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The left supramarginal gyrus contributes to finger positioning for object use: a neuronavigated transcranial magnetic stimulation study

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Abstract

In everyday actions, we grasp dozens of different manipulable objects in ways that accommodate their functional use. Neuroimaging studies showed that grasping objects in a way that is appropriate for their 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 involved in specifying the position of fingers onto the object from those implementing the motor programme 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 where the thumb or the index finger was expected to contact the object during its normal utilization or where a given attribute of the same object 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 of finger positions but not judgements of 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, at least the left SMG is involved in specifying the appropriate position of the thumb and index onto the object.

Introduction

Our ability to use objects in a fast and efficient way presupposes the existence of mechanisms that determine how and where to grasp them. 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) (Johnson-Frey *et al.*, 2005; Kroliczak & Frey, 2009; Brandi *et al.*, 2014). 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 specifying the position of fingers onto an object to use it.

Up to now, the identification of the brain areas involved in finger positioning for object use has remained problematic because previous research on this issue has mostly relied on tasks requiring action execution, making it difficult to discriminate between the areas specifying fingers position and those implementing the motor programme to perform the appropriate action (Johnson-Frey *et al.*, 2005; Kroliczak & Frey, 2009; Brandi *et al.*, 2014). 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 make manipulation-related judgements on the basis of pictures of objects. A functional magnetic resonance imaging (fMRI) study showed that deciding whether two objects are used with the same manipulation pattern increases 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 retrieving information important for object use, but brain imaging results are not immune to the possibility that the task

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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–object interactions from those involved in motor execution using mental imagery or action judgement tasks, but their results do not suffice to establish the causal implication of the activated regions because fMRI data are of correlative nature (Decety *et al.*, 1994; Grafton *et al.*, 1996; Binkofski *et al.*, 1999; Moll *et al.*, 2000; Grezes & Decety, 2001; Imazu *et al.*, 2007; Vingerhoets *et al.*, 2010, 2013). In theory, lesional studies should provide more convincing evidence by showing that the integrity of a given region is necessary to specify the appropriate hand shape and finger configuration 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 judgements that require to access knowledge of the hand posture required to use objects (Buxbaum *et al.*, 2000; Buxbaum & Saffran, 2002; Buxbaum *et al.*, 2005; Kalénine *et al.*, 2010). This observation was replicated using repetitive transcranial magnetic stimulation (rTMS) in healthy participants while they judged whether two objects displayed on a screen shared a designated attribute: left SMG disruption slowed down judgements about the hand configuration associated with object use but not judgements about the functional interaction between two objects (Pelgrims *et al.*, 2011) or their context of use (Andres *et al.*, 2013). However, 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. Previous TMS studies (Pelgrims *et al.*, 2011; Andres *et al.*, 2013) did not allow us to decide whether the involvement of SMG was driven by motor or non-motor attributes of the objects because participants could make the judgements by relying either on the hand configuration evoked by the two objects or on the object parts shared by the two objects. Moreover, another study revealed an association between inferior frontal lesions, encompassing PMv and deficits in judging the adequacy of hand and finger configurations for object use, whereas no association was observed between parietal lesions and deficits in these judgements (Pazzaglia *et al.*, 2008). Current results from brain imaging and lesional studies thus remain controversial and subject to alternative interpretations. Finally, in most of these studies, manipulation knowledge was broadly defined, and its assessment was largely undifferentiated, dealing with the hand configuration but also the movement direction and amplitude or more formal aspects of object use. This has contributed to limit conclusions about the role of the implicated brain regions.

In this study, we targeted a specific aspect of hand–object interactions, which is the spatial relationship between the fingers and the object, and tested the causal role of left SMG, AIP and PMv in specifying the position of fingers onto an object in order to use it. We applied rTMS over left SMG, AIP and PMv while healthy participants made spatial judgements about object attributes (‘Object task’) or about the position of the thumb and index finger 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 is involved in specifying the finger positioning for object use, rTMS over this region will delay the judgements in the Finger task but not in the Object task.

Methods

Participants

Sixteen right-handed males (mean age ± standard deviation, $M \pm$ SD: 25.4 ± 3.6 years) participated in this study. They were free of any history of neurological deficits and showed no contraindications for TMS (Rossi *et al.*, 2009). The experiment was undertaken with the understanding and written consent of each subject and conforms to the Declaration of Helsinki. The biomedical ethics committee of the Université catholique de Louvain approved all experimental procedures.

Stimuli and tasks

Stimuli consisted of colour pictures of 28 familiar manipulable man-made objects (see Table S1). The object picture (maximum 5 degrees of visual angle) 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.* either the ‘thumb’ or the ‘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.* rounded, flat, wooden, bottom, pierced, hollow or metallic), 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 bottom); 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 (M = 28.5, SD = 2.2 years) while they used the objects to exclude those for which finger positioning differed among users. We then asked a second sample of 10 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 data of these participants, we selected a subset of objects that were judged as fast and accurately in the two tasks (mean response latency (RL): $t < 1$; error rate: $t < 1$). The successful matching of the two tasks was further demonstrated by the absence of differences in RL 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.

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 judgement tasks with ten objects that were not used in the TMS experiment.

During the TMS experiment, the two tasks were repeated four times in a row while rTMS was applied over the four mentioned target sites, *that is* SMG, AIP, PMv and vertex, 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.

During a block, a finger name or object attribute to be identified was cued by written instructions displayed on the screen every two to five 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 trial sequence. Each trial started with the display of a fixation cross on the screen centre for 200 ms, followed by a 500 ms blank interval, and the object picture that remained visible until the participant's response (Fig. 1). The next trial started after 5000 ms. A voice key connected to E-Prime V1.0 (Schneider *et al.*, 2002) was used to measure the latency of verbal responses ('red' or 'blue'), and accuracy was monitored online by the experimenter. Verbal responses were preferred to manual responses to avoid interference between manual response movements and finger position judgements.

TMS protocol

We delivered repetitive TMS (10 Hz, five pulses, 400 ms) by means of a 35 mm inner diameter polyurethane-coated figure-of-eight coil connected to the Rapid Magstim stimulator (Magstim Company, Whitland, UK). This parameter combination has been used in more than 50 studies without generating any side effect (Rossi *et al.*, 2009). 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 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 *et al.*, 2001). The intensity was set to 65% to fit the parameters of previous TMS studies investigating hand–object interactions (Pelgrims *et al.*, 2011; Andres *et al.*, 2013). The first pulse occurred 100 ms 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 coregistration with individual anatomical magnetic resonance images using a home-made neuronavigation system (Noirhomme *et al.*, 2004). The coregistration proceeded in three steps: (i) 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.); (ii) 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; (iii) 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 centre 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 millimetre. 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 (Fig. 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

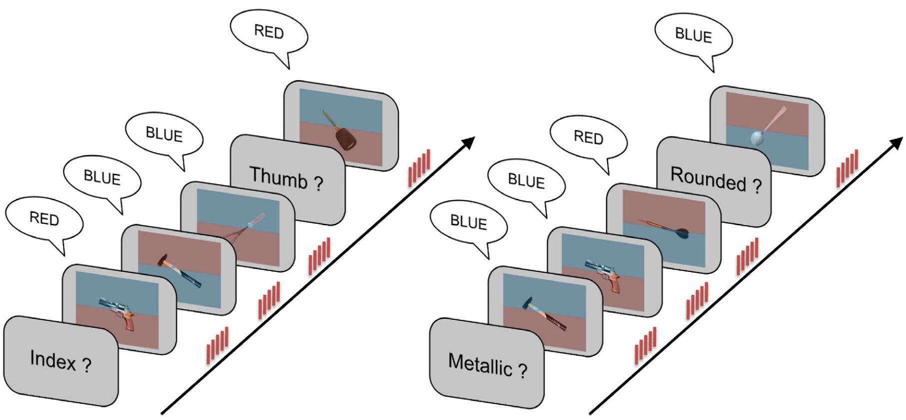

FIG. 1. In the Finger task, participants were asked to name the colour of the part of the image (lower or upper half) where a given finger (*e.g.* index or thumb) was expected to contact the object during normal conditions of use. In the Object task, participants were asked to name the colour of the part of the image (lower or upper half) where a given feature of the object (*e.g.* metallic or rounded part) was located. The finger or the object feature was cued by a question displayed in advance to a series of 2 to 5 object images. Repetitive TMS (65%, five pulses, 400 ms) was applied in every trial, the first pulse occurring 100 ms after the onset of the object picture. [Colour figure can be viewed at wileyonlinelibrary.com].

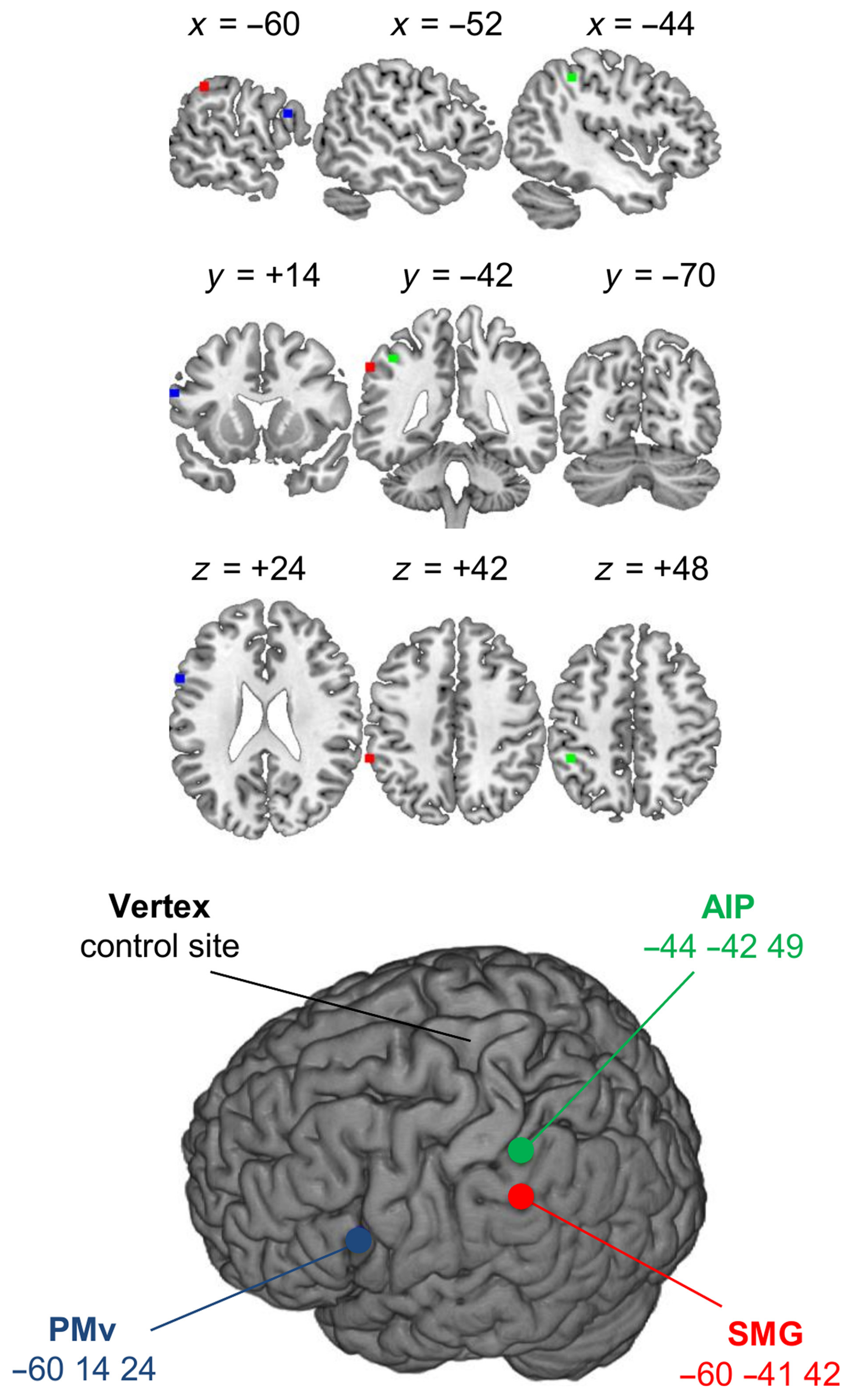

FIG. 2. Illustration of the TMS sites in left SMG, left AIP and left PMv on sagittal, coronal, axial and 3D views of the brain. The MNI coordinates (*x*, *y*, *z*) were obtained using an online neuronavigation technique (Noirhomme *et al.*, 2004). [Colour figure can be viewed at wileyonlinelibrary.com].

identification on functional MR images obtained for each participant during a relevant task (Sparing *et al.*, 2008; Sack *et al.*, 2009). In this 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: (i) rigid and scale transformations and (ii) non-rigid basis-spline transformations. The mean MNI coordinates of SMG (mean x, y, z and standard deviation: $M = -60, -41, 42$; SD = 4, 12, 6 mm), AIP ($M = -44, -42, 49$; SD = 9, 7, 3 mm) and PMv ($M = -60, 14, 24$; SD = 3, 3, 8 mm) fitted with the x, y, z coordinates gathered in previous fMRI studies demonstrating the involvement of these regions in object use (Johnson-Frey *et al.*, 2005; Kroliczak & Frey, 2009; Brandi *et al.*, 2014).

Data analysis

Trials in which a participant's response failed to trigger the voice key (0.97%) and trials with a RL falling outside a 500–2500 ms range (1.53%) were discarded from subsequent analyses. We modelled the probability of making an error by means of a generalized mixed model, using a probit binary link function (binomial distribution), with the TASK, the SITE and the TASK by SITE interaction as fixed effects and the differences between participants as a random effect. The mean RL (ms) of correct trials was computed for each participant and condition, and these values were entered in a repeated-measure ANOVA with the TASK (Finger and Object) and the SITE (SMG, AIP, PMv and vertex) as within-subject factors. *Post hoc* analyses were conducted on the significant effects using the Tukey HSD test ($\alpha = 0.05$), and Bayesian paired samples t-tests performed with a default Cauchy prior width of $r = 0.707$ for effect size on the alternative hypothesis (Rouder *et al.*, 2012). These analyses, performed with the Bayes Factor R package (Morey & Rouder, 2015), yield Bayes Factors (BFs; Dienes, 2014; Rouder *et al.*, 2009) obtained by dividing the likelihood of the alternative hypothesis (H_1) by that of the null hypothesis (H_0). Therefore, BF varies between 0 and ∞ where values below 1 provide increasing evidence in favour of the null hypothesis and values above 1 increasing evidence for the alternative theory.

Results

The analysis of errors showed no significant effect of the TASK, $F_{1,3486} = 0.51$, $P = 0.37$, the SITE, $F_{3,3486} = 1.5$, $P = 0.21$, and no significant TASK by SITE interaction, $F_{3,3486} = 1.09$, $P = 0.35$. The error rate was similar in the Finger task ($M = 6.4\%$, SD = 7%) and in the Object task ($M = 5.9\%$, SD = 5.1%).

The analysis of RLs showed no effect of the TASK, $F_{1,15} = 2.84$, $P = 0.11$, $\eta_p = 0.16$, a marginal effect of the SITE, $F_{3,45} = 2.35$, $P = 0.085$, $\eta_p = 0.14$, and a two-way interaction between TASK and SITE, $F_{3,45} = 5.94$, $P = 0.002$, $\eta_p = 0.28$. As illustrated in Fig. 3, RLs differ between sites in the Finger task, $F_{3,45} = 5.49$, $P = 0.003$, $\eta_p = 0.27$. *Post hoc* comparisons using Tukey HSD test ($\alpha = 0.05$) indicated that disruption of left SMG functioning ($M = 1059$ ms, SD = 162 ms) led to a significant RL increase compared to the vertex ($M = 962$ ms, SD = 166 ms), while this was not the case following disruption of the left PMv ($M = 934$ ms, SD = 125 ms), or the left AIP ($M = 967$ ms, SD = 121 ms). The results of the corresponding two-tailed Bayesian paired samples t-tests yielded BFs (H_1/H_0) of 7.86, 0.26 and 0.35 for the comparison of the vertex and the SMG, the AIP and the PMv. According to Jeffreys (1961), this constitutes substantial evidence in favour of the alternative hypothesis for SMG stimulation, substantial evidence in favour of the null for AIP and anecdotal evidence in favour of the null for PMv (Wetzels & Wagenmakers, 2012). In the Object task, the effect of SITE was not significant, $F_{3,45} = 0.45$, $P = 0.72$, $\eta_p = 0.03$, indicating that there was no RL difference between left SMG ($M = 953$ ms, SD = 90 ms), the vertex ($M = 968$ ms, SD = 149 ms), left PMv ($M = 934$ ms, SD = 136 ms) and left AIP ($M = 956$ ms, SD = 81 ms). Further comparisons using paired samples t-tests indicated an absence of RL difference between the two tasks when TMS was applied over the vertex, AIP or PMv (all ts < 1), whereas

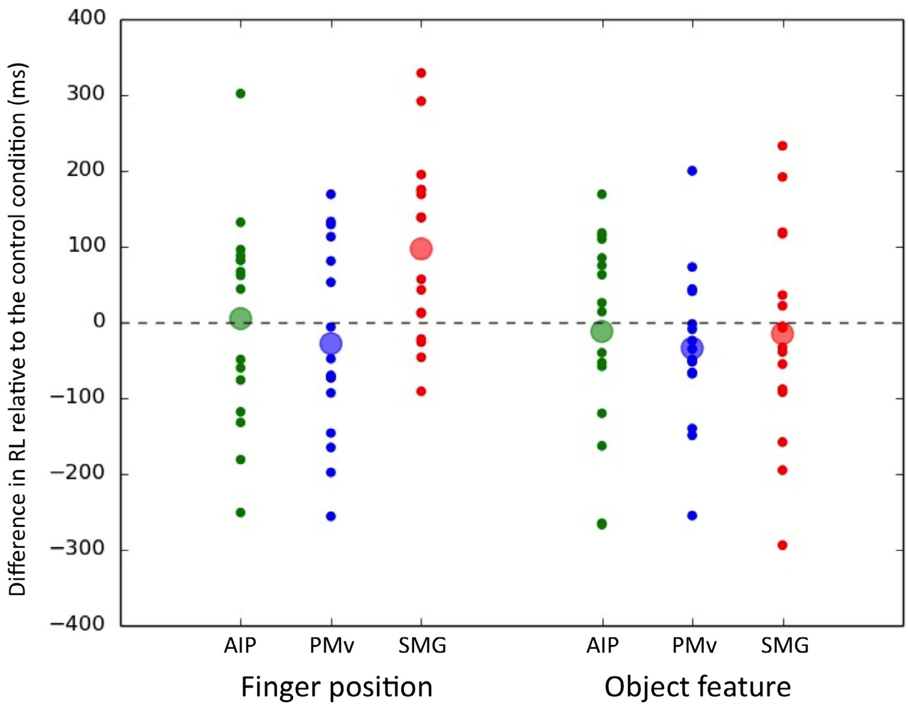

FIG. 3. TMS over left SMG selectively interfered with judgements of finger position. The disruptive effect of TMS (Y axis) was estimated by subtracting each participant's RL in the control condition from the RL measured in the condition of interest. Each small dot represents the mean RL from a single participant. Large dots represent the group average. Positive values indicate that TMS over the target site (AIP, PMv or SMG) delayed responses compared to the control condition (*i.e.* TMS over the vertex). [Colour figure can be viewed at wileyonlinelibrary.com].

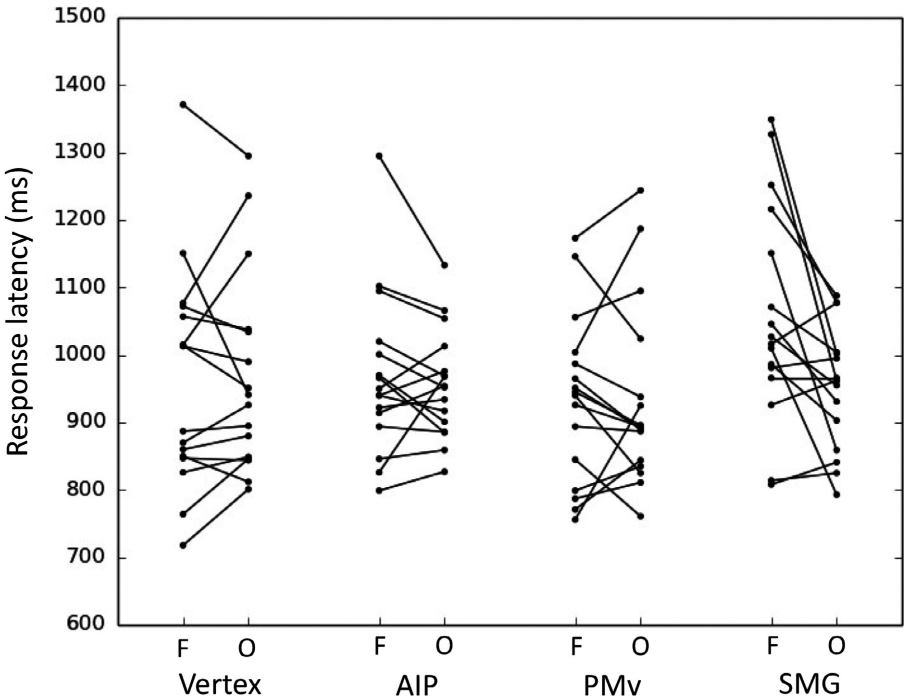

FIG. 4. The connected dots represent the mean RL (ms) of each participant, in the Finger task (F) and in the Object task (O), as a function of the stimulated region (vertex, AIP, PMv or SMG).

RLs were larger in the Finger task compared to the Object task when rTMS was applied over SMG, $t(15) = 3.08$, $P = 0.008$ (see Fig. 4).

Discussion

Our results provide direct evidence that left SMG plays a causal role in specifying the position of fingers onto an object to use it. Repetitive TMS applied over left SMG delayed spatial judgements about finger positions by 100 ms when compared to the control site, whereas response latencies did not show any significant increase when rTMS was applied over left AIP or PMv. 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 manipulate 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 their manner of manipulation (Buxbaum *et al.*, 2000; Kalénine *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 motor or perceptual processes unrelated to finger positioning. 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 vs. 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. The results go beyond the scope of previous evidence because they demonstrate the causal role of left SMG in specifying 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.

Uncovering the source of this effect – determining the nature of the processes or representations hampered by rTMS on the SMG and involved in specifying the finger positioning for object use – was beyond the scope of this study, and we have no direct evidence that speaks to this issue. We see at least two possible, non-mutually exclusive, mechanisms by which the SMG may contribute to specifying finger positioning for object use. A first possibility is that the SMG houses abstract representations of finger positions required for proper object use. A second is that the SMG is involved in a mental simulation process (Jeannerod, 1994), sometimes described as technical reasoning (Osiurak & Badets, 2016) or mechanical problem solving (Goldenberg & Hagmann, 1998), that would integrate information about the putative actor's finger configuration, retrieved elsewhere, with the particular shape and position of the object to be grasped. In line with the latter, several fMRI and TMS studies evidenced a role of left SMG in left-right judgements on rotated hand drawings (Kosslyn *et al.*, 1998; Parsons *et al.*, 1998; Pelgrims *et al.*, 2009), a task that has long been considered as relying on motor imagery. However, a closer look at the literature on motor imagery 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 *et al.*, 2012; Vannuscorps & Caramazza, 2015, 2016). Furthermore, other sources of data indicate that AIP and PMv do play a role in the mental imagery of grasp movements (Rizzolatti *et al.*, 2002; Aflalo *et al.*, 2015). If SMG was contributing to hand configuration through mental imagery, then rTMS over AIP or PMv should have disrupted performance as well. Future studies are thus needed to elucidate this question.

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 *et al.*, 2015). Left SMG, in particular, was sensitive to the manipulatory pattern of objects irrespective to their physical appearance. It is worth noting that, in the present study, spatial judgements only assessed where to position the thumb or index finger onto an object, while functional use also often requires knowing how to position the fingers relative to each other and not just the thumb and index. Future studies should investigate the role of left SMG in configuring the whole hand for object use, as this may constitute a distinct source of difficulties for patients suffering from apraxia (Sirigu *et al.*, 1995). Aside from its role in finger positioning, left SMG is also likely to contribute 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 (Kalénine *et al.*, 2010). Another reported a correlation between the existence of brain damage in the left inferior parietal lobe, including the SMG, and the severity of amplitude and timing errors of patients asked to pantomime tool use (Buxbaum *et al.*, 2014). 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 thus seems confined to motor attributes such as finger position and possibly other aspects of hand/arm movements (Buxbaum *et al.*, 2014).

Our failure to find evidence for an effect of the 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 (Ehrsson & Fagergren, 2001; Tunik *et al.*, 2005; Davare *et al.*, 2006, 2007, 2010; Cavina-Pratesi *et al.*, 2010). 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 *et al.*, 2009, 2010). But several results indicate that AIP and PMv actually 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 *et al.*, 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 (Jacobs *et al.*, 2010; Gallivan *et al.*, 2013). In the light of the present results, we suggest that AIP and PMv are not essential to define the position of fingers onto the object but well to implement this information into an action plan that can be translated in muscle recruitment with the contribution of the primary motor cortex. This conjecture obviously requires additional evidence. Our findings indeed provided only substantial and anecdotal evidence in favour of the null for AIP and PMv, respectively. However, it is compatible with the role of AIP-PMv in the cortical motor hierarchy (Gallivan *et al.*, 2013) and with their functional connectivity pattern (Koch *et al.*, 2007; Olivier *et al.*, 2007; Davare *et al.*, 2009). 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 *et al.*, 2007; Whitney *et al.*, 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.

Finally, as we only tested male participants, the present conclusions should be limited to the neural representation of the motor attributes of objects in the men's brain. Further research is needed to test the causal implication of the left SMG, AIP and PMv in women and evaluate the impact of gender differences. So far, one fMRI study has reported that, compared to men, women showed greater activity in the left SMG when simulating tool use actions (Wadsworth & Kana, 2011). But the cognitive strategy used by the participants and their familiarity with the presented tools remains a potential source of gender differences, which was not controlled in this fMRI study and should be taken into account in future investigations (see Jordan *et al.*, 2002; Seurinck *et al.*, 2004; Hugdahl *et al.*, 2006; Vingerhoets, 2008).

Conclusion

The combined use of TMS 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 specifying the position of fingers for object use. 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 Homo sapiens (Peeters *et al.*, 2009). Future research will have to address the fundamental questions of the nature of the representations and types of processes housed in the SMG and attempt to clarify how SMG works in concert with other parts of the brain, notably the AIP, the PMv and the posterior temporal cortex, to support efficient object grasping and use.

Supporting Information

Additional supporting information can be found in the online version of this article:

Table S1. List of the 28 objects used in the study.

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Conflict of interest

The authors have no conflicts of interest to declare.

Author contributions

All authors contributed to the conception of the work. MA and BP ran the study. EO provided technical support and expertise. BP analysed the data. MA and GV interpreted the data and drafted the manuscript. BP and EO amended the first draft. MA, BP and GV dealt with the revision process.

Data accessibility

The data supporting the results will be deposited to Figshare on the Author's behalf with a CC-Zero licence. The data will be assigned a single DOI and will be automatically and permanently associated with the HTML version of the manuscript.

Abbreviations

AIP, anterior intraparietal area; fMRI, functional magnetic resonance imaging; M, mean; MNI, Montreal neurological institute ; PMv, ventral premotor cortex; RL, response latency; rTMS, repetitive transcranial magnetic stimulation; SD, standard deviation; SMG, supramarginal gyrus.

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