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TMS-induced modulation of action sentence priming in the ventral premotor cortex

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ABSTRACT

Despite accumulating evidence that cortical motor areas, particularly the lateral premotor cortex, are activated during language comprehension, the question of whether motor processes help mediate the semantic encoding of language remains controversial. To address this issue, we examined whether low frequency (1 Hz) repetitive transcranial magnetic stimulation (rTMS) of the left ventral premotor cortex (PMv) can interfere with the comprehension of sentences describing manual actions, visual properties of manipulable and non-manipulable objects, and actions of the lips and mouth. Using a primed semantic decision task, sixteen participants were asked to determine for a given sentence whether or not an auditorily presented target word was congruent with the sentence. We hypothesized that if the left PMv is contributing semantic information that is used to comprehend action and object related sentences, then TMS applied over PMv should result in a disruption of semantic priming. Our results show that TMS reduces semantic priming, induces a shift in response bias, and increases response sensitivity, but does so only during the processing of manual action sentences. This suggests a preferential contribution of PMv to the processing of sentences describing manual actions compared to other types of sentences.

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1. Introduction

How do listeners process the speech signal to understand language? Do linguistic–semantic representations draw on sensory-motor experiences? The extent to which language and other cognitive processes are grounded in sensory-motor representations (i.e., embodied) has been debated for centuries, often as part of a more general discussion of the relation between mind and body. The idea of a separation between mind and body was already present in the writings of Greek philosophers such as Plato about 400 years BC, but was formalized in the 17th century by René Descartes (1637). More recently, cognitive neuroscience has been built on deconstructing the mind-body dualism. An important practical problem for dualism arose with the Piagetian notion that knowledge is acquired through sensory and motor experiences (e.g., Piaget & Inhelder, 1969), and over the past decade, the issue of cognitive and language embodiment has resurfaced again and has led to heated debates. This resurgence of interest is largely due to the discovery of "mirror neurons" in the macaque ventral

premotor cortex (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Mirror neurons are neurons that discharge when a monkey executes a specific goal-directed action or when he observes a similar action; these sensory-motor neurons appear to be involved in action understanding (see for example Rizzolatti & Craighero, 2004). This major breakthrough was quickly followed by attempts to identify regions with analogous properties in the human brain, and with some caveats, the data support the existence of a number of such regions. One such region in the frontal lobe is found in the posterior part of the inferior frontal gyrus (IFG) and in the ventral premotor cortex (PMv) (e.g., Buccino et al., 2001, 2005; Buccino, Sato, Cattaneo, Roda, & Riggio, 2009; Decety, Chaminade, Grezes, & Meltzoff, 2002; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Grafton et al., 1996; Grezes et al., 2001; Hari et al., 1998; Iacoboni et al., 1999). According to advocates of language embodiment (e.g., Beilock et al., 2008; Gallese & Lakoff, 2005; Glenberg, 1994; Fischer & Zwaan, 2008; Martin & Chao, 2001; Pulvermuller, 1996, 2001), understanding the meaning of action words and sentences involves activating the motor circuits required to produce the action being described. For instance, hearing the word "kick" would engage neural circuits overlapping with those involved in kicking. One postulate is that the relation between action, language and the motor system is mediated by a putative human mirror neuron system with mirror properties and involves an automatic action

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simulation process that is necessary to comprehend action words and sentences (e.g., Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Buccino et al., 2001; Tettamanti et al., 2005). Alternatively, linguistic representation may be embodied via other kinds of mechanisms not involving neurons with mirror-like properties. Furthermore, grounding of word meaning into motor circuits may or may not be an automatic and necessary part of language comprehension.

Consistent with the general idea of language embodiment, behavioral studies have shown evidence for a link between actions and language (Chambers et al. (2004); Gentilucci, Benuzzi, Bertolani, Daprati, & Gangitano, 2000; Glenberg & Kaschak, 2002; Glenberg, Sato, & Cattaneo, 2008; Glenberg, Sato, Cattaneo, Riggio, et al., 2008; Sato, Mengarelli, Riggio, Gallese, & Buccino, 2008). Moreover, several brain imaging studies have revealed increased activation in motor regions, primarily in the ventral premotor cortex (PMv) during auditory word/sentence listening/reading (e.g., Aziz-Zadeh et al., 2006; Hauk, Johnsrude, & Pulvermuller, 2004; Tettamanti et al., 2005; Tremblay & Small, 2011; Skipper, Nusbaum, & Small, 2005). In particular, in a previous study, we showed that listening to and repeating action and object-related sentences activate the left PMv (Tremblay & Small, 2011). Nevertheless, brain-imaging studies, for all their advantages, cannot answer the question of whether PMv is critical or accessory to language comprehension, and further, whether the importance of PMv depends upon the semantic content of the sentences. Indeed, some authors argue that activation in PMv is not related to semantic analyses *per se*, but rather reflects processes secondary to linguistic interpretation, as might be expected in a complex neural network mediating modality-independent comprehension (see Mahon & Caramazza, 2008, and Hickok, 2009, for critical reviews of the "mirror neuron theory" of language).

One useful approach to solving this problem is to use brain stimulation methods such as transcranial magnetic stimulation (TMS) to reveal potential causal relationships (or lack thereof) between specific brain regions and cognitive and linguistic processes. TMS can be used to temporarily and non-invasively disrupt the function of a given cortical region, thereby creating what is often referred to as a reversible (or "virtual") lesion. Virtual lesions have been described as "*a means of adding neural noise to a task*" (Walsh & Pascual-Leone, 2003). The study of "virtual" lesions has advantage over the study of "real" lesions in that it is not complicated by compensatory mechanisms (e.g., plasticity) and it has precise spatial localization of a few centimeters (see for example Paus, 1999; Paus & Wolforth, 1998). Hence, the idea here is to create a lesion in the left PMv to determine whether this region is critical for language comprehension. This approach has been used by Buccino et al. (2005), Pulvermuller, Hauk, Nikulin, and Ilmoniemi (2005) and Glenberg, Sato, Cattaneo, Riggio, et al. (2008) to test the role of the primary motor cortex during action verb and sentence processing, and by Cattaneo, Devlin, Salvini, Vecchi, and Silvanto (2010) to demonstrate that the left PMv contributes category-specific semantic information during word processing. In the Cattaneo et al. study, participants were primed with the word "Tool" or the word "Animal", and then presented with a target word belonging to one or the other category. Participants made a forced choice on whether the target word was a tool or an animal. Under normal circumstances, this type of decision is faster when the prime and the target words are congruent (i.e., it results in a facilitation effect, called "semantic priming", Meyer & Schvaneveldt, 1971). When a single TMS pulse was applied over the left PMv, it reduced priming in the congruent tool trials (i.e., trials in which the prime was the word "Tool" and the target was a tool word). In contrast, identical stimulation had no effect when the target stimulus was an exemplar of the "Animal" category, regardless of whether the target word was congruent or incongruent with
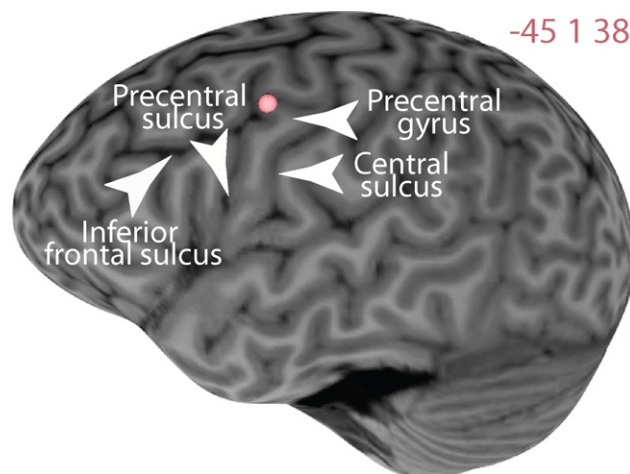

Fig. 1. Mean location of the rTMS stimulation and associated Talairach coordinates in the ventral premotor cortex (PMv), shown on the lateral surface of a Brainsight 3D rendered brain.

the prime. These results provide evidence that PMv is contributing semantic information in a category-specific way.

In the present study, we sought to extend these results by examining whether stimulation of the left PMv interferes with sentence processing in relation to different semantic content. To investigate this issue, sixteen healthy right-handed participants underwent rTMS (1 Hz, 15 min, 110% of the resting motor threshold) and sham stimulation to the left PMv (Fig. 1) and subsequently performed a primed semantic decision task. On each trial, a sentence was presented auditorily through loudspeakers, and was quickly followed by a single word, also presented auditorily, which was either congruent (e.g., "I plug the cable"/"outlet") or incongruent ("The hammer is rusty"/"gown"), with the sentence meaning. Participants performed a two-button alternative forced choice on whether or not the target word was congruent with the sentence. The sentences described manual, object-directed actions (e.g., "I plug the cable."), visual properties of manipulable objects (e.g., "The cable is long."), visual properties of non-manipulable objects (e.g., "The roof is flat."), and orofacial actions (e.g., "I smack my lips."). We chose to use sentences describing manual actions and manipulable objects based on our previous finding of strong brain activation in PMv while participants processed and produced action and object sentences (Tremblay & Small, 2011). In that study, PMv was strongly activated for both object sentences and action sentences. Hence, here we wanted to examine whether rTMS would disrupt semantic priming in both action sentences and object sentences. Sentences describing non-manipulable objects were added to test whether comprehending sentences describing objects with fewer motor affordances would also require a contribution of PMv. Finally, the sentences containing orofacial actions were included to test the specificity vs. generality of the contribution of PMv to semantic processing. Indeed, previous neuroimaging studies have shown distinct activation peaks in the ventral premotor cortex and the inferior frontal gyrus during the semantic processing of manual vs. orofacial action-related language, respectively (Hauk et al., 2004; Tettamanti et al., 2005). Based on these findings, if PMv is specifically involved in the processing of either of these types of semantic content, then stimulation of this region should disturb semantic priming on congruent/incongruent trials, compared to no stimulation. Furthermore, since listening to action- and object-related sentences has been shown to activate the left PMv (Tremblay & Small, 2011), we expected rTMS to decrease semantic priming in the action and manipulable object sentences.

2. Material and methods

2.1. Participants

Sixteen healthy right-handed (Oldfield, 1971) native speakers of English (mean 20.37 ± 1.32; 7 males), with a mean of 13.75 ± 1.4 years of education, were recruited to participate in this experiment. All participants had normal pure-tone thresholds and normal speech recognition scores (95.75% accuracy on the Northwestern University auditory test number 6). The Institutional Review Board for the Division of Biological Sciences at The University of Chicago approved the study. Participants were screened for any relative or absolute contraindication to rTMS before their arrival at the laboratory and again upon their arrival, and were excluded if any of these were present (Wasserman, 1998, updated in Rossi, Hallett, Rossini, & Pascual-Leone, 2009). Informed written consent was obtained from each participant.

2.2. Experimental procedures

The experiment entailed two visits on two different days. During the first visit, participants underwent structural magnetic resonance imaging and a set of behavioral tests, including (1) the Edinburgh Handedness Inventory; (2) a standard semantic (category) fluency task (animals and vegetables), (3) audiometric testing to evaluate hearing (pure-tone air conduction thresholds for the following frequencies: 250, 500, 1000, 2000, 3000, 4000, 6000, and 8000 Hz), and (4) speech discrimination testing (SDT) to evaluate participants' ability to identify speech sounds. Speech discrimination procedures measure a person's ability not only to hear words but also to identify them. We used the Northwestern University auditory test number six (form A). The procedure includes the presentation of 50 monosyllabic words at an easily detectable intensity level and the calculation the percentage of words correctly identified.

The second visit was divided into two 15-min sessions during which participants underwent rTMS and sham stimulation. The rTMS and sham sessions were separated by 1 h and fully counterbalanced across participants. Following completion of each session, participants had to complete two tasks: (1) a simple reaction time task (control) and then (2) a primed semantic decision task. During both tasks, participants were seated on a padded armchair in front of a computer monitor. During the control task, participants fixated a small crosshair presented in the middle of a computer screen. On each trial, the crosshair moved to the left or to the right. Participants were asked to determine the direction of movement as quickly as possible by pressing one of two buttons on a keyboard with their right-hand. For the primed semantic decision task, a set of short concrete sentence was presented through loudspeakers, at a level that was individually adjusted for each participant. Each sentence was followed, after 500 ms, by a congruent or incongruent target word representing an object or an object part (but not an action) (e.g., "The hammer is rusty"/"Nail"; "I cut the tape"/"Milk"). Participants were asked to decide whether the target word was semantically related to the sentence by pressing one of two keyboard buttons as quickly as possible with their right-hand (2-alternative forced-choice). The response key designation was fully counterbalanced across participants. Half the sentence-word pairs were congruent. If participants failed to respond, the trial was automatically terminated after 2000 ms.

The stimuli consisted of 240 sentences that were recorded in a soundproof booth by a male speaker and digitized to disk. The resulting sound files were intensity normalized using Sound Studio 3 (Felt Tip Software) and each sound file length was set to 1800 ms. The sentences were divided into four semantic categories: (1) object-directed manual actions (e.g., "I squeeze the ball"), (2) manipulable objects (e.g., "The ball is red"), (3) non-manipulable objects ("The nursery is pink") and (4) orofacial actions ("I bite my lower lip"). The same set of object words was used in the manipulable object and manual action conditions. The sentences were matched on number of syllables ($F_{(3,236)} = .185$, $p = .91$) and number of words ($F_{(3,236)} = 1.83$, $p = .14$), with an average of 5.51 syllables (±1.2) and 4.57 words (±.95) across sentence types.

In addition to the sentences, a set of 240 target words (all nouns) was recorded by the same speaker. In order to compare the linguistic properties of the target words across sentence types, we ran a series of one-way ANOVAs for each property that we controlled for (familiarity, frequency, imageability, concreteness and number of syllables). These linguistic properties were extracted from the MRC Psycholinguistic Database available online at http://www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm, with the exception of the word frequency, which was extracted from the SUBTLEXus database (Brysbaert & New, 2009), available online at http://expsy.ugent.be/subtlexus/. None of the following showed a main effect of condition: familiarity (printed) ($F_{(3,221)} = 1.10$, $p = .65$), concreteness ($F_{(3,163)} = .63$, $p = .60$), imageability ($F_{(3,165)} = 1.02$, $p = .39$), frequency ($F_{(3,239)} = 1.86$, $p = .14$). The number of syllables per target word was similar across the different sentence types ($F_{(3,221)} = 1.25$, $p = .31$).

This experimental setup resulted in a 4 × 2 × 2 design with Sentence (Manual action, orofacial action, manipulable object and non-manipulable object), Congruency (congruent, incongruent) and Stimulation (SHAM/TMS) as within-subject factors. There were 240 trials in total, which were equally divided into 8 conditions comprising 30 trials each. During the experiment, all conditions were presented in a pseudo-random order, with the constraint that the same condition could not repeat on more than two consecutive trials. Half of the trials were presented after sham stimulation, the other half after rTMS. Trial assignment was randomized for

each subject. In addition to the priming task, participants also completed a short control experiment (20 trials) during which they watched a moving target ("+") on a computer screen and, on each trial, had to determine whether it moved to the left or to the right. The control task was performed immediately after each stimulation period, TMS and sham (henceforth SHAM). Each trial ended when a response was recorded or after 2000 ms if no response occurred. This task was included to control for a potential motor effect of rTMS, and it was performed after the rTMS and sham sessions.

2.3. Transcranial magnetic stimulation

2.3.1. MRI acquisition and co-registration

A high-resolution T1-weighted MRI scan was obtained for each participant on a Philips Achieva Quasar Dual 16 Channel 3T MRI scanner (Phillips, Andover, USA) at The University of Chicago (matrix 256 mm × 256 mm, 176 slices, 1 mm × 1 mm × 1 mm, no gap). Once obtained, the anatomical MRI was incorporated into BrainSight 2 (Rogue Research, Montreal, Canada) to guide coil placement. For each participant, an MRI-to-head co-registration was performed. The position of four anatomical landmarks (tip of the nose, bridge of the nose, superior-lateral edge of the tragus of left and right ears), previously identified on participant's MRI, was assessed using an infrared tracking system (Polaris, Northern Digital, Waterloo, Canada). Upon successful co-registration, infrared tracking was used to monitor the position of the coil with respect to the participant's brain.

2.3.2. Resting motor threshold (RMT)

Stimulation was performed with a Double 70 mm Air Film coil combined with a Magstim Rapid2 biphasic stimulator (Magstim Company, Dyfed, UK). The Air film coil allows for quiet, temperature-regulated stimulations using managed ambient airflow and integrated temperature-regulated fan technology. For the determination of each subject's resting motor threshold (RMT), the TMS coil was placed over the participant's left motor cortex hand area with the coil held tangentially to the skull, and the handle pointing posteriorly and inferiorly. Single pulses were delivered to the motor cortex, with the intensity of the stimulation adjusted until a motor evoked potential (MEP) in the right hand was visually observed by one of the investigators in 5 out of 10 trials. The location of the stimulation was adjusted to locate the maximally excitable hand area of the precentral gyrus.

2.3.3. rTMS stimulation

The intensity of the stimulation was set at 110% of participants' RMT, which ranged from 60 to 81% of the output capacity of the stimulator, with a mean of 68%. The coordinates of stimulation sites were determined individually for each participant using Brainsight 2 software based on their own macroscopic gyral anatomy. First, we identified the inferior frontal sulcus (IFS) and the precentral gyrus. The stimulation site was then set to the anterior most part of the precentral gyrus at the level of the IFS, corresponding to the superior part of the ventral premotor cortex (sPMv). This stimulation site was based on a previous fMRI study during which participants were presented with similar action and object-related sentences (Tremblay & Small, 2011). In that study, the sPMv was also identified on each individual's cortical surface using the automated parcellation scheme implemented in Freesurfer (Desikan et al., 2006; Fischl et al., 2002, 2004), which uses a probabilistic labeling algorithm that incorporates the anatomical conventions of Duvernoy (1991), and thus is based on macroanatomical landmarks. For this reason, we believe that the procedure for identifying subject-specific stimulation targets in sPMv used in the current study was most appropriate to ensure compatibility with sPMv results reported in Tremblay and Small (2011).

The results of this study show that the left sPMv, is active during the processing of sentences describing actions and objects across a number of tasks (passive listening, repetition and generation). Moreover, the magnitude of the activation in this region was modulated by the semantic content of the sentence (action, object), suggesting of a role for this region in sentence-level semantics. It is for this reason that in the present study, we wanted to examine whether stimulating the sPMv would interfere with sentence processing.

Stimulation was applied in one offline train of 900 pulses delivered at a rate of 1 Hz for 15 min. This type of design is usually referred to as "conventional slow", or "low frequency", rTMS protocol (Rossi et al., 2009). Here we used a conventional slow paradigm with an intensity level of 110% of RMT, that is, a low frequency–high intensity protocol or LFHI. Similar rTMS protocols have been shown to produce inhibitory modulation of motor cortical excitability (Fierro et al., 2001; Fitzgerald, Fountain, & Daskalakis, 2006). Moreover, we previously used similar parameters to decrease the sensitivity of sPMv during phonological tasks (Sato, Tremblay, & Gracco, 2009). These stimulation parameters resulted in a disruption in behavioral performance during a phonological segmentation task. Therefore, based on these previous studies, here we used a LFHI protocol to inhibit activation in sPMv during sentence processing. Importantly, these parameters are well within the published Safety Guidelines for rTMS (Wasserman, 1998, revised in Rossi et al., 2009).

To control for some of the sensations that participants experience during rTMS, we used sham stimulation, during which a tape-recorded sample of the discharging stimulator (which produces a relatively loud clicking sound) was presented through small computer speakers located close to the participant to control for the acoustic stimulation experienced during rTMS. Moreover, the coil was positioned on the

scalp exactly as it was during the rTMS stimulation, thereby approximating the scalp contact experienced during rTMS. The rTMS and sham sessions were separated by 1 h and fully counterbalanced across participants. The use of sham as a control condition is helpful to establish that any rTMS-related effect is not related to the unspecific effect of the sensations associated with rTMS, though it does not account for the sensations associated with actual scalp stimulation.

At the beginning of the session, participants were told that they were to experience brain stimulation at various intensity levels; they were not told that they were to experience sham stimulation. To further establish the specificity of the observed effects, we also used a control task (simple reaction time) described in a previous section. The use of a control task is helpful in establishing whether stimulation to a region, regardless of the task, can affect behavior (i.e., it tests for an effect of stimulation specificity). Used jointly, these controls (sham stimulation, control task) help establish the specificity of the stimulation.

2.4. Data analysis

2.4.1. Control task

For the analysis of RT in the control task, we sought to make sure that TMS to PMv did not decrease RT or accuracy in a simple choice-reaction time task, thereby making unreliable our dependent measure. We therefore computed two planned repeated measure contrasts (Jaccard, 1998; Rosenthal, Rosnow, & Rubin, 2000). For this analysis, we removed error trials and data points that were two standard deviations above or below the mean for each participant. In all, 9% of trials contained errors of omission or commission (337 trials) and 3503 trials contained none. Of these error-free trials, 121 (mean per subject 7.56 ± 2.25) were removed because RT fell within our definition of outliers, leaving a total of 3382 trials in the analysis, representing over 88% of all experimental trials. The resulting RTs were log transformed to satisfy the assumption of normal distribution. Accuracy was defined as the percentage of correct responses for each subject. Errors included both misses (no response) and incorrect responses.

2.4.2. Primed semantic decision task

2.4.2.1. RT. For the primed semantic decision task we first compared the RT for the congruent and incongruent trials to examine the effectiveness of our priming paradigm in inducing a facilitation effect (shorter RT's) in the congruent trials compared with the incongruent trials. RT was defined as the time from the target stimulus offset to the onset of the subject's response. Outliers, defined as data points that were two standard deviations above or below the mean for each participant and each condition, were removed from the analysis. Error trials were also removed from this analysis. RTs were log transformed to satisfy the assumption of normal distribution.

We then calculated an index of semantic priming by subtracting the mean RT in the congruent trials from the mean RT in the incongruent trials for each participant. A positive value indicates that mean RT in the congruent trials was faster than in the incongruent trials, which indicates a facilitation effect. These values were first entered in a 4×2 ANOVA with repeated measures on sentence (manual action, orofacial action, manipulable object and non-manipulable object) and stimulation (SHAM, TMS).

To better interpret these results, we performed an analysis of the degree of priming associated with particular sentence types. We did this by measuring facilitation effects in the sham trials using one-sample t-tests against zero. To evaluate the extent to which TMS can modulate priming, we compared these priming scores for the TMS and SHAM trials, for the sentence types that were associated with the expected facilitation using a set of focused, FDR-corrected planned repeated measure contrasts.

2.4.2.2. Accuracy. For accuracy, our hypothesis was that TMS would reduce accuracy, and that, consequently, there should be a difference in participants' accuracy patterns during TMS and SHAM. To test this hypothesis, we conducted FDR-corrected repeated measures comparisons, one for each semantic condition showing the expected RT facilitation effect during SHAM, comparing the percentage of correct responses for each sentence type, during SHAM and TMS. The percentage of correct responses was calculated separately for each experimental condition for each subject. Errors included both misses and incorrect responses.

2.4.2.3. Sensitivity and response bias. In addition to looking into participants' accuracy, we also calculated (1) a measure of bias-corrected sensitivity or d-prime (d'), which measures the extent to which participants can discriminate between related and unrelated pairs (a d' of zero indicates chance discrimination) and (2) a measure of response bias (β), which measure an individual's disposition toward one response or another (congruent vs. incongruent). Increases in d' indicate improvements in discrimination ability, whereas decreases in d' indicate a decrease in discrimination ability. This analysis was carried out to examine whether rTMS influences sentence processing, more specifically, to test if rTMS modulates the ability to determine whether a sentence and a target word are semantically related. For each subject, we computed the hit rate in the congruent trials (i.e., the rate of choosing congruent when congruent) for each sentence type for the sham and rTMS trials separately, as well as the false alarm rate in the incongruent trials (i.e., the rate of choosing congruent when incongruent). For hit rates of 1.0 or false alarm rates of 0, a correction

was applied. False alarm rates of zero were corrected using the following formula: $1/(2N)$ where N is the maximum number of false alarms. For hit rates of zero, we used the following correction: $1 − 1/(2N)$, where N now represents the number of targets. The d' for 2-alternative forced choice (2AFC) paradigm was calculated according to the following formula: $d'(2\text{AFC}) = \sqrt{2}[z(\text{hit rate}) − z(\text{false alarm rate})]$, as described in Macmillan and Creelman (1991) (see http://psy2.ucsd.edu/~kang/sdt/sdt.htm). A set of focused contrasts was then computed to examine the effect of TMS separately for each of the sentence types. Response bias (β) was calculated using the following formula: $\beta_{(2\text{AFC})} = e^{(d'^* \sqrt{2}(z(\text{hit rate}) + z(\text{false alarm rate})))/−2}$. All statistical analyses were conducted using PASW 18 (SPSS Inc., Chicago, IL).

3. Results

3.1. Control task

Participants' performance in the control task was not affected by rTMS. Participants' reaction times were similar after rTMS and after sham stimulation, with a mean of 322.77 ms after sham, and a mean of 322.16 ms after rTMS ($t_{(15\text{df})} = .06$, $p = .95$). Likewise, the number of accurate responses was unaffected by rTMS, with a mean percentage of correct responses of 94.33% after sham, and 96.33% after TMS ($t_{(15\text{df})} = .84$, $p = .42$).

3.2. Primed semantic decision task

3.2.1. Reaction time (RT) for correct responses

The results of the repeated-measure ANOVA revealed a significant main effect of sentence ($F_{(3,45)} = 4.42$, $p = .008$), and a significant main effect of Stimulation ($F_{(1,15)} = 5.92$, $p = .028$), with decreased priming after TMS compared to SHAM (means $\pm$ SD: 22 ms $\pm$ .041, 3 ms $\pm$ .037), but no Sentence by TMS interaction ($F_{(3,45)} = .82$, $p = .49$).

Although no sentence by TMS interaction was observed in the ANOVA, a series of one-tailed paired-sample t-tests revealed that only the manual action sentences ($t_{(15\text{df})} = 3.414$, $p = .002$) and the manipulable object sentences ($t_{(15\text{df})} = 1.93$, $p = .036$) showed the expected facilitation effect, but no such effect was found for the non-manipulable object ($t_{(15\text{df})} = −.93$, $p = .18$) and the orofacial action sentences ($t_{(15\text{df})} = .10$, $p = .46$).

The results of this analysis are shown in Fig. 2. To further test a possible TMS-induced modulation of semantic priming, the remaining analyses therefore focused on the manipulable object sentences and on the manual action sentences.[1] As shown in Fig. 3, additional RT analyses revealed a significant reduction of priming (incongruent RT − congruent RT) following TMS for the manual action sentences ($t_{(15\text{df})} = 2.88$, $p = .011$, $q = .025$), but not for the manipulable object sentences ($t_{(15\text{df})} = 1.17$, $p = .26$). As can been seen in the figure, for the manual action sentences, the facilitation effect for the congruent trials disappears following TMS.

3.2.2. Accuracy

The percentages of correct responses for each condition are listed in Table 1. Given that semantic priming during SHAM was only observed for manipulable object and manual action sentences, the analysis of accuracy focused on these sentences. These analyses revealed a significant effect of TMS on the percentage of accurate responses for the manual action sentences ($t_{(15\text{df})} = −2.2$, $p = .022$; $4.58\% \pm 8.33$ SEM): participants were less accurate in the congruent than in the incongruent trials in the Sham trials; following rTMS,

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[1] We did not conduct further analyses on the two types of sentences for which no priming effect was found (non-manipulable object sentences and orofacial action sentences), because the objective of this study was to examine how rTMS to PMv could disrupt priming, which would require the presence of priming in the SHAM trials. It is possible that some intrinsic properties of these semantics categories could have interfered with the task leading to the observed absence of a semantic priming effect, such as concreteness and semantic neighborhood density.
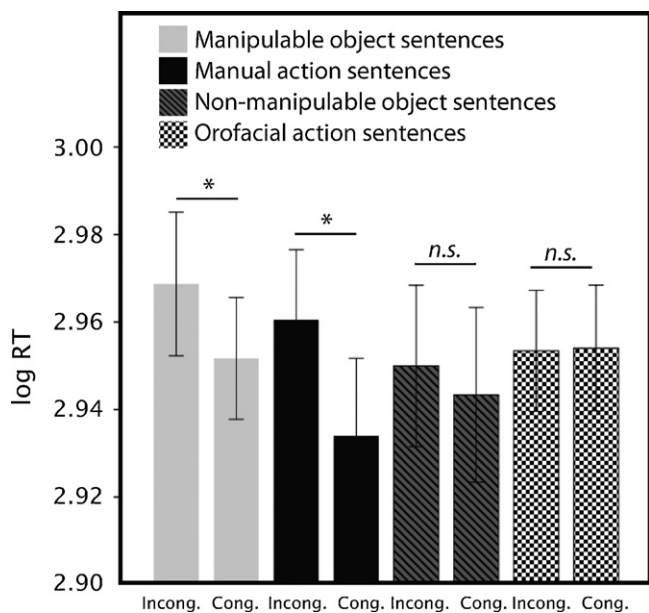
Fig. 2. RT for each of the sentence type, presented separately for the congruent and incongruent trials. Note the facilitation effect (faster RTs) for the manipulable object and manual action sentences. Error bars represent the confidence interval of the mean. The asterisks indicate a statistically significant difference while "n.s." indicates a non-significant difference.
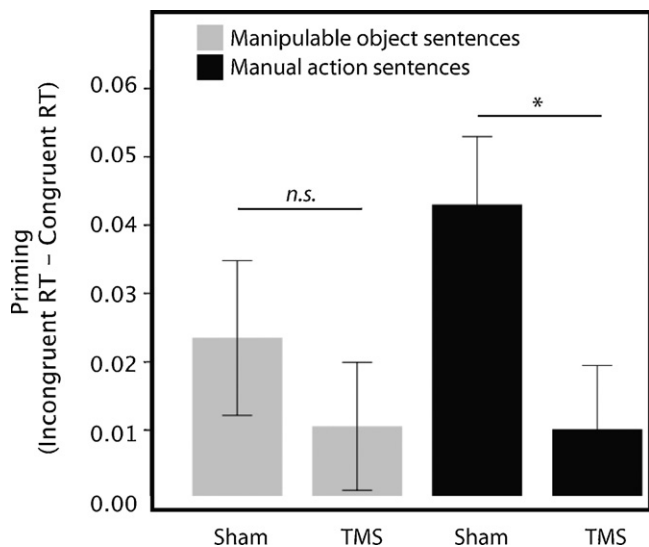

Fig. 3. Effect of prime-target congruency on RT for the manipulable object and manual action sentences, during Sham and TMS. Note the significant decrease in priming for the manual action sentences following rTMS. Error bars represent the confidence interval of the mean. The asterisks indicate a statistically significant difference. n.s. indicates a non-significant difference.

Table 1

Percentage of accurate responses in the primed semantic decision task.

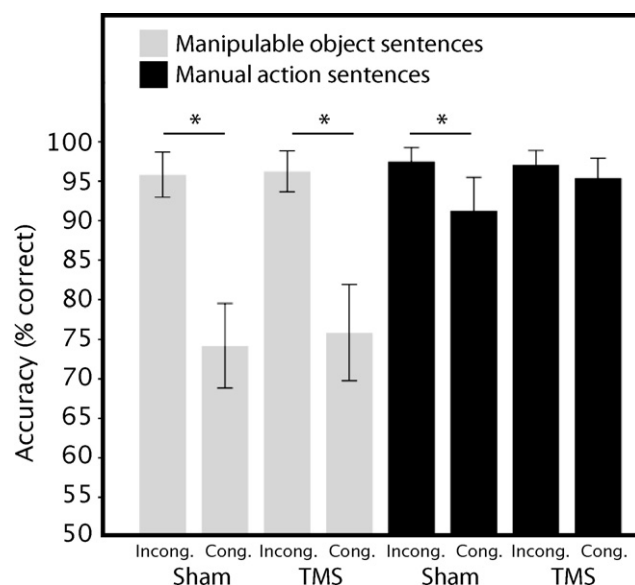| Sentence type	Trial type	Percentage of accurate responses
Non-manipulable object sentences	Congruent	87.5
	Incongruent	96.9
Manipulable object sentences	Congruent	75.0
	Incongruent	96.0
Manual action sentences	Congruent	93.3
	Incongruent	97.3
Oro-facial action sentences	Congruent	89.2
	Incongruent	96.7

Fig. 4. Effect of prime-target congruency on accuracy measured as percentage of correct responses, separately for the Sham and TMS trials, for the manipulable object and manual action sentences, Error bars represent the confidence interval of the mean. The asterisks indicate a statistically significant difference in accuracy for congruent and incongruent trials.

participants' accuracy was similar in the congruent and incongruent trials. No such effect was found for the manipulable object sentences ($t_{(15df)} = .337$, $p = .37$; $1.25\% \pm 14.85$ SEM), where participants were more accurate in the congruent than the incongruent trials, before and after TMS. Fig. 4 shows the accuracy results for the manipulable object sentences and the manual actions sentences during SHAM and rTMS trials.

3.2.3. Sensitivity (d′) and response bias

To further examine the effect of rTMS on participants' performance, more specifically, to examine a possible rTMS-induced shift in sensitivity, we computed a measure of unbiased sensitivity (d′). A set of focused contrasts indicated that rTMS slightly, but significantly, shifted sensitivity in the manual action sentences ($t_{(15df)} = 2.3$, $p = .036$). The mean sensitivity ($\pm$SD) was 2.2 ($\pm$.3 SD) following SHAM and 2.4 ($\pm$.2 SD) following rTMS. No such shift was found for the manipulable object sentences ($t_{(15df)} = .029$, $p = .98$). Fig. 5 shows the d′ values for manipulable object and the manual actions sentences during SHAM and rTMS trials.

In addition, we also examined a potential change in response bias by computing response bias (β), which measures an individual's disposition toward one response or another (congruent vs. incongruent) in the manipulable action sentences following SHAM and rTMS. A paired directional sample t-test indicated a slight decrease in response bias following rTMS ($t_{(15df)} = 2.11$, $p = .026$). The mean response bias (toward responding "incongruent") was higher in the SHAM trials (1.81 ± 1.03 SD) than in the rTMS trials ($1.36 \pm .71$ SD).

4. Discussion

In the present study, we asked whether the motor system – more specifically the left ventral premotor cortex – contributes information that is critical to comprehend sentences with different semantic content. The relation between mind and body has fascinated scientists for centuries, yet many questions remain highly contentious today. Regarding the present study, the main point of contention is related to the importance of sensory and motor information in the comprehension of meaningful linguistic units such as
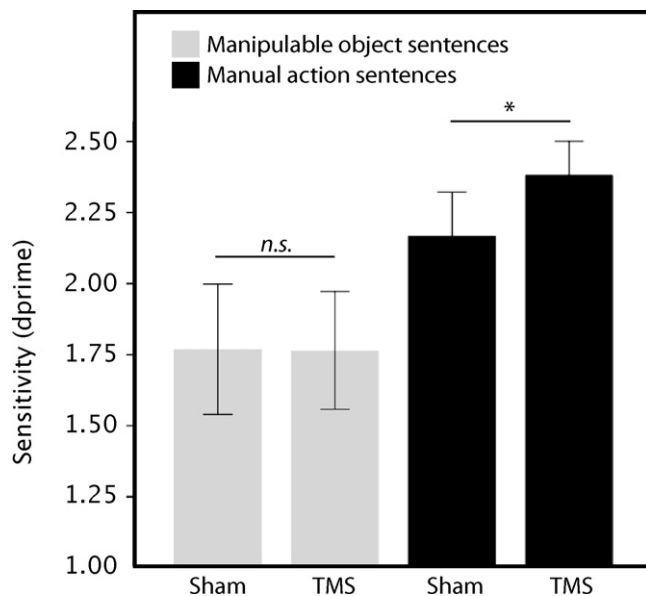
Fig. 5. d' (sensitivity) values for the manipulable object and manual action sentences, Error bars represent the confidence interval of the mean. The asterisks indicate a statistically significant difference in sensitivity during sham and TMS. n.s. indicates a non-significant difference.

words and sentences. For instance, does understanding the word "grasp", *depend on* activating the neural circuits associated with the physical act of grasping, or can the meaning of this word be understood without engaging these motor circuits, using only a symbolic (disembodied) representation of grasping? In the present study we used repetitive transcranial magnetic stimulation (rTMS) to create a reversible "lesion" to the left ventral premotor cortex (PMv) and examined the consequences of the lesion on the processing of sentences describing first person actions and objects. This is the first study, to the best of our knowledge, to examine the issue of language embodiment by looking at the effect of a virtual lesion to PMv during a sentence-processing task.

The main finding of this study is that inhibitory rTMS to the left PMv modulates the processing of sentences describing manual actions, an effect that is not found during the processing of object-related sentences. This modulation is manifested behaviorally in three different ways: (1) as a shift in response bias; (2) as an increase in sensitivity; and (3) as a decrease in semantic priming following rTMS. More specifically, in the absence of rTMS, participants were faster in responding to congruent trials compared to incongruent trials (semantic priming), and consequently, they also made slightly more mistakes (although accuracy was high throughout), reflecting a slight bias toward responding "incongruent". Semantic priming refers to the well-established finding that participants respond faster to a target word when it is preceded by a semantically related (congruent) word than when it is preceded by an unrelated (incongruent) word (e.g., Meyer & Schvaneveldt, 1971). Following rTMS, this facilitation effect was lost; that is, participants were equally fast on the congruent and incongruent trials; their performance accuracy increased, as well as their sensitivity. Finally, their tendency to respond "incongruent" disappeared. In sum, rTMS appears capable of modulating sentence processing on multiple levels, not only influencing processing speed, but also response patterns. Importantly, these rTMS-induced changes were highly specific, only occurring when participants processed action-related sentences.

Two main conclusions can be drawn from these findings. First, these results suggest that the left PMv is involved in comprehension-related processes, at least during the processing of

short concrete first person sentences describing manual actions. This effect cannot be attributed to a general slowing of RT, for there was no effect of rTMS on the simple RT task that was used as control. Here we contend that the effect that we observed is specifically related to a disruption in the semantic priming of sentences describing manual actions *per se*, which suggests that the left PMv is an integral part of a distributed sentence comprehension network. Admittedly however, participants were still capable of comprehending the manual action sentence tasks following rTMS despite the observed behavioral changes, consistent with the notion that the left PMv participates in the process, but may be used in certain situations to decrease ambiguity but not others. We postulate that this is based on the value of the motor information, the costs of computing it, and its utility. It is possible that PMv is particularly important for language comprehension in cases where covert simulation or motor imagery would resolve the meaning of an otherwise ambiguous sentence describing an action.

It is also possible that the role of PMv during language processing is related to post-lexical processes such as post-lexical meaning integration mechanisms, post-lexical semantic relatedness judgments or even motor imagery, particularly because our stimulus onset asynchrony (SOA) was long, providing more time for participants to process the prime sentences, and because we used a task with a binary response mode (related, unrelated). Consistent with a post-lexical hypothesis, Tomasino, Werner, Weiss, and Fink (2007) recently showed that activation magnitude in M1 and PM decreases when people listen to negative action phrases compared to positive action phrases ("Don't grasp" vs. "Do grasp"), a finding that challenges a strong version of a simulation account which predicts that action words should modulate the motor system automatically, independent of the linguistic context. Relatedly, it has been shown that TMS to M1 affects the processing of first person action words more so than that of third person action verbs, suggesting that (Duscherer & Holender, 2005) M1 contribution to language comprehension does not reflect an automatic, obligatory process but rather context-dependent, self-centric processes (Papeo, Corradi-Dell'acqua, & Rumiati, 2011). In the present study, participants performed an explicit semantic judgment task (prime-target association) with long SOAs; our results show that this task is disrupted following rTMS to the left PMv, reflecting the involvement of PMv in either pre- or post-lexical processes, or both. Prior work has shown that priming effects are modulated by the value of the response associated with the target, suggesting that the change in response bias found here likely reflects a change in post-lexical decision process (Duscherer & Holender, 2005). Future studies investigating the role of PMv as well as other premotor areas in language are necessary to gain a more comprehensive understanding of the importance of the information that is contributed by these regions, the kind of processes it informs (pre- vs. post-lexical processes, semantic vs. decisional processes, etc.) and contexts within which this information is integrated.

The second main conclusion that can be drawn from these results is that processing sentences describing first person manual actions relies more heavily on sensory-motor representations in the left PMv than processing sentences describing physical objects. This should not be taken to imply that sensory-motor representations play no part in the conceptual representation of object sentences. On the contrary, there is neuroimaging and neurophysiological evidence for activity of the PMv during object observation (e.g., Binkofski et al., 1999; Buccino et al., 2009; Chao & Martin, 2001; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Grezes, Tucker, Armony, Ellis, & Passingham, 2003). There is also evidence that processing object sentences activates the motor system (Tremblay & Small, 2011), and that state-dependent TMS applied to PMv interferes with priming of tool words (Cattaneo et al., 2010). It could be argued that differences in the structure of the sentences

are driving the difference in the processing of the manual action and object sentences. For instance, the object sentences ended with an adjective (e.g., "The box is blue") while the action sentences ended with a noun (e.g., "I wrap the box"). However, we do not think that the observed effect of rTMS on the manual action sentence is reducible to this structural difference, for it was not present between the orofacial action sentences (e.g., "I kiss the baby") and the manual action sentences, and yet rTMS only affected processing of the manual action sentences. In line with these previous findings, our results suggest that the left superior part of PMv, while involved in the processing of object words, is not absolutely necessary for object-related sentence comprehension. Furthermore, these results also suggest that sensory-motor representations are engaged during linguistic processing in a different manner and to a different extent depending on the specific language task (i.e., word vs. sentence processing). Additional studies are required to further characterize the role of the sensory-motor system in language. Nevertheless, the present study is the first to show that semantic priming can be disrupted by rTMS of the left PMv, suggesting that this region is indeed causally related to the semantic encoding of manual action-related sentences.

Finally, we ought to remark on the fact that the present results emphasize the importance of using different experimental techniques to characterize neural processes associated with complex behavior such as language. Using fMRI, we recently found that the left PMv is strongly active during the processing of both object and action related sentences (Tremblay & Small, 2011). Our current results demonstrate that despite a strong neural response, inhibiting the normal functioning of the left PMv does not affect the ability to process object related sentences.

Acknowledgements

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