select the appropriate hand configuration but to single out object parts in order to facilitate motor judgements. Current results from brain imaging and lesional studies thus remain controversial and subject to alternative interpretations.

In the present study, we focussed on a specific aspect of hand-object interactions, which is the spatial relationship between the fingers and the object, with the aim to refine the role of the aforementioned brain regions in defining hand configuration. In order to test the causal role of left SMG, AIP and PMv in coding the relative position of fingers while using an object, we applied rTMS over each region while healthy participants made spatial judgements about object attributes ("Object task") or about the position of the fingers onto the objects under normal conditions of use ("Finger Task"). We presented the same objects in the two

tasks that were closely matched in terms of visual display, response requirements and task difficulty. Thus, if a given region was involved in finger positioning, rTMS over this region should delay spatial judgements in the "Finger task" but not in the "Object task".

2. Methods

2.1. Participants

Sixteen right-handed males (mean age ± standard deviation: 25.4 ± 3.6 years) participated in this study. They were free of any history of neurological deficits and showed no contra-indications for TMS (Rossi, Hallett, Rossini, Pascual-Leone, & Group, 2009). The biomedical ethics committee of the Université catholique de Louvain approved all experimental procedures.

2.2. Stimuli and Tasks

Stimuli consisted in colour pictures of 28 familiar manipulable man-made objects (maximum 5 degrees of visual angle). The object picture was centred on a light grey background on which was superimposed a translucent bicolour image where the upper and the lower half were respectively red and blue or the reverse. In the "Finger task", the images were preceded by instructions referring to a finger (*i.e.*, "thumb", "index") and participants were asked to name the colour of the image part ("red" or "blue") where the fingertip is expected to contact the object under normal conditions of use. In the "Object task", the images were preceded by instructions referring to a physical characteristic (*i.e.*, metallic, rounded, pierced, hollow, flat, wooden, base) and participants were asked to name the colour of the part of the image ("red" or "blue") where this feature of the object was present. In the Finger task, orientation of the objects was always congruent with the way they are typically used by right-handed people (*i.e.*, the graspable part oriented rightward). The same orientation was adopted in the Object task, except for four objects whose target attribute was the part on which they rest (*i.e.*, the base); these objects were displayed upside-down in half of the trials to make sure participants inspected object parts before they answered the spatial judgement; the other objects were displayed in an upright orientation in all trials. The same set of 28 object pictures

was presented in the two tasks. They were selected from a larger set of 89 object pictures on the basis of two pilot studies. We first videotaped four right-handed males (mean age ± standard deviation: 28.5 ± 2.2 years) while they used the objects in order to exclude those for which finger positioning differed among users. We then asked a second sample of ten right-handed males (mean age ± standard deviation: 26.4 ± 3.2 years) to perform the Finger and the Object task (without TMS) and, based on the average data over these participants, we selected a subset of objects that were judged as fast and accurately in the two tasks (mean response latency, RL: $t<1$; mean error rate: $t<1$). The successful matching of the two tasks was further demonstrated by the absence of differences in RT and error rate in the control condition of the TMS experiment (see Results). None of the subjects who participated in the pilot studies was included in the subsequent TMS experiment.

2.3. Procedure

The experiment was performed in a dimly illuminated room. Participants sat comfortably in an armchair, 60 cm in front of a computer screen, and were instructed to keep their hands at rest on their lap in a half-pronated position throughout the experiment. Before the TMS experiment, participants were asked to name all the objects displayed sequentially on a computer screen to make sure all objects were correctly recognized. Then, they practiced the two judgment tasks with ten object pictures that were not used in the TMS experiment.

During the TMS experiment, each of the two tasks was repeated four times in row while rTMS was applied over a different site, resulting in a total of eight blocks. Half of the participants started with the Finger task and the other half with the Object task. The order in which the different sites were stimulated was the same for each task but it was counterbalanced across participants. The same set of 28 object pictures was presented in each block with half of the trials calling for a "red" response and the other half for a "blue" response; the pictures were presented in a random order with the only constraint that the same response (“red” or “blue”) never occurred more than three times in a row. In two successive blocks, the association between a picture and a response ("blue" or "red") was changed in half of the trials by varying colour assignment on the screen.

The finger name or object attribute to be identified was cued by written instructions displayed on the screen in-between sub-blocks of 3 to 5 trials; participants were required to read out the instruction (*e.g.*, "Where do you place the thumb?", "Where is the wooden part?") and keep it in memory throughout the sub-block. Each trial started with the display of a fixation cross on the screen centre for 200 msec, followed by a 500 msec blank interval, and the object pictures that remained visible until the participant's response (Figure 1). The next trial started after 5000 msec. A voice key connected to E-Prime V1.0 (Schneider, Eschman, & Zuccolotto, 2002) was used to measure the latency of verbal responses ("red" or "blue") and accuracy was monitored on-line by the experimenter. Verbal responses were preferred to manual responses to avoid interference between manual response movements and finger position judgements.

2.4. TMS protocol

We delivered repetitive TMS (10 Hz, 5 pulses, 400 msec) by means of a 35 mm inner diameter polyurethane-coated figure-of-eight coil connected to the Rapid Magstim stimulator (Magstim Company, Whitland, UK). The small size of the coil allowed more focal stimulation than larger standard coils and its polyurethane coating allowed a closer contact with the subject's scalp. The coil was held tangentially to the skull with the handle pointing laterally and backwards and was located either over the left SMG, PMv, AIP or over the vertex, used as a control site. The TMS intensity was set arbitrarily to 65 % of the stimulator output because the excitability of the stimulated areas was not directly measurable and the excitability of the primary motor cortex, sometimes used as a guide, is not always correlated with the excitability of other cortical areas (Stewart, Walsh, & Rothwell, 2001). The first pulse occurred 100 msec after the display of the object image. During the whole experiment, participants wore earplugs to attenuate the sound of TMS and a closely fitting EEG cap to mark the stimulation sites after co-registration with individual anatomical magnetic resonance (MR) images using a home-made neuronavigation system (Noirhomme et al., 2004). The co-registration proceeded in three steps: (1) the coordinates of about 200 points distributed randomly on the participant's scalp, in the physical space, were obtained using a digitized pen receiver connected to a forehead reference allowing for head movements (Polhemus Isotrak II system, Kaiser

Aerospace Inc.); (2) the registration process created a transformation matrix that minimized the mean square distance between these points and a segmented scalp surface extracted from the MRI; (3) the figure-of-eight coil was digitized by pointing the pen to three points at the intersection of the coil windings, where the magnetic field is maximal, and these points were converted within the transformation matrix; the position of the coil relative to the scalp was then indicated through the visualization interface. A normal to the plane of the coil was drawn from its center to the brain, revealing the impact point of TMS both on a segmented brain surface and on the MR images, with a spatial accuracy close to the millimeter. The TMS sites were localized by a trained experimenter based on anatomical landmarks. To target SMG, the coil was placed below the intraparietal sulcus, in front of the Jensen sulcus, over the rostral part of SMG. AIP was targeted by positioning the coil at the intersection between the intraparietal sulcus and the postcentral sulcus and PMv was located over the caudal portion of the pars opercularis of the inferior frontal gyrus (Figure 2). Comparative studies showed that using the structural (anatomical) brain image of each participant, with frameless stereotaxic neuronavigation, to identify the TMS sites was as reliable as basing their identification on functional MR images obtained for each participant during a relevant task (Sack et al., 2009; Sparing et al., 2008). In the present study, the location of the TMS sites was further validated by a post-hoc probabilistic approach. After the experiment, individual coordinates of the TMS sites were normalized with respect to the Montreal Neurological Institute (MNI) brain atlas. This normalization was performed by normalizing each individual MRI onto the MNI brain template by means of an iterative algorithm that looks for the optimal projection of a given brain onto the MNI brain (Noirhomme et al., 2004). This algorithm solved the best transformation parameters optimizing the mutual information metric between the individual and MNI brains by using sequentially two types of transformations: (1) rigid and scale transformations and (2) nonrigid basis-spline transformations. The mean coordinates of SMG (xyz ± *SD*: -60±4, -41±12, 42±6 mm), AIP (-44±9, -42±7, 49±3 mm) and PMv (-60±3, 14±3, 24±8 mm) fitted with the xyz coordinates gathered in previous fMRI studies demonstrating the involvement of these regions in object use (Brandi et al., 2014; Johnson-Frey et al., 2005; Kroliczak & Frey, 2009).

2.5. Data Analysis

Trials in which the participant's response failed to trigger the voice key (0.9 %) and trials with an RL falling outside a 500-2500 msec range (1.4 %) were discarded from subsequent analyses. The mean error rate (%) and the mean RL (msec) of correct trials were computed for each participant and condition. These values were entered in two ANOVAs with TASK (Finger and Object) and SITE (SMG, AIP, PMv and Vertex) as within-subject factors. Post-hoc analyses were corrected for multiple comparisons by using Tukey t-tests.

3. Results

The ANOVA on error rates revealed no effect of TASK, $F(3,45)=0.43$, $p=.52$, $\eta_p=.03$, or SITE, $F(2,30)=0.69$, $p=.56$, $\eta_p=.04$, and no interaction between these factors, $F(3,45)=0.99$, $p=.41$, $\eta_p=.06$. The error rate was similar in the Finger task (M = 6.4, SD = 0.7) and in the Object task (M = 5.9, SD = 0.5).

The ANOVA on RLs showed no main effect of TASK, $F(3,45)=2.60$, $p=.13$, $\eta_p=.15$, but a significant main effect of SITE, $F(3,45)=3.06$, $p=.038$, $\eta_p=.17$, and a two-way interaction between TASK and SITE, $F(3,45)=6.19$, $p=.001$, $\eta_p=.29$. As illustrated in Figure 3, the effect of rTMS in the Finger task, $F(3,45)=6.41$, $p=.001$, $\eta_p=.30$, showed that disruption of left SMG functioning (M = 1070, SD = 177) led to a significant RL increase compared to the vertex (M = 962, SD = 166), $t(15)=4.59$, $p=.012$), to left PMv (M = 934, SD = 124), $t(15)=5.78$, $p=.001$, or to left AIP (M = 967, SD = 121), $t(15)=4.34$, $p=.018$. In the Object task, there was no RL difference between left SMG (M = 956, SD = 97), the vertex (M = 967, SD = 149), left PMv (M = 934, SD = 136), and left AIP (M = 960, SD = 83; all ts<1). Further comparisons indicated an absence of RL difference between the two tasks when TMS was applied over the vertex, AIP or PMv (all ts<1), whereas RLs were larger in the Finger task compared to the Object task when rTMS was applied over SMG, $t(15)=3.01$, $p=.05$.

4. Discussion

Our results provide direct evidence that left SMG plays a causal role in selecting the hand configuration appropriate for object use by coding the relative position of the fingers onto the object. Repetitive TMS applied over left SMG delayed spatial judgements about finger

positions by 100 msec when compared to the control site, whereas response latencies remained remarkably stable when rTMS was applied over left AIP, PMv or the vertex. Moreover, rTMS had no effect on spatial judgements about object parts, confirming that the role of left SMG is determined by motor rather than non-motor attributes of objects. Alternative interpretations in terms of visual processing, response selection or task difficulty do not stand because spatial judgements about finger position and object parts were entirely matched on all these aspects.

Previous fMRI studies revealed increased activity in left SMG while making a judgement about how to position one's fingers on a given object (Boronat et al., 2005; Canessa et al., 2007). Lesional mapping studies corroborated this view by showing that patients with parietal lesions, encompassing left SMG, have difficulties in shaping the hand adequately for using objects (Martin et al., 2015) as well as to match objects according to the hand posture required to use them (Buxbaum et al., 2000; Kalenine et al., 2010). However, these results are subject to limitations inherent to the size and extent of natural brain lesions. Moreover, action execution and object matching tasks left open the possibility that left SMG contributes to perceptual or motor processes unrelated to hand shape selection. Finally, the contribution of left SMG had never been directly compared to the contribution of functionally connected areas, AIP and PMv, which are also known to be involved in object use. To overcome these limitations, we used rTMS to disrupt the normal functioning of these areas in healthy participants making judgements about motor *versus* non-motor attributes of manipulable objects. We focussed on a specific aspect of hand-object interactions, which is the spatial relationship between the fingers and the object, with the aim to refine the role of the aforementioned brain regions in defining the hand configuration appropriate to object use. The results go beyond the scope of previous evidence because they demonstrate the causal role of left SMG in coding the spatial relationship between the fingers and the object to be used and they further indicate that this role is not mediated by the processing of non-motor attributes of objects or by functional interactions with left AIP or PMv.

It might be argued that rTMS over left SMG did not affect the coding of finger position *per se* but a mental imagery process by which participants imagined the action after they had selected the hand configuration required for object use. Several fMRI and TMS studies

evidenced a role of left SMG in left-right judgements on rotated hand drawings (Kosslyn, Digirolamo, Thompson, & Alpert, 1998; Parsons, Gabrieli, Phelps, & Gazzaniga, 1998; Pelgrims, Andres, & Olivier, 2009), a task that has long been considered as relying on motor imagery. However, a close look at the literature indicates that the hand laterality judgement task is not a reliable tool to assess the contribution of a given area to motor imagery. We found for instance that individuals with a congenital absence of upper limbs perform similarly to normally limbed individuals in hand laterality judgements, meaning that performance in this task is not strictly dependent on motor imagery and may thus reflect other strategies (Vannuscorps & Caramazza, 2015; Vannuscorps, Pillon, & Andres, 2012). Moreover, other sources of data indicate that AIP and PMv do play a role in the mental imagery of grasp movements (Aflalo et al., 2015; Rizzolatti, Fogassi, & Gallese, 2002). If judging the position of one's fingers on an object had required motor imagery, then rTMS over AIP or PMv should have disrupted performance as well. Thus, motor imagery does not represent a valid account of our results (see also Vannuscorps & Caramazza, 2016).

None of the dorsal stream areas included in the present study was essential for perceiving the spatial configuration of object parts, corroborating the view that these areas are not concerned by non-motor attributes of objects. Similar results were obtained in a brain imaging study in which classifiers were trained on one pair of objects and then tested on a distinct pair to decode brain activity related to motor attributes of objects over and above their non-motor attributes (Chen, Garcea, & Mahon, 2015). Left SMG, in particular, was sensitive to the manipulatory pattern of objects irrespective to their physical appearance. Aside from its role in hand configuration, little is known about the potential contribution of left SMG to the processing of other motor attributes, such as movement amplitude (*e.g.*, using an axe to cut down a tree requires a larger movement amplitude than using a hammer to drive in a nail) or movement direction (*e.g.*, using a hammer requires back and forth movements). One lesional mapping study incriminated left SMG lesions in the difficulties of patients in detecting errors of body posture, movement amplitude or timing in an action recognition task (Kalenine et al., 2010). In contrast, past studies showed that left SMG is not essential to access knowledge about the function of a given object (Buxbaum et al., 2000), its functional complementarity with other objects (Pelgrims et al., 2011) or its context of use (Andres et al., 2013). The

contribution of left SMG is thus confined to motor attributes such as hand configuration and possibly other aspects of hand/arm movements.

The absence of impairment after rTMS over left AIP or PMv is at odds with previous findings in action execution and observation tasks. Indeed, several fMRI and TMS studies evidenced the role of left AIP and PMv in transforming the geometrical properties of an object into an appropriate grip (Cavina-Pratesi et al., 2010; Davare, 2006; Davare, Andres, Clerget, Thonnard, & Olivier, 2007; Davare, Rothwell, & Lemon, 2010; Ehrsson & Fagergren, 2001; Tunik, Frey, & Grafton, 2005). Some authors proposed to differentiate the role of SMG and AIP-PMv by making a distinction between object use and object grasping (Binkofski & Buxbaum, 2013). From this viewpoint, the contribution of AIP-PMv would be restricted to elementary sensorimotor mechanisms that shape the hand to the object size, allowing object grasping but not functional use (Randerath, Goldenberg, Spijkers, Li, & Hermsdörfer, 2010). In everyday life, however, object grasping is rarely dissociated from its functional use, except in situations where grasping is performed only to transport the object. Moreover, several results indicate that AIP and PMv contribute to more elaborate aspects of object use than just grasping. Increased activity has been observed in left AIP while participants named tools, although tool-selective activity was found in a separable locus than grasp-related activity (Valyear, Cavinapratesi, Stiglick, & Culham, 2007). AIP and PMv are also active whether grasping is executed with the hand or with a tool, suggesting that the role of these areas is not bound to body-specific representations (Gallivan, McLean, Valyear, & Culham, 2013; Jacobs, Danielmeier, & Frey, 2010). In the light of the present results, we suggest that AIP and PMv are not essential to define the appropriate hand configuration for object use but well to implement this configuration into an action plan that can be translated in muscle recruitment with the contribution of the primary motor cortex. This interpretation requires additional evidence but it is compatible with the role of AIP-PMv in the cortical motor hierarchy (Gallivan et al., 2013) and with their functional connectivity pattern (Davare, Montague, Olivier, Rothwell, & Lemon, 2009; Koch et al., 2007; Olivier, Davare, Andres, & Fadiga, 2007). A remaining issue concerns the finding that apraxic patients with left inferior frontal lesions, encompassing PMv, experience difficulties in judging the correctness of an observed hand/finger configuration related to object use (Pazzaglia et al., 2008). Although this finding is

reminiscent of impaired coding of finger position, we suggest it may actually reflect the contribution of the inferior frontal cortex to more general cognitive control processes. Indeed, in that study, the task put high demands on semantic control and feature selection, two processes that depend on the integrity of the inferior frontal cortex (Goldenberg, Hermsdorfer, Glindemann, Rorden, & Karnath, 2007; Whitney, Kirk, O'sullivan, Lambon Ralph, & Jefferies, 2011). Hence, the semantic distractors included in the task (*i.e.*, the correct gesture associated with an incorrect object) required inhibiting concurrent associations between objects and actions in semantic memory, while the spatial distractors (*i.e.*, incorrect hand/finger configurations) differed from the correct configuration in a very subtle way. It is unclear how each type of distractors influenced task difficulty because performance was quantified as a composite score but the authors did not control for the influence of cognitive control deficits in apraxic patients, limiting the interpretation of the results in terms of impaired coding of finger position. Based on currently available data, we therefore argue that defining the appropriate hand configuration for object use is a specific competence of left SMG.

5. Conclusion

The combined use of transcranial magnetic stimulation and spatial judgements that require to infer finger position from object pictures, without making any hand movement, allowed us to demonstrate the causal role of left SMG in coding the spatial relationship between the fingers and the object to be used. Moreover, left SMG interference delayed spatial judgements about finger position but not about object parts, in line with the view that dorsal stream areas only deal with aspects related to object use, a competence that has evolved with the expansion of the inferior parietal cortex in Homosapiens (Peeters et al., 2009).

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Figure legends

Figure 1. A. In the Finger task, participants were asked to name the colour of the part of the image where a given finger (*e.g.*, thumb) was expected to contact the object during normal conditions of use. **B.** In the Object task, participants were asked to name the colour of the part of the image where a given feature of the object (*e.g.*, wooden handle) was located. The finger or the object feature was cued by a question displayed in advance to a series of 3 to 5 object images. Repetitive TMS (65%, 5 pulses, 400 msec) was applied in every trial, the first pulse occurring 100 msec after the onset of the object image.

Figure 2. Illustration of the TMS sites in left SMG, left AIP and left PMv on sagittal, coronal, axial and 3D views of the brain. The MNI coordinates (x, y, z) were obtained using an on-line neuronavigated technique (Noirhomme et al., 2004).

Figure 3. TMS over left SMG selectively interfered with judgements on finger position. The graph represents the mean response latencies and standard errors in the Finger task and in the Object task as a function of the TMS site. The asterisk indicates a significant difference between the two tasks.

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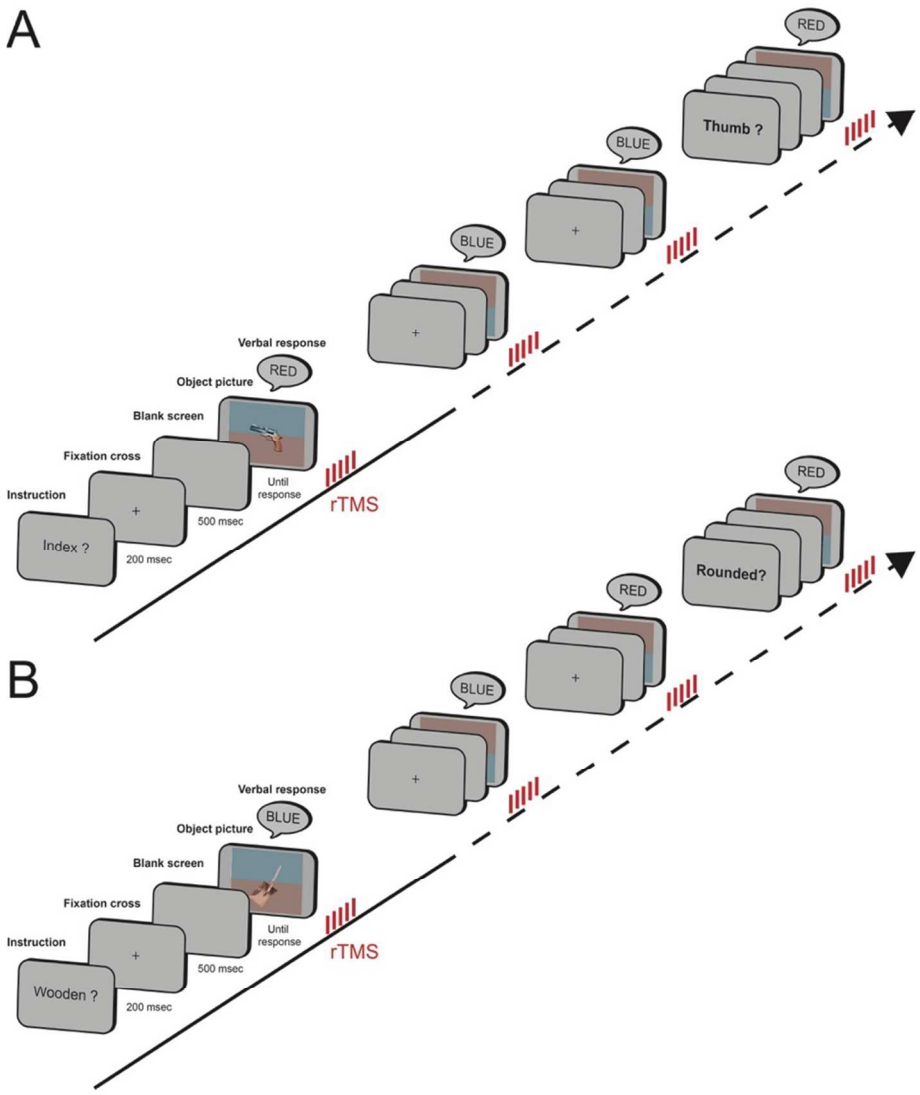

Figure 1. A. In the Finger task, participants were asked to name the colour of the part of the image where a given finger (e.g., thumb) was expected to contact the object during normal conditions of use. B. In the Object task, participants were asked to name the colour of the part of the image where a given feature of the object (e.g., wooden handle) was located. The finger or the object feature was cued by a question displayed in advance to a series of 3 to 5 object images. Repetitive TMS (65%, 5 pulses, 400 msec) was applied in every trial, the first pulse occurring 100 msec after the onset of the object image.

Figure 1
338x447mm (72 x 72 DPI)

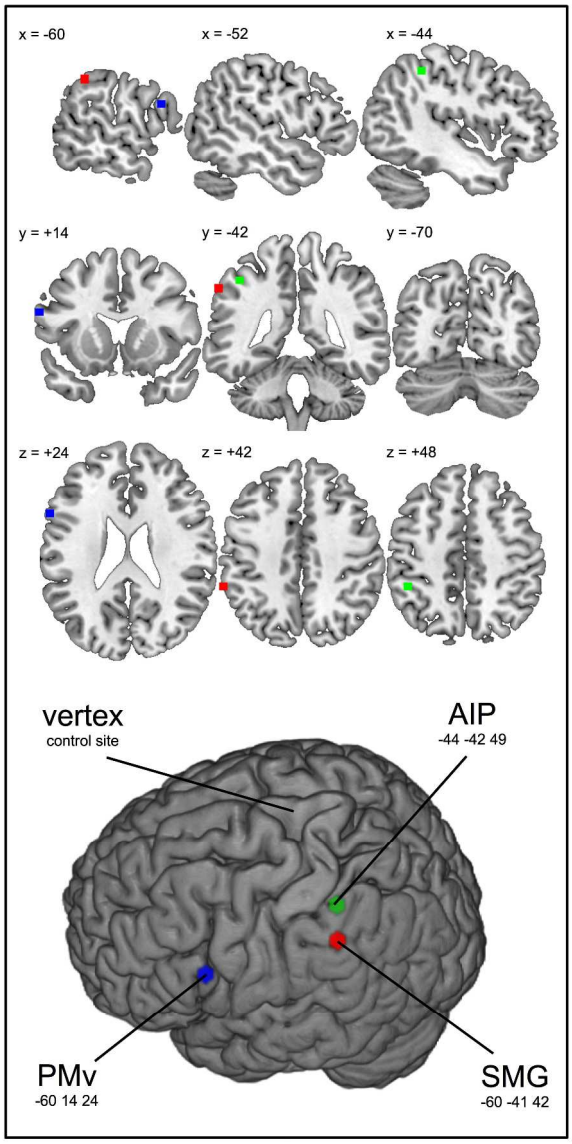

Figure 2. Illustration of the TMS sites in left SMG, left AIP and left PMv on sagittal, coronal, axial and 3D views of the brain. The MNI coordinates (x, y, z) were obtained using an on-line neuronavigated technique (Noirhomme et al., 2004).
Figure 2
834x1638mm (72 x 72 DPI)

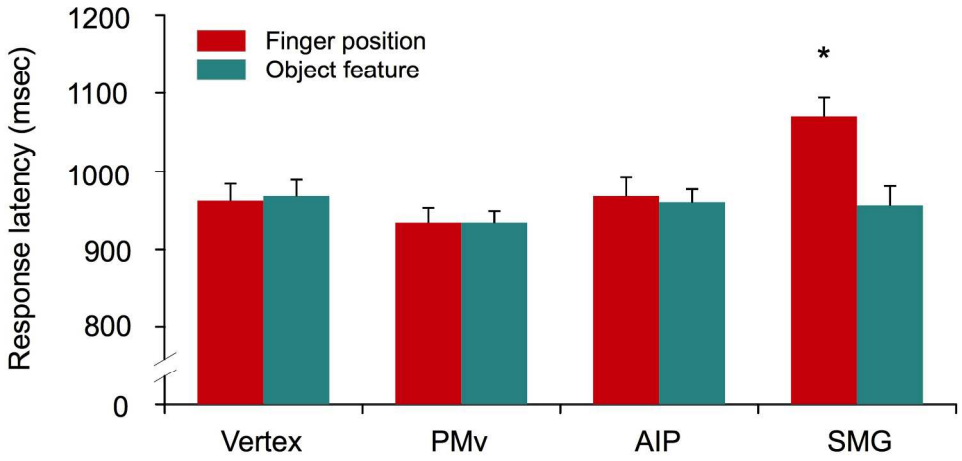

Figure 3. TMS over left SMG selectively interfered with judgements on finger position. The graph represents the mean response latencies and standard errors in the Finger task and in the Object task as a function of the TMS site. The asterisk indicates a significant difference between the two tasks.
Figure 3
833x418mm (72 x 72 DPI)