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CORTEX 49 (2013) 2097-2105



Research report

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Distinct contribution of the parietal and temporal cortex to hand configuration and contextual judgements about tools

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ARTICLE INFO

Article history: Received 5 June 2012 Reviewed 7 July 2012 Revised 12 October 2012 Accepted 23 November 2012 Action editor Georg Goldenberg Published online 10 December 2012

Keywords: Action Semantic memory Transcranial magnetic stimulation Upper-limb apraxia

ABSTRACT

Neuropsychological studies showed that manipulatory and semantic knowledge can be independently impaired in patients with upper-limb apraxia, leading to different tool use disorders. The present study aimed to dissociate the brain regions involved in judging the hand configuration or the context associated to tool use. We focussed on the left supramarginalis gyrus (SMG) and left middle temporal gyrus (MTG), whose activation, as evidenced by functional magnetic resonance imaging (fMRI) studies, suggests that they may play a critical role in tool use. The distinctive location of SMG in the dorsal visual stream led us to postulate that this parietal region could play a role in processing incoming information about tools to shape hand posture. In contrast, we hypothesized that MTG, because of its interconnections with several cortical areas involved in semantic memory, could contribute to retrieving semantic information necessary to create a contextual representation of tool use. To test these hypotheses, we used neuronavigated transcranial magnetic stimulation (TMS) to interfere transiently with the function of either left SMG or left MTG in healthy participants performing judgement tasks about either hand configuration or context of tool use. We found that SMG virtual lesions impaired hand configuration but not contextual judgements, whereas MTG lesions selectively interfered with judgements about the context of tool use while leaving hand configuration judgements unaffected. This double dissociation demonstrates that the ability to infer a context of use or a hand posture from tool perception relies on distinct processes, performed in the temporal and parietal regions. The present findings suggest that tool use disorders caused by SMG lesions will be characterized by difficulties in selecting the appropriate hand posture for tool use, whereas MTG lesions will yield difficulties in using tools in the appropriate context.

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1. Introduction

One hallmark of higher primates is the development of a seemingly unlimited dexterity, leading to an unmatched ability to use tools. The evolution of this function has also conferred, especially in the human brain, a unique status to tool representations (Johnson-Frey, 2004; Peeters et al., 2009). Indeed, many neuropsychological studies have contributed to demonstrate that tools form a particular category, which can be selectively impaired, or preserved, following brain damage (for a review, see Capitani et al., 2003; Pillon and d'Honincthun, 2011; Vannuscorps and Pillon, 2011). Functional magnetic resonance imaging (fMRI) studies have corroborated this view by showing that tools benefit from a distinct representation in the ventral stream. Indeed, tool identification activates a specific area in the fusiform gyrus located nearby the lateral region dedicated to the animal category (Chao et al., 1999), the face fusiform area (Kanwisher et al., 1999) and a more medial region extending to the parahippocampal place area (Epstein and Kanwisher, 1998).

The cortical network underlying tool representations has also been found to extend outside the ventral stream. In particular, fMRI studies have shown the involvement of the left supramarginalis gyrus (SMG) and the left middle temporal gyrus (MTG) in processing tools and actions (Binder et al., 2009; Chao et al., 1999; Johnson-Frey et al., 2005; Mahon et al., 2007). As a component of the dorsal stream, SMG is thought to underlie the pragmatic processing of actions. Indeed, it has been shown that SMG activation is more related to the hand configuration required to use tools than to their actual function (Boronat et al., 2005; Canessa et al., 2008; Kellenbach et al., 2003). MTG lies in-between the ventral and dorsal streams, as defined in seminal papers (Goodale and Milner, 1992; Milner and Goodale, 1995; Mishkin and Ungerleider, 1982; Ungerleider and Mishkin, 1982), and both fibre tractography and resting-state functional connectivity studies revealed that this region is interconnected with a widely distributed network of areas located in the inferior temporal, frontal and parietal lobes (Turken and Dronkers, 2011; de Zubicaray et al., 2011). In addition, functional imaging data have shown that, in humans, MTG activation is enhanced when the hand posture adopted to grasp a tool is consistent with its conventional use, reflecting the responsiveness of this area to learnt semantic associations (Valyear and Culham, 2010; Vingerhoets et al., 2011).

Lesions of the left parieto-temporal junction often lead to upper-limb apraxia, a disorder affecting the normal use of tools in the absence of elementary sensorimotor disturbances (Buxbaum et al., 2000; Moreaud et al., 1998; Rapcsak et al., 1995; Rosci et al., 2003; Rothi et al., 1991; Sirigu et al., 1995). Neuropsychological studies have showed that some patients are unable to retrieve the manipulatory pattern associated to tool use, whereas they are still able to understand their function (Buxbaum and Saffran, 1998; Buxbaum et al., 2000; Buxbaum and Saffran, 2002). This selective impairment of manipulatory knowledge is generally accompanied by an inability to pantomime or recognize tool use gestures (Buxbaum et al., 2000). In contrast, other patients were found to experience difficulties in recognizing tools or in describing their function, although they were still able to demonstrate how these tools are used (Buxbaum et al., 1997; Sirigu et al., 1991; Ochipa et al., 1989). These data strengthen the hypothesis that semantic associations between tools and actions are processed independently of the spatio-temporal features of tool—hand interactions.

However, in patients, the respective contribution of SMG and MTG to the processing and/or representation of tool use remains difficult to evaluate because the lesions often overlap these two areas as well as frontal areas (Goldenberg and Spatt, 2009; Kalénine et al., 2010). In a previous study, we used repetitive transcranial magnetic stimulation (rTMS) to interfere transiently with the functioning of SMG while participants performed judgements about the hand configuration required to use tools or about the functional interactions between tools. Results showed increased reaction times (RTs) in the hand configuration task only but, since less than 33% of the tools were similar across tasks, we could not exclude that perceptual attributes of certain tools had facilitated functional judgements (Pelgrims et al., 2011).

In order to address the issues left unanswered by previous studies, we designed a new TMS experiment in which healthy participants judged the same set of tool pictures as a function of their context of use or the hand configuration required to use them. To provide a direct test for the double dissociation between the two tasks, we applied TMS over left MTG or left SMG of each participant. Although fMRI studies have occasionally revealed bilateral MTG activations during action judgements (Canessa et al., 2008), we focussed on the left hemisphere contribution because apraxia is mostly observed after left-sided lesions (Frey, 2008; Johnson-Frey et al., 2005). Based on the brain imaging and neuropsychological evidence reviewed above, we predicted that contextual judgements about tool use should be selectively slowed down by TMS over left MTG, whereas TMS over left SMG should delay judgements about the hand configuration required for tool use.

2. Methods

2.1. Participants

Sixteen male volunteers, free of neurological history, and aged between 25 and 30 years (mean age: 27.6 years) participated in the present study. They were all right handed according to the Edinburgh handedness inventory (Oldfield, 1971). The experimental procedure was approved by the Ethics Committee of the Université catholique de Louvain and all subjects gave their written informed consent.

2.2. Tasks and stimuli

Experiments were performed in a dimly illuminated room. Subjects sat comfortably in an armchair, 60 cm in front of a computer screen, with their elbows flexed and their hands at rest in a half-pronated position over the side supports of the armchair. They were told not to move and not to look at their hands during task performance. They wore earplugs to protect against the noise generated by TMS.

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The subjects had to perform two judgement tasks. In a Hand Configuration task, they had to decide whether the two objects displayed on the computer screen are normally used with an identical hand configuration whereas the Context task consisted in deciding whether both objects are usually used in the same context. Subjects were required to respond, as quickly as possible, by "oui" (yes) or "non" (no). Each trial began with the presentation of a cross (200 msec) displayed on the screen centre and followed by a 500 msec mask. Two colour pictures of tools were then displayed vertically on a mid-grey background (visual angle of 5°) until a response was given (Fig. 1A). The next trial started 4800 msec after the participant's response. A microphone was used to record verbal responses and the RT was measured on-line by using E-Prime V1.0 (Psychology Software Tools, Pittsburgh, USA). The errors were encoded by the experimenter.

Seventy-two pictures of tools were used to create two different sets of 36 pairs, one for each task (see Supplementary Table). These pairs were selected from a larger set of pairs evaluated successively by two additional groups of 12 male participants who did not participate in the TMS study. The selected pairs showed a minimal agreement of 90% across the responses of the first group of participants who performed the two tasks without time constraint. To ascertain that each task targeted a specific feature of tool use, we asked the other group to rate the similarity between hand configurations (1 = completely dissimilar; 5 = very similar) for the 36 pairs of tools used in the Hand Configuration task and for those used in the Context task (see Fig. 2A). The same pairs of tools were also rated according to the similarity between contexts of use (see Fig. 2B). For compatible pairs, similarity between hand configurations was rated higher in the Hand Configuration task than in the Context task (Wilcoxon's signed rank test, p < .001). In contrast, the tools belonging to compatible pairs of the Context task were closer in terms of context of use than those of the Hand Configuration task (Wilcoxon's signed rank test, p < .001). As illustrated in Fig. 2B, incompatible trials elicited low ratings for both criteria and these ratings did not differ across tasks (all p > .1).

2.3. Practice and TMS sessions

At the beginning of the experimental session, subjects were first asked to name each object used in the practice and TMS sessions in order to ascertain that they were able to recognize all of them. Then for each task, subjects performed 24 practice trials with objects different from those used in the TMS sessions. Each block in both the training and TMS sessions included the same number of compatible ("yes") and incompatible ("no") trials; in addition, the same response ("yes" or "no") never occurred more than three times in a row. Although the same objects were presented in both the Hand Configuration and Context tasks, inside different pairs, a possible interference between responses in trials of the two tasks involving the same object was reduced by controlling the distribution of the objects in the compatible and incompatible trials: half of the objects were presented in a compatible trial in one task and in an incompatible trial in the other task.

The main experiment consisted of six blocks of 36 trials resulting from the combination of the two tasks and three sites of stimulation, namely the left SMG, left MTG and Vertex,



Fig. 1 – A. Time course of the stimulus presentation and rTMS application. For the sake of clarity, the two objects are displayed horizontally on this figure (see Methods). B. Examples of compatible ("yes") and incompatible ("no") trials for the Hand Configuration and Context judgement tasks.

used as a control site. The three TMS conditions were counterbalanced and both tasks were interleaved but half of the subjects began the experiment with the *Hand Configuration* task whereas the other half began with the *Context* task. The order of the trial presentation and the position (up or down) of the objects on the screen differed between the three TMS conditions of each task.

2.4. TMS protocol

rTMS (10 Hz, five pulses, 400 msec) was delivered using a Rapid Magstim model 200 stimulator (Magstim Company, Whitland,

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Fig. 2 – A. Ratings of similarity between hand configurations (1 = completely dissimilar; 5 = very similar) for the compatible and incompatible pairs of tools in the *Hand Configuration* task and for the compatible and incompatible pairs of tools in the *Context* task. B. Ratings of similarity between contexts of use for the same pairs of tools.

UK) through a 70 mm diameter figure-of-eight coil. The coil was held tangential to the skull with the handle pointing laterally and backward, and located over the left SMG, the left MTG, or the Vertex. The TMS intensity was fixed arbitrarily at 65% of the machine output. The rTMS train was delivered 100 msec after the stimuli presentation. Given that the next trial started 4800 msec after the participant's response (mean RT \pm standard deviation (SD): 1073 \pm 234 msec) and that the rTMS train started 800 msec after the onset of the fixation cross, the inter-train interval was longer than 5000 msec, in line with the safety recommendations for the use of 10 Hz rTMS (Rosci et al., 2003). The subjects wore a closely fitting

electroencephalography (EEG) cap used to mark the different stimulation sites that were precisely located by means of an on-line neuronavigation technique using individual anatomical magnetic resonance images (MRI; see Noirhomme et al., 2004 for technical details). The co-registration between TMS site and anatomical MRI proceeded in three steps. First, 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.). Second, 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. Third, Montreal Neurological Institute (MNI) coordinates of group functional MRI data were used as a guide to localize broadly the target brain areas in left MTG and SMG (Canessa et al., 2008; Johnson-Frey et al., 2005; Mahon et al., 2007). The fMRI studies were chosen because they provide functional data about the involvement of SMG and MTG in the perception of tools versus animals (Mahon et al., 2007), in the planning of manipulation versus control movements (Johnson-Frey et al., 2005), or in similar judgements as those performed in the present study (Canessa et al., 2008). The transformation matrix was used to project the MNI coordinates reported in each fMRI study on 2D and 3D views of the participant's brain. The ultimate coil position was determined based on the following anatomical landmarks in order to take into account the inter-subject variability: to target left MTG, we positioned the coil over the posterior part of this area, under the ascending branch of the superior temporal sulcus; the other target site was the superior part of the anterior bank of left SMG, under the junction of the postcentral and intraparietal sulci. The position of the figure-ofeight coil relative to the scalp was known by digitizing three points at the intersection of the windings. A normal to the plane of the coil was drawn from its centre to the brain, revealing the impact point of TMS on the cortex. The coil was moved accordingly until its digitized position matched the target site on the visual interface. This method allows the visualization of the target sites on individual brain images with a remarkable accuracy (<1 mm) in comparison with other methods (Andres et al., 2011; Sparing et al., 2008). After the experiment, the individual coordinates of the target sites were collected in order to double-check their location and provide an estimate of inter-subject variability. The mean normalized MNI coordinates for SMG were -60 ± 4 , -34 ± 12 , 46 \pm 7 mm (mean \pm SD, n = 16) and those for MTG were -60 ± 4 , -50 ± 10 , -1 ± 10 mm (see Fig. 3A).

2.5. Data analysis

The statistical analysis was performed on error rates and RTs, defined as the time between the appearance of the picture on the computer screen and the onset of the verbal response. Error trials (*Hand Configuration*: $5.5 \pm 3.4\%$; Context: $5.8 \pm 3.8\%$) as well as trials with an RT falling outside the range of 500 to 3500 msec (*Hand Configuration*: $.57 \pm .6\%$; Context: $.23 \pm .4\%$) were discarded from the RT analysis. The percentage of excluded trials was similar across tasks and sites (all *F* values < 1). Mean RTs were computed on the remaining



Fig. 3 – A. Representation of the stimulation sites in SMG (green) and MTG (red), as determined by an on-line neuronavigation technique (Noirhomme et al., 2004). The open black circles indicate the mean MNI coordinates of each site (SMG: x = -60, y = -34, z = 46; MTG: x = -60, y = -50, z = -1) and the ellipses represent the 95% confidence interval of the normalized coordinates calculated for each subject. B. Mean RT and standard error (SE) in the Hand configuration and the Context tasks, respectively, as a function of the TMS condition. Asterisks indicate a significant difference between two conditions (p < .05).

trials (91%) for each subject and condition. The effects of rTMS on RTs were analysed by means of a repeated-measure (RM) analysis of variance (ANOVA) with TASK (*Context vs Hand Configuration*) and SITE (SMG vs MTG vs Vertex) as within-subject factors. When appropriate, post-hoc comparisons were performed using Tukey t-tests.

3. Results

The RM ANOVA performed on RTs showed a main effect of TASK [F(2,30) = 16.24, p < .001], with longer RTs in the Hand

Configuration than in the Context task, and an interaction between TASK and SITE [F(2,30) = 20.951, p < .001]. As shown in Fig. 3B, in the Hand Configuration task, a left SMG virtual lesion led to an increase in the mean RT (1208 \pm 250 msec) when compared with the Vertex [mean \pm SD: 1085 \pm 174 msec; Tukey t-test, t(15) = 3.586, p < .043] or the MTG condition $[1061 \pm 266 \text{ msec}; t(15) = 4.259, p < .014];$ no difference was found between the MTG and Vertex conditions in the Hand Configuration task [t(15) < 1]. In contrast, in the Context task, a virtual lesion of left MTG led to longer RTs (1114 \pm 280 msec) than in the Vertex [983 \pm 178 msec; t(15) = 5.454, p < .002] and SMG conditions [990 \pm 192 msec; t(15) = 5.15, p < .003]; no difference was found between these two latter conditions [t(15) < 1]. The RT difference between the MTG and Vertex conditions was larger in the Context task than in the Hand Configuration task [139 \pm 35 msec vs $-23 \pm$ 48 msec; t(15) = 4.78, p < .01], whereas the RT difference between the SMG and Vertex conditions was larger in the Hand Configuration task than in the Context task [123 \pm 48 msec vs 7 \pm 23 msec; t(15) = 2.62, p < .05].

There was no difference in error rate between conditions (all F values < 1). The mean rate and SD was 5.5 \pm 3.4% in the Hand Configuration task and 5.8 \pm 3.8% in the Context task.

4. Discussion

The use of TMS to create virtual lesions of the parietal or temporal cortex allowed us to demonstrate a specific contribution of these regions to the ability of judging the hand configuration or the context associated to tool use. Our results confirmed that left SMG is involved in coding the appropriate hand posture for using tools effectively. Interestingly, we found that the role of SMG is limited to the pragmatic processing of tool use, as suggested by an absence of deficit in judgements about the context of tool use after SMG virtual lesions. The present study also extends previous findings about the critical role of left MTG in implementing representations of conceptual features of tool use and further indicates that, in contrast to SMG, this area is not involved in retrieving the correct hand posture to handle tools. Because the two tasks made use of the same tool pictures and were supposed to elicit the same verbal responses, it is unlikely that TMS impaired perception, or response preparation, in one task and not in the other. The manipulatory or contextual relationship between tools led to similar ratings in the two tasks, except in compatible trials where ratings dissociated as a function of the task. The double dissociation also excludes the possibility that the deficits reported in the present study could be due to differences in task difficulty. It is worth noting that, in the present study, hand configuration judgements took more time than contextual judgements, leading to the possibility that this task was more vulnerable to SMG stimulation simply because it was more effortful. However, this possibility is refuted by previous findings showing that several control tasks matched in response speed with hand configuration judgements were not affected by TMS applied over SMG (Pelgrims et al., 2011).

The present TMS study shows that the left MTG contributes to processes and/or representations that are necessary

for Context but not Hand Configuration judgements. The RT increase observed in Context judgements cannot be attributed to impaired perception or response selection because these two processes are also involved in Hand Configuration judgements which were not affected by TMS over left MTG. The ability to judge the context of tool use relies on a large range of other processes and/or representations, such as tool recognition and retrieval of information about its function, the circumstances of its use (e.g., the typical location, the associated objects), its mechanism of action (e.g., the duration, the motion, the needed energy) and the consequences of its use (e.g., the changes of the initial state, the sound emitted by tool use). The present results do not allow us to specify further the kind of information processed by left MTG during Context judgements. Neuroimaging evidence shows that MTG activation is one of the most robust finding in tasks involving tool recognition or retrieval of semantic information about tools (for a review, see Binder et al., 2009; Martin, 2007). Moreover, damage of the left posterior MTG is often observed in patients with selective difficulties to identify tools when compared to living objects (Brambati et al., 2006; Tranel et al., 2003; Vannuscorps and Pillon, 2011). However, the exact role of left MTG in conceptual processing of tools remains very much debated. According to sensory-motor theories, information about tools is stored and processed in the same neural sub-systems as those recruited for tool perception and manipulation (Barsalou, 2008; Gallese and Lakoff, 2005; Martin et al., 2000; Warrington and Shallice, 1984). Because the posterior MTG encompasses extrastriate visual areas (MT+) specialized for motion perception (Sack et al., 2006) and motion imagery (Seurinck et al., 2011), it has been proposed that MTG would contribute to tool identification by providing information about the characteristic motion of tools (Beauchamp et al., 2002, 2003; Beauchamp and Martin, 2007; Martin et al., 2000). Domain-specific theories assume that the representation of conceptual knowledge in the human brain is primarily determined by evolutionary adaptations (Caramazza and Shelton, 1998). One theory proposes that a specialized system has evolved for the conceptual processing of tools because their fast recognition and efficient use improve the ability of humans to survive in a particular environment (Mahon and Caramazza, 2003, 2009). Another theory proposes that the distinctive representation of tools in the human brain results from a more general adaptation for efficiently designing means to achieve specific goals (Vannuscorps and Pillon, 2011; Pillon and d'Honincthun, 2011). According to this theory, tools are processed by a domain-specific conceptual system that apprehends all kinds of man-made objects and actions in terms of the goals they allow to achieve. Such a system was initially proposed to account for neuropsychological observations that could not be explained by other theories. In particular, this hypothesis was motivated by the finding that conceptual deficits for tools usually extend over all kinds of man-made objects - including tools but not only and actions, without being necessarily constrained by the intrinsic properties of objects and actions, such as their sensory or motor attributes (Vannuscorps and Pillon, 2011; see also Pillon and d'Honincthun, 2010). Lesion data from these neuropsychological studies and others (Tranel et al., 2003) converge with brain imaging evidence (Johnson-Frey et al.,

2005; Kellenbach et al., 2003; Noppeney et al., 2005) to show that left MTG is a potential candidate for the neural substrate of a conceptual system representing knowledge about all kinds of man-made objects and actions. The present study does not allow us to distinguish between sensory-motor and domain-specific theories but it indicates that the processes and/or representations supported by left MTG, being modality-specific or modality-independent, are involved in *Context* and not *Hand Configuration* judgements.

The present study also converges with our, and other, previous results to indicate that the ability to judge the hand configuration associated with tool use depends on left SMG (Boronat et al., 2005; Canessa et al., 2008; Pelgrims et al., 2009, 2011). In line with this view, it could be assumed that, in the dorsal stream, left SMG is involved in identifying tool affordances (Grèzes et al., 2003). Indeed, in the Hand Configuration task, when the use of a pair of tools required a comparable hand posture, their graspable parts also showed some visual similarities. The deficit found when TMS was applied over SMG could therefore reflect the involvement of this area in high-level perceptual processes dedicated to tool use. Because a comparable activation was found in SMG after the visual display of tool pictures and after the auditory presentation of their names and because this activation was also observed when tool names were presented to congenitally blind subjects, it is unlikely that the contribution of SMG to tool processing exclusively depends on visual experience (Mahon et al., 2010). It is possible, however, that SMG codes the tool properties that are relevant for hand conformation in a multimodal manner or independently of the input modality (see for example Noppeney et al., 2006). Alternatively, SMG may play a role in analysing the spatial relationships between tool and hand position (Goldenberg, 2009; Goldenberg and Hagmann, 1998) or in retrieving familiar gesture memories (Rothi et al., 1991). Deciphering the different processes and/or representations involved in Hand Configuration judgements goes beyond the scope of this study and will require further observations from case studies. The crucial finding of our study is that these processes and/or representations are at least partially distinct from those required to perform Context judgements (see also Pelgrims et al., 2011). In order to provide a full-blown explanation of tool processing in the human brain, this division of labour should be accounted by sensorymotor and domain-specific theories in the future.

Previous neuropsychological studies suggest that impaired knowledge of the manipulatory pattern or the context of tool use can lead to distinct disorders (Buxbaum et al., 2000; Ochipa et al., 1989; Sirigu et al., 1991). Hence, patients unable to retrieve manipulatory knowledge experience difficulties to shape their hand appropriately when asked to pantomime or to imitate tool use gestures (Buxbaum et al., 2000), whereas impaired access to conceptual knowledge hampers the ability of patients to select the appropriate tool for a given action or to match tools according to their function (Ochipa et al., 1989; Sirigu et al., 1991). Based on the present results, we propose that these two profiles of upper-limb apraxia can be accounted by the specific effects of SMG and MTG lesions on the ability to define the hand configuration or the context associated to tool use. A lesion of SMG should result in inappropriate hand conformation, which will affect tool use but also imitation

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tasks because these tasks put strong demands on the ability to adjust the hand posture relative to the tool and/or to the body. Clinical studies converge to show that deficits in actual tool use (Goldenberg and Spatt, 2009) or imitation tasks (Goldenberg and Karnath, 2006) result indeed from SMG lesions. It is worth noting, however, that the causal relationship between SMG and hand posture is not exclusive and that the contribution of the inferior frontal gyrus might also be critical, especially in pantomime tasks (Goldenberg et al., 2007; Bohlhalter et al., 2011) or imitation tasks that require subjects to reproduce complex finger configurations (Goldenberg and Karnath, 2006). The inability to retrieve semantic information necessary to reconstruct the context of tool use, after MTG lesions, should lead to a predominance of tool substitution errors as well as difficulties to match tools according to their function, the sound they emit, or the approximate duration of the action for example. Clinical studies confirmed that patients with such difficulties show overlapping lesions in MTG (Goldenberg and Spatt, 2009; Kalénine et al., 2010; Tranel et al., 2003). Obviously, our results are still insufficient to validate fully this neurofunctional model of upper-limb apraxia since the tasks used in the present study did not require gesturing. In particular, it is unknown whether SMG also contributes to specify the spatial trajectory or the timing of tool use gestures, as predicted by the errors of apraxic patients impaired in pantomime and imitation tasks. Moreover, it is worth noting that, in some patients, conceptual deficits mainly affect the ability to embed segments of actions into a correct sequence (e.g., making coffee or wrapping a gift; Rumiati et al., 2001; Schwartz et al., 1998). Recent studies suggest that the hierarchical processing of actions rather depends on frontal areas (Clerget et al., 2009; Fazio et al., 2009; Goldenberg et al., 2007). Further research is therefore needed to elucidate these issues but we believe that focussing on the causal relationship between brain damage and cognitive functions should help us to establish fine-grained distinctions between the clinical profiles observed in upper-limb apraxia.

5. Conclusion

Whereas fMRI studies showed that the cortical network underlying tool processing is very large and encompasses both the ventral and dorsal streams, the present study highlights the distinct contribution of two main nodes of this circuit in implementing different characteristics of tool representation. Indeed, we found that SMG plays a role in processing incoming information about tools to shape hand posture, whereas MTG ensures the retrieval of semantic information necessary to create a contextual representation of tool use. These findings illustrate how neuromodulation data could help us to decipher the cognitive underpinnings of tool use disorders in the near future.

Acknowledgements

This work was supported by grants from the "Actions de recherches concertées" (ARC, Académie Louvain), the Fonds

Spéciaux de Recherche (FSR) of the Université catholique de Louvain and the "Fonds de la Recherche Scientifique Médicale" (FRSM). M.A. was a Postdoctoral Researcher at the "Fonds National de la Recherche Scientifique" (FRS-FNRS). B.P. was a Research Fellow at the "Fonds National de la Recherche Scientifique" (FRS-FNRS).

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2012.11.013.

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