Role of medial premotor areas in action language processing in relation to motor skills

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ABSTRACT

The literature reports that the supplementary motor area (SMA) and pre-supplementary motor area (pre-SMA) are involved in motor planning and execution, and in motor-related cognitive functions such as motor imagery. However, their specific role in action language processing remains unclear. In the present study, we investigated the impact of repetitive transcranial magnetic stimulation (rTMS) over SMA and pre-SMA during an action semantic analogy task (SAT) in relation with fine motor skills (*i.e.*, manual dexterity) and motor imagery abilities in healthy non-expert adults. The impact of rTMS over SMA (but not pre-SMA) on reaction times (RT) during SAT was correlated with manual dexterity. Specifically, results show that rTMS over SMA modulated RT for those with lower dexterity skills. Our results therefore demonstrate a causal involvement of SMA in action language processing, as well as the existence of inter-individual differences in this involvement. We discuss these findings in light of neurolinguistic theories of language processing.

KEYWORDS

language embodiment; supplementary motor area; pre-supplementary motor area; fine motor skills; transcranial magnetic stimulation; motor imagery

HIGHLIGHTS

1. The role of medial premotor areas in action language processing is unclear.
2. rTMS was administered over SMA and pre-SMA during an action language task.
3. The results show that SMA is involved in human action language processing.
4. This involvement is correlated with dexterity, but not with motor imagery skills.
5. The impact of rTMS over SMA is stronger for those with lower dexterity.

1. INTRODUCTION

The motor system is known to be engaged during motor-related cognitive tasks such as motor imagery (Decety et al., 1994 ; Roth et al., 1996), action observation (Decety et al., 1994; Grafton, Arbib, Fadiga, & Rissolatti, 1996), speech perception (Pulvermüller, Shtyrov, Ilmoniemi, & Marslen-Wilson, 2006; Tremblay & Small, 2010) and action language processing (Hauk, Johnsrude, & Pulvermüller, 2004 ; Tettamanti et al., 2005). During action language processing, the left motor and pre-motor areas are activated, including the primary motor cortex (M1) (Kana et al., 2015 ; Kana, Blum, Ladden, & Ver Hoef, 2012), the ventral premotor cortex (de Vega et al., 2014 ; Rueschemeyer, Ekman, van Acheren, & Kilner, 2014; Rueschemeyer, Rooij, Lindemann, Willems, & Bekkering, 2010 ; Tremblay, & Small, 2011; Wheatley, Weisberg, Beauchamps, & Martin, 2005), and the dorsal premotor cortex (de Vega et al., 2014 ; de Zubicaray, Arciuli, & McMahon, 2013 ; Kana et al., 2015, 2012). Activation in the supplementary motor area (SMA) and pre-supplementary motor area (pre-SMA), two premotor areas located in the medial wall of the cerebral hemispheres, have also been shown in relation to action language processing. Pre-SMA activation has been observed during the processing of isolated action words (*i.e.*, action verbs and tool nouns) in passive reading and listening (Hauk et al., 2004; Postle, McMahon, Ashton, Meredith, & de Zubicaray, 2008; Tremblay & Small, 2011; Urrutia, Gennari, & de Vega, 2012; Yang & Shu, 2014) and in more complex tasks including grammatical category judgment (de Zubicaray et al., 2013), lexical decision (Rueschemeyer et al., 2010 ; Tomasino, Weiss, & Fink, 2010) and go-no go tasks (Sakreida et al., 2013). Action sentence processing has been associated with the activation of both SMA and pre-SMA (Boulenger, Hauk, & Pulvermüller, 2009 ; de Vega et al., 2014 ; Desai, Binder, Conant, Mano, & Seidenberg, 2011 ; Kana et al., 2015, 2012 ; Moody-Triantis, Humphreys, & Gennari, 2014 ; Schuil, Smits, & Zwaan, 2013 ; Tomasino, Fabbro, & Brambilla, 2014 ; Tremblay & Small, 2011). However, a number of studies did not report activation in either SMA nor pre-SMA during action language processing (Bedny, Caramazza, Grossman, Pascual-Leone, & Saxe, 2008;

Carota, Moseley, & Pulvermüller, 2012; Desai, Conant, Binder, Park, & Seidenberg, 2013; Ghio & Tettamanti, 2010 ; Ghio, Vaghi, Perani, & Tettamanti, 2016; Hauk & Pulvermüller, 2011 ; Hoenig, Sim, Bochev, Herrnberger, & Kiefer, 2008; Kemmerer, Castillo, Talavage, Patterson, & Wiley, 2008; Moody & Gennari, 2010; Raposo, Moss, Stamatakis, & Tyler, 2009; Samur, Lai, Hagoort, & Willems, 2015; Tettamanti et al., 2005, 2008; van Dam, Rueschemeyer, & Bekkering, 2010; van Dam, van Dijk, Bekkering, & Rueschemeyer, 2012; Willems, Toni, Hagoort, & Casasanto, 2010). Hence, the importance and specific role of these regions in action language processing remain far from being elucidated. More generally, the potential role that the motor system plays during action language processing remains unclear, and is still highly debated within the cognitive neuroscience community (Glenberg, Witt, & Metcalfe, 2013; Mahon, 2015; Zwaan, 2014). Moreover, despite accumulating evidence for a role for SMA and pre-SMA in several aspects of language processing and production, these regions are still absent from most neurobiological models of language, partly due to a lack of research focus on the potential involvement of areas other than the “classical language areas” in language processing (Tremblay & Dick, 2016). It is possible that the contribution of SMA and pre-SMA to action language understanding and action semantics is linked to motor-related processes such as motor imagery, the mental process of imagining an action without motor execution. Consistent with this notion, the SMA and pre-SMA are often activated during motor imagery in right-handed healthy adults, as revealed by functional magnetic resonance imaging (fMRI) studies using motor imagery tasks of finger tapping (Berman, Horovitz, Venkataraman, & Hallett, 2012; Burianová, Lee, Grady, & Moscovitch, 2013; Guillot et al., 2008, 2009; Hanakawa et al., 2003; Hanakawa, Dimyan, & Hallett, 2008; Kasess et al., 2008; Lacourse, Orr, Cramer, & Cohen, 2005; Wang, Chen, Gong, Shen, & Gao, 2010; Xu et al., 2014), fist squeezing (Mizuguchi et al., 2013 ; Mizuguchi, Nakata, & Kanosue, 2014a ; Pilgramm et al., 2016), finger or hand extension/flexion (Gérardin et al., 2000 ; Mizuguchi, Nakata, & Kanosue, 2014 b ; Pilgramm et al., 2016), finger opposition (Dechent, Merboldt, & Frahm, 2004; Macuga & Frey, 2012; Sauvage, Poirriez, Manto, Jissendi,

& Habas, 2011; Sharma & Baron, 2013; Solodkin, Hlustik, Chen, & Small, 2004), object manipulation (Johnson, 2002; Oosterhof, Tipper, & Downing, 2012) and other manual actions and movements (Formaggio, Storti, Cerini, Fiaschi, & Manganotti, 2010; Lorey et al., 2009, 2010, 2011; Stippich, Ochmann, & Sartor, 2002; Szameitat, McNamara, Shen, & Sterr, 2012).

The role of motor imagery in action language processing has scarcely been addressed. Only a few studies have investigated the relationship between action language processing and motor imagery (Papeo, Rumiati, Cecchetto, & Tomasino, 2012; Tomasino, Fink, Sparing, Dafotakis, & Weiss, 2008; Tomasino, Werner, Weiss, & Fink, 2007; Willems et al., 2010; Yang & Shu, 2014; Hauk, Davis, Kherif, & Pulvermüller, 2008). Using fMRI, Tomasino et al. (2007) have shown activation in M1 during action word reading and simultaneous motor imagery, but not during action word reading and simultaneous letter detection. This suggests that M1 activation is related to the secondary task (*i.e.*, motor imagery) rather than to action language processing *per se*. In a subsequent study, TMS over M1 was shown to slow reaction times during a motor imagery task but not during action language reading (Tomasino et al., 2008). Yang & Shu (2014) have shown that SMA and pre-SMA are more strongly activated when action verb reading is accompanied by motor imagery than when it is not. In contrast, Willems et al. (2010) showed that motor imagery and action language reading elicited different cortical networks, none of which included SMA or pre-SMA. Across these four studies, however, the lack of separate language and imagery tasks does not allow for a clear distinction between action language and motor imagery processes. In contrast, Papeo et al. (2012) used two separate tasks and showed motor activation (particularly in M1) during reading of action and state verbs after completion of a motor imagery task (*i.e.*, mental rotation of hands, with the explicit instruction to execute motor imagery). However, since motor imagery was tested before the language task, one cannot rule out that motor imagery *primed* motor activation during reading of both action and state verbs. This suggests that the motor activation observed during language processing may have resulted from explicit motor imagery, rather than from the spontaneous use of motor imagery during language processing. Hence, the role of motor imagery during action language processing remains to be clarified.

Interestingly, studies on motor imagery have focused on *explicit* motor imagery, which is the conscious, voluntary act of imagining oneself in action. As Willems et al. (2010) noted, it is unlikely that everyday action language processing would rely upon a conscious self-initiated cognitive process such as explicit motor imagery. *Implicit* motor imagery, on the other hand, is an unconscious cognitive strategy allowing for the completion of other cognitive tasks (Jeannerod & Frak, 1999) such as determining hand laterality in a hand mental rotation task (e.g., Ferri, Frassinetti, Ardizzi, Costantini, & Gallese, 2012). However, only a few studies have examined the neural correlates of implicit motor imagery (de Lange, Helmich, & Toni, 2006; Ferri et al., 2012; Seurinck, Vingerhoets, De Lange, & Achten, 2004 ; Vingerhoets, de Lange, Vandemaele, Deblaere, & Achten, 2002 ; Zapparoli et al., 2014). Results from half of these studies suggest an activation of pre-SMA during the mental rotation of hands (Ferri et al., 2012 ; Zapparoli et al., 2014). Whether action language relies upon implicit motor imagery, and whether pre-SMA is similarly involved in both processes remains to be determined.

To explore the activation of motor and premotor areas during action language processing, a few fMRI studies have examined the direct link between motor execution and action language processing (Hauk et al., 2004 ; Moody-Triantis et al., 2014 ; Peck, Bradbury, Psaty, Brennan, & Holodny, 2009 ; Postle et al., 2008 ; Schuil et al., 2013). In three of these studies, motor execution was used as a localizer task in order to determine whether action language related motor activation was somatotopically organized (Hauk et al., 2004 ; Postle et al., 2008 ; Schuil et al., 2013). Motor execution consisted in repetitive meaningless movements of left and right foot and hand (Hauk et al., 2004 ; Schuil et al., 2013) or of the mouth, tongue and hand (Postle et al., 2008). Hauk et al. (2004) and Postle et al. (2008) showed somewhat somatotopic activation. In contrast, Schuil et al. (2013) showed a lack of somatotopy in motor activation during reading of literal and non-literal action sentences. Instead, activation was modulated by the literalness of sentences, suggesting that the motor system responded to the semantic content of action sentences. Using a different approach, Moody-Triantis et al. (2014) created a motor execution task (*i.e.*, instruction-guided motor execution) and used an action language task (*i.e.*, passive reading), in which action execution and action sentence processing were matched (*e.g.*, “I am pressing both buttons with my right fingers,” “I am pushing one left button”), thus providing both tasks with identical semantic context. Results from this study indicated that SMA was activated during both action execution and action sentence processing, although activation for motor execution was more posterior within SMA. Peck et al. (2009) also compared cerebral activation during a motor task (*i.e.*, sequential finger tapping) and during an action language task (*i.e.*, covert action verb generation) and showed that SMA was activated during motor execution while pre-SMA was activated during action language processing. Since action language processing seems to be related to both SMA and pre-SMA activation, and given that studies comparing motor execution and motor imagery have shown that medial premotor activation was more anterior (pre-SMA) for movement imagery than for movement execution (SMA) (Gérardin et al., 2000 ; Hanakawa et al., 2003 ; Lacourse et al., 2005 ; Lorey et al., 2013 ; Macuga & Frey, 2012), it is conceivable that the processing of action language involves the pre-SMA in relation to motor imagery processes and the SMA in relation to motor execution and late stage motor planning components (e.g., selection of motor plans, movement sequencing).

The present study aimed to clarify the role of SMA and pre-SMA in action language processing, and to determine whether this role is related to implicit motor imagery and/or motor execution mechanisms. Our main hypotheses were that, (1) if action language processing relies (at least in part) upon implicit motor imagery, rTMS to the pre-SMA will impact semantic processing, and this impact will be related to motor imagery abilities, and (2) if semantic processing relies (at least in part) upon motor-related mechanisms, rTMS to the SMA will impact semantic processing, and this impact will be related to motor execution abilities. Specifically, we expected these effects to occur for the processing of human action but not for non-human action sentences.

To achieve these goals, a deep semantic processing task was created and validated as part as Study 1: the *semantic analogy task (SAT)*. SAT consists in listening to analogy sentences such as “ciseaux est à découper ce que crayon est à dessiner”/“scissors is to cut what pencil is to draw” and in determining whether they are true or false. This task was created to induce a deeper semantic processing than is typically required in classical language tasks such as lexical decision. Study 1 included three sub-studies that aimed to validate the tasks that were used in the rTMS experiment (Study 2). Study 1a included online semantic questionnaires to select the best word pairs for the creation of SAT, Study 1b validated SAT, and Study 1c validated the implicit motor imagery expertise task. In Study 2, semantic processing of action language was measured with SAT, motor imagery abilities were measured using a task of mental rotation of hand, and manual motor execution abilities were measured using a standardized manual dexterity task.

2. STUDY 1a: ONLINE QUESTIONNAIRES

A total of 1026 native speakers of Canadian French aged between 18 and 45 years filled the questionnaires in Study 1a. The study was approved by the Committee on research Ethics of the research center of the Institut universitaire en santé mentale de Québec (CR-IUSMQ) (project #2014-378). In two complementary online questionnaires (www.limesurvey.com), participants had to determine the degree to which two French words (*e.g.,* “ciseaux/couper”/“scissors/to cut”) were semantically associated. 256 pairs composed of a verb (64 verbs were tested) and a noun (128 nouns were tested) were tested. Half of the pairs were manual human actions (*e.g.,* “scissors/to cut”), while the other pairs were non-human actions (*e.g.*, “plane/to land”). A one-way analysis of variance (ANOVA) with Action (Human, Non-human) as the independent factor showed that the pairs did not differ across action categories in terms of the number of syllables ($F_{(1,89)} = .941$, $p = 1.34$, $\eta_2 = .01$). In half of the trials, words were highly associated (*e.g.*, “scissors/to cut”) while in the other half they were poorly associated (*e.g.,* “scissors/to draw”). Each verb was presented four times. The strength of semantic association was determined on a six-point Likert scale ranging from 0 to 5. Participants were instructed to answer as fast and as spontaneously as they could. A 2x2 repeated-measure ANOVA with Congruency (Congruent, Incongruent) and Action (Human, Non-human) as within-subject factors was performed on the percentage of correct responses using SPSS (23.0.0.2, IBM) for Macintosh. There was a significant effect of Congruency ($F_{(1,59)} = 3091.98$, $p < .001$, $\eta_2 = .98$), confirming that highly semantically associated pairs were significantly different from the poorly associated pairs. There was no other effect. All 256 word pairs tested in these questionnaires were used in the behavioural validation of SAT.

3. STUDY 1b: BEHAVIOURAL VALIDATION OF SEMANTIC ANALOGY TASK (SAT)

Ten healthy native speakers of Canadian French participated in this validation study (6 females, mean age 27.10, SD = 7.75). Participants were recruited through emails sent to Université Laval students and employees, and posters distributed within the general community of Quebec City. They were right-handed (Oldfield, 1971), had normal or corrected-to-normal vision and no self-reported history of speech, voice, language or neurological disorder. Participants were screened for normal cognitive functioning using the Montreal Cognitive Assessment (MoCA) (Nasreddine et al., 2005). Given the auditory nature of SAT, pure-tone audiometry (PTA) was used to identify potential hearing loss (in decibels) in the listener’s two ears at 0.5, 1 and 2 kHz using an AC40 Interacoustics clinical audiometer in a sound-attenuated room (Génie Audio Inc, Saint-Laurent, Canada). PTA indicated normal hearing (< 25 dB of hearing loss) in all participants. Informed written consent was obtained for each participant. This study was approved by the Committee on research Ethics of the CR-IUSMQ (project #2015-392).

In this study, we used the word pairs validated in Study 1a to ensure that human and non-human actions were processed in a similar timeframe and with a similar accuracy level as part of SAT. The stimuli were produced at a mean speech rate of 3.5 syllables per second by a 24-year-old male speaker and recorded in a double-walled sound-attenuated room at 44 kHz with a lavaliere microphone (MX150, Shure, Chicago, USA). Stimuli were analogy sentences such as "*ciseaux* est à *découper* ce que *crayon* est à *dessiner*"/"*scissors* is to *cut* what *pencil* is to *draw*." Half of the sentences included two pairs of human actions, while the other half included two pairs of non-human actions. Half of the sentences were congruent while the other half was incongruent (e.g., "*ciseaux* est à *découper* ce que *crayon* est à *creuser*"/"*scissors* is to *cut* what *pencil* is to *dig*"). Incongruent sentences were used as fillers and were not analyzed. The order of presentation of the verb and noun ("*marteau* est à *clouer* ce que *crayon* est à *dessiner*" vs. "*clouer* est à *marteau* ce que *dessiner* est à *crayon*"/"*hammer* is to *nail* what *pencil* is to *draw*" vs. "*to nail* is to *hammer* what *to draw* is to *pencil*") was counterbalanced across sentences and conditions. Participants were comfortably seated in a double-walled sound-attenuated room, facing a computer screen. Sentences were amplified (HP4, Presonus, Baton Rouge, USA) and presented through TMS-compatible, non-metallic insert earphones (Etymotic Research, Elk Grove Village, IL, USA). A GO sign appeared on the screen after the end of the auditory sentence, signalling that an answer was required. Participants were asked to determine whether the content of the sentence was true or false by responding as rapidly and accurately as possible by pressing one of two buttons of a response pad with the index and middle finger of their right hand (RB-840 model, Cedrus, San Pedro, California, US). Inter-stimuli intervals of different lengths (500 ms, 750 ms, 1000 ms) were randomly assigned to trials in order to prevent a habituation bias. The task was comprised of 256 trials and lasted approximately 20 minutes. This task requires the activation of lexical and semantic representations of words and the syntactic-semantic processing of statements (*e.g.,* "scissors is to cut"). SAT also involves working memory and executive functions abilities. Working memory is needed to maintain the first statement in memory during the processing of the second statement. Executive functions are involved (*e.g.* attentional control) in the comparison of the two statements required to judge the semantic correctness of the sentence. However, the experimental conditions in SAT only differ in terms of semantic category: human vs. non-human actions. SAT therefore allowed us to examine the impact of rTMS on SMA and pre-SMA during the processing of human actions and non-human action sentences.

Separate one-way ANOVAs with Action (Human, Non-human) as the independent factor were performed on the percentage of correct responses and reaction time (RT) (for correct responses only) using SPSS (23.0.0.2, IBM). There was no effect of Action on accuracy ($F_{(1,9)}$ = .00, p = 1.00, η_2 = .00) or RT ($F_{(1,9)}$ = .08, p = .78, η_2 = .01). These results therefore confirm that the human and non-human conditions have a similar difficulty level. Two word pairs per category were discarded because of low accuracy ratings. The final stimulus lists for SAT used in Study 2 thus contained 30 pairs.

4. STUDY 1c: VALIDATION OF THE IMPLICIT MOTOR IMAGERY TASK

Ten right-handed (Oldfield, 1971) adults participated in this study (5 females, mean age 24.36, SD = 5.33), which aimed to ensure that the implicit motor imagery task was challenging allowing us to identify various levels of performance. Informed written consent was obtained for each participant. Recruitment procedure, as well as inclusion and exclusion criteria were identical to those used for the validation of SAT. This study was approved by the Committee on research Ethics of the CR-IUSMQ (project #2015-392).

A mental rotation of hand task, which has been used to assess implicit motor imagery abilities (*e.g.*, Butson, Hyde, Steenbergen, & Williams, 2014; Conson et al., 2013; Tomasino, Budai, Mondani, Skrap, & Rumiati, 2005; Vromen, Verbunt, Rasquin, & Wade, 2011), was adapted to measure expertise in implicit motor imagery. Stimuli were 3D hand pictures created by Yves Almécija (CeRCA, Poitiers, France), used in previous research on motor imagery (Meugnot, Agbangla, & Toussaint, 2016; Meugnot & Toussaint, 2015). Stimuli represented right and left hands, in two different views (*i.e.*, back and palm of the hand), in four different angles: 40 º, 80 º, 120 º, 160 º. Half of the images were presented in a lateral view (*i.e.*, tip of hand away from mid-body line), while the other half was presented in a medial view (*i.e.*, tip of hand toward mid-body line). In total, 36 different hand pictures were presented in each block. The novelty in our version of the task was the creation of six blocks differing only in the time allowed for response (block 1: 2000 ms, block 2: 1750 ms, block 3: 1500 ms, block 4: 1250 ms, block 5: 1000 ms, block 6: 750 ms). Stimuli were pseudo-randomized within each block for each participant and visually presented on a screen. The mental rotation task consisted in determining whether each hand was left or right. Participants answered with index and middle fingers of their right hand using a response pad (RB-830, Cedrus, San Pedro, CA, USA). Their left hand was immobile, and in the same position as the right hand. To monitor the absence of hand movements during motor imagery, physiological data were acquired throughout the mental rotation task, using a multi-channel surface EMG system (MP150, Biopac Systems Inc, Goleta, CA, USA), measuring the electrical potential reaching muscles in the right hand. A pair of small bipolar disposable surface electrodes (EL504, Biopac Systems Inc, Goleta, CA, USA) were placed on participants' skin approximately 1 cm apart on the belly of the first dorsal interosseous (FDI) muscle of the right hand. The EMG signal was filtered using a 500 Hz low-pass anti-aliasing filter and a 10 Hz high-pass filter. A 55-65 notch filter was used to remove electrical noise from the signal. No hand contractions, defined as a 50 ms burst of a mean amplitude at least twice that of the preceding 50 ms of signal, were visually identified in the EMG signal. In addition, an HDR-CX320 video camera (Sony) was used to record participants' hands, thus providing a second source of hand movement monitoring. This examination confirmed that participants' hands remained still during the entire task. As the break off point (*i.e.* first block with 50 % or less accuracy) differed across participants, the percentage of correct responses for the entire task (*i.e.*, average of the six blocks) was considered the most sensitive measure of expertise and was calculated for each participant.

The results revealed a mean accuracy of 64.74% (SD = 18.06, range 39.58 – 91.67), with accuracy declining as speed increased, thus validating the use of this task in Study 2 to measure individual differences in mental rotation expertise.

5. STUDY 2: rTMS

5.1. Participants

Sixteen (16) healthy native speakers of Canadian French participated in this study. Participants were recruited through emails sent to Université Laval students and employees, employees of the IUSMQ, as well as through posters and flyers distributed in the general community. Two participants did not complete all tasks and were excluded from analyses. The fourteen (14) remaining participants (mean age 28.79, SD = 6.86; range: 18–40 years of age; 7 women) were right-handed (Oldfield, 1971), had normal or corrected-to-normal vision and no self-reported history of speech, voice, language or neurological disorder. Participants were screened for normal cognitive functioning using Montreal Cognitive Assessment (MoCA) (Nasreddine et al., 2005). PTA indicated normal hearing (< 25 dB of hearing loss) in all participants at 500 Hz, 1000 Hz and 1500 Hz. Informed written consent was obtained for each participant. The study was approved by the Committee on Research Ethics of the CR-IUSMQ (project #2016-149).

5.2. Experimental Procedure

The experiment included two visits on two different days. During the first visit, participants underwent structural magnetic resonance imaging (MRI). Eight participants already had an MRI that was kept in the lab’s participant databank (Banque de données sur l’Audition et la Communication Humaine “BACH,” approved by our local research ethics committee, project #369-2014); for those participants, the study entailed only one visit. During the main visit, participants completed SAT with rTMS. A behavioural mental rotation task was used to measure participants' level of expertise in implicit motor imagery (For details, see section 4). Visual inspection of video and EMG recordings showed that no movement was executed during the motor imagery task. Finally, manual dexterity was measured with the Grooved Pegboard 32025 (Lafayette Instrument Company). This standardized and normalized test consists in placing small pegs in randomly oriented slots as rapidly as possible. Pegs have a key along one side and therefore require to be rotated before being inserted in the boards' holes. Performance is measured as completion time, in seconds. In this study, rTMS was also administered during a motor imagery task; these data are not presented in this article.

5.3. Experimental Design

Stimuli for SAT were sentences from the validation study: two lists of 120 sentences using 30 human action verbs and 30 non-human action verbs (see supplementary material 1). Each verb was paired with two strongly and two poorly associated nouns. The lists were counterbalanced across participants, and stimuli were pseudo-randomized within each list for each participant. All verbs were presented in the rTMS and no rTMS trials. Motor imagery was assessed following the semantic analogy task to avoid motor imagery priming in SAT. The dexterity task was administered last. SAT was administered before the motor imagery and Grooved Pegboard tasks in order to avoid priming motor imagery.

5.4. rTMS

Participants were seated in a padded TMS chair with their head comfortably held in place by a headrest (Rogue Research, Montreal, Canada). Prior to the rTMS session, the position of the computer screen was adjusted to ensure that each participant could read the instructions and see the GO signal properly. All stimuli were presented via a computer controlled by the Presentation software (version 18.1, www.neurobs.com). Participants performed SAT using TMS-compatible non-metallic insert earphones, which provide a 30 dB+ external noise reduction (Etymotic Research, Elk Grove Village, IL, USA).

5.4.1. MRI acquisition and co-registration

A high-resolution T1-weighted anatomical MRI scan was obtained for all participants on a 3T Philips Achieva TX MRI scanner at the Clinique Mailloux in Québec City (matrix 256 mm x 256 mm, 180 slices, 1 mm^3, no gap). Prior to the rTMS session, the anatomical MRI was incorporated into Brainsight 2 (Rogue Research, Montreal, Canada). Six anatomical landmarks (tip and bridge of the nose, external corner of the eyes when possible, and the intersection of the helix and tragus for the ears) were identified on participants' T1 image to guide MRI-to-head co-registration using an infrared tracking system (Polaris, Northern Digital, Waterloo, Canada).

5.4.2. Resting motor threshold (RMT)

Stimulation was performed with a figure-of-eight Air Film Magstim coil combined to a Magstim $Rapid_2$ stimulator (Magstim Company, Dyfed, UK). To establish the resting motor threshold (RMT) of each participant, the TMS coil was placed over the hand area ("hand knob") of the participants left M1, previously identified on the participant's MRI scan. The coil was held tangentially to the skull with the handle pointing posteriorly and inferiorly. Single pulses were delivered to M1 and the intensity of the stimulation was adjusted until a motor evoked potential (MEP) in the right FDI (EMG Isolation Unit, Brainsight 2, Rogue Research, Montreal, Canada) was observed in 5 of 10 trials with a minimum amplitude of 50 μV (Rossini, et al., 1994). For two participants, whose RMT was not reached at 85 % of stimulator output capacity, stimulation intensity was fixed at this maximal intensity. Stimulation intensity ranged from 59 % to 85 % (mean = 72.21 %, SD = 8.51) of the output capacity of the stimulator.

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5.4.3. rTMS stimulation

The coil was held by an experimenter throughout the rTMS session. Trains of six (6) pulses were administered at a frequency of 10 Hz (train duration = 500 ms). The stimulation intensity was set to 110 % of the participant's RMT. These stimulation parameters were well within rTMS safety guidelines (Rossi, Hallett, Rossini, & Pascual-Leone, 2009; Wassermann, 1998) and have been used on SMA and pre-SMA in the past (Tremblay, & Gracco, 2009). Stimulation was administered 550 ms before the beginning of the trial in half of the trials. Each participant underwent two blocks of rTMS: one block over the left SMA and one over the left pre-SMA. Since action language induces left-lateralized activation in motor areas in right-handers (Hauk, & Pulvermüller, 2011; Willems, Hagoort, & Casasanto, 2010), left SMA and pre-SMA were targeted in the present study. SMA and pre-SMA were localized on individual T1-weighted images using macro-anatomical landmarks as well as knowledge derived from previous fMRI studies. SMA and pre-SMA were ventrally delimited by the cingulate sulcus. The caudal boundary of the SMA is the precentral sulcus (Bozkurt et al., 2016). The rostral frontier of pre-SMA was defined as an imaginary vertical line passing through the genu of the corpus callosum (Matelli et al., 1991; Picard & Strick, 2001). An imaginary vertical line passing through the anterior commissure (*i.e.,* the VAC line) was drawn to separate SMA from pre-SMA (Picard & Strick, 2001). In order to ensure the distinct rTMS stimulation of SMA and pre-SMA, the stimulation targets (respective MNI coordinates: -3, -8, 66, and -3, 15, 60) were selected to be apart by a minimum of 20 mm on the y-axis based on a previous study from our group that dissociated the role of pre-SMA and SMA during action selection (Tremblay, & Gracco, 2009). Importantly, these coordinates were chosen to be within the range of coordinates previously reported in the literature in relation to action language processing (Supplementary material S2). The location of the targets is shown in Figure 1. The order of stimulation of these two areas was randomized across participants.

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5.5. Data analysis

Analyses were run on congruent sentences only. First, outliers (*i.e.,* data located 2 SD from the mean) in RTs and accuracy data were discarded from the analyses. This led to the exclusion of one participant from the RT analyses. An analysis of covariance (ANCOVA) with Area (SMA, pre-SMA) and Stimulation (TMS, No TMS) as within-subject independent factors was performed on accuracy (the percentage of correct responses) and RTs (for correct responses only) using SPSS (23.0.0.2, IBM). For both Accuracy and RT, the dependant variable was a difference score (*i.e.,* human action score — non-human action score). Motor imagery and dexterity were included in the analyses as continuous quantitative between-subject covariates. The dexterity score was the mean time for completing the Grooved Pegboard with the right and left hands expressed in seconds. The motor imagery expertise score was the mean percentage of correct responses across the six blocks of the task. Post-hoc paired samples Student t-tests and Pearson's correlations were conducted to decompose significant interaction effects. For all ANOVAs, measures of effect sizes are provided in the form of partial eta squared (η_{p2}), which are reported for all main effects and interactions. When comparing two means, we report effect sizes in the form of Cohen *d* statistics.

INSERT FIGURE 3 ABOUT HERE AS A ONE-COLUMN FIGURE

5.6 Results

All accuracy scores and RTs for Study 1 and Study 2 are reported in Supplementary Materiel S3. The analysis of accuracy revealed no significant differences between conditions, as reported in Table 1. The analyses of RTs showed a significant main effect of Area ($F_{(1,10)} = 8.69$, $p = .01$, $\eta_2 = .47$), indicating a greater difference in RTs between human and non-human actions during the stimulation of SMA compared to pre-SMA. The interaction between Area and Stimulation was also significant ($F_{(1,10)} = 6.66$, $p = .027$, $\eta_2 = .40$), as well as the interaction between Area and Dexterity ($F_{(1,10)} = 8.76$, $p = .014$, $\eta_2 = .47$), and the interaction between Area, Stimulation and Dexterity ($F_{(1,10)} = 5.96$, $p = .035$, $\eta_2 = .37$). No interaction involving motor imagery reached significance (see Table 1). A paired samples Student t-test was performed to decompose the Area x Stimulation interaction. This analysis revealed a smaller TMS-NoTMS difference for pre-SMA than for SMA, but these effects were not significant (RTs between no TMS and TMS conditions for SMA ($t_{(12)} = -.73$ $p = .48$, d = .36) or pre-SMA ($t_{(12)} = -1.07$ $p = .31$, d = .49)). To decompose the Area x Dexterity interaction, a Pearson's correlation analysis was run. This analysis revealed a significant correlation between RTs and dexterity when rTMS was applied over SMA ($r_{(11)} = .69$, $p = .01$, $r_2 = .48$) but not pre-SMA ($r_{(11)} = -.15$, $p = .64$, $r_2 = .02$). Pearson's correlations were also run to decompose the Area x Stimulation x Dexterity interaction (see Figure 2). This analysis revealed that RTs were correlated to the dexterity score only when rTMS was applied over the SMA ($r_{(11)} = .59$, $p = .035$, $r_2 = .34$). All correlation results are reported in Table 2. Additional correlations were conducted to clarify the effect of rTMS over the SMA in relation to dexterity. First, a measure of the general impact of rTMS over SMA on RT was computed according to the following formula: $f(x) = |(x_{\mathrm{H}} - x_{\mathrm{NH}})_{\mathrm{TMS}} - (x_{\mathrm{H}} - x_{\mathrm{NH}})_{\mathrm{NOTMS}}|$, where x_{H} is the mean RT for human actions and x_{NH} the mean RT for non-human actions. The analysis showed a significant positive relationship between dexterity and the impact of rTMS over SMA ($r_{(11)} = .70$, $p = .01$, $r_2 = .49$). That is, lower dexterity was associated with stronger SMA effect on RT (Figure 3). Two additional correlations were performed, using the following formula: $f(x) = |x_{\mathrm{TMS}} - x_{\mathrm{NOTMS}}|$, to determine whether the impact of rTMS over SMA was due to an impact of rTMS on human actions or non-human actions. These analyses revealed a significant correlation between dexterity and the impact of rTMS over SMA for human ($r_{(11)} = .49$, $p = .04$, $r_2 = .24$) but not for non-human actions ($r_{(11)} = .12$, $p = .36$, $r_2 = .01$). These results are illustrated in Figure 4.

INSERT FIGURE 4 ABOUT HERE AS A TWO-COLUMN FIGURE

Finally, additional correlations were conducted to determine whether the impact of rTMS over SMA (SMA_rTMS_Hum), dexterity and motor imagery were correlated. The results revealed that dexterity and motor imagery expertise were significantly correlated ($r_{(11)}$ = -.60, p = .03, r_2 = .35), but that motor imagery and SMA_rTMS_Hum were not ($r_{(11)}$ = .01, p = .98, r_2 = .00).

6. DISCUSSION

In the past decades, an increasing number of studies have examined the involvement of the motor system in action language processing. The aim of this rTMS study was to determine whether medial premotor areas were involved during an action language task requiring deep semantic processing, and, further, to determine if this involvement was linked to motor imagery expertise and/or motor skills (manual dexterity) in order to reveal the underlying neurobiological mechanisms. Results showed that SMA was involved in action language processing, and that this involvement was related to individual differences in manual dexterity, with rTMS having a greater impact on RTs during SAT for participants with lower dexterity. In contrast, expertise in motor imagery did not modulate the involvement of SMA nor pre-SMA during action language processing. These findings are discussed in the following sections.

6.1. Involvement of SMA in Action Language Processing

Research on action language and the motor system has produced diverging theoretical positions regarding the necessity of the involvement of motor/premotor areas in action language processing (*e.g.,* Mahon & Caramazza, 2008; Pulvermüller, 2005). Research has shown that the involvement of the motor system in action language processing is not homogeneous, and that it can be modulated by a number of different factors. Specifically, studies have examined the linguistic characteristics that modulate motor/premotor activation during action language processing, such as grammatical categories (*e.g.,* Boulenger, Décoppet, Roy, Paulignan, & Nazir, 2007 ; Fargier & Laganaro, 2015 ; Pulvermüller, Cook, & Hauk, 2012), degree of abstractness (*e.g.,* Aziz-Zadeh & Damasio, 2008; Desai et al., 2013; Glenberg et al., 2008; Troyer, Curley, Miller, Saygin, & Bergen, 2014), or semantic context of action sentences (*e.g.*, Aravena et al., 2012). However, only few studies have explored the potential relationship between action language processing and motor imagery (Papeo et al., 2012 ; Tomasino et al., 2008, 2007 ; Willems et al., 2009 ; Yang & Shu, 2014) or motor skills (Moody-Triantis et al., 2014 ; Peck et al., 2009). In the present study, the involvement of SMA and pre-SMA in action language processing was examined in relation to both motor imagery and motor execution. Results show that rTMS over SMA impacted human action language processing. This effect was not observed for non-human actions. In an electroencephalography study (van Elk, van Schie, Zwaan, & Bekkering, 2010), motor and premotor responses were recorded during listening of sentences containing action verbs that were associated either with human or animal nouns, which is at odds with the present finding. However, the verbs used in that study (*e.g.*, “jump”) referred to actions that can be executed by both humans and animals, whereas the verbs presented in our study were specifically linked to human or non-human actions, the latter not being associated with human motor plans (*e.g.*, “hatch”). The specificity of the rTMS effect therefore suggests that SMA involvement in human action language is related to motor planning.

Results also show that human action language processing was associated with SMA, but not pre-SMA. This finding is consistent with the study by Moody-Triantis et al. (2014) who showed activation in SMA during both motor execution and action language processing. SMA and pre-SMA present distinct anatomical and functional characteristics. Human brain dissection (Bozkurt et al., 2016; Vergani et al., 2014; Catani et al., 2012) and diffusion imaging studies (Bozkurt et al., 2016 ; Vergani et al., 2014; Catani et al., 2012 ; Lehéricy et al., 2004) have allowed for the direct and indirect observation of white matter tracts connecting SMA and pre-SMA to cortical and subcortical structures in the human brain. These studies have revealed that SMA and pre-SMA present major differences in their connectivity patterns, similar to the macaque monkey (*e.g.,* Luppino, Matelli, Camarda, & Rizzolatti, 1993). Indeed, SMA is connected to primary motor cortex (M1) (Bozkurt et al., 2016; Vergani et al., 2014) while pre-

SMA has no connection to M1, but is connected to the prefrontal cortex (Bozkurt et al., 2016). Furthermore, SMA, similarly to M1, is connected to the caudal part of the striatum (Lehéricy et al., 2004), while pre-SMA is connected to the more rostral part of the striatum. In addition, microsurgical anatomy has shown that SMA contains 10% of corticospinal cells while pre-SMA contains close to none (Bozkurt et al., 2016). Taken together, these results demonstrate that SMA is in a much closer relation to motor execution than pre-SMA, having direct access to M1 and to the descending pathways. This notion is supported by human studies which showed that while pre-SMA seems to be involved in high order motor planning functions such as motor inhibition (*e.g.,* Obeso, Robles, Marrón, & Redolar-Ripoll, 2013), switching (*e.g.,* Rushworth, Hadland, Paus, & Sipila, 2002), sequencing (*e.g.,* Forstmann et al., 2008) or in intention of action (*e.g.,* Lau, Rogers, Ramnani, & Passingham, 2004), SMA is involved in motor execution (*e.g.,* Macuga & Frey, 2012; Peck et al., 2009) and in the late stage of motor planning (*e.g.,* Amador & Fried, 2004; Tankus, Yeshurun, Flash, & Fried, 2009). Intracranial electrophysiology (with depth electrodes), which possesses better spatial and temporal resolutions than other brain imaging methods, has been used to study the functions of SMA in macaque monkeys (Chen, Scangos, & Stuphorn, 2010; Hoshi & Tanji, 2004) and humans (Amador & Fried, 2004; Tankus et al., 2009). During cued motor tasks, pre-SMA was involved in earlier motor planning stages, while SMA participated in the later motor planning stages and motor execution (Amador & Fried, 2004; Hoshi & Tanji, 2004). Specifically, results suggested that SMA is involved in the selection of the appropriate arm (Hoshi & Tanji, 2004) or appropriate hand (Amador & Fried, 2004). SMA also seems to exert a proactive control over motor execution (Chen et al., 2010). In that study, the electrophysiological activity of SMA was correlated with the modulation of RTs in a stop-signal task, with a shortening of RTs after several correct responses and a lengthening of RTs after several errors, suggesting a role of SMA in the anticipation and inhibition of movements. In addition, Tankus et al. (2009) have shown that, during a simple 2D maze computer game, firing rates of 51.3 % of the recorded units in the SMA were correlated with motion speed, and that 82.5

% of the recorded units were direction-selective, suggesting that SMA is involved in the programming of hand motion speed and direction. Thus, the impact of rTMS over SMA during human action language processing in our study suggests that SMA involvement in action language could be linked to movement planning, including limb selection, anticipation and inhibition of movement, and encoding of hand motion speed and direction. Our study is the first to show a causal role of SMA in action language processing. Further research is needed to replicate these results and identify the precise nature of SMA's involvement in language semantic processing.

6.2. Motor Imagery

In the present study, expertise in implicit motor imagery was not correlated with the impact of rTMS on neither SMA nor pre-SMA during SAT, suggesting that implicit motor imagery is not involved in deep semantic processing of human action sentences. Although motor imagery and action language processing were not associated, dexterity was correlated with the impact of rTMS over SMA during SAT and with motor imagery expertise, suggesting that motor imagery and action language processing, though not directly related to one another, are both linked to fine manual motor skills. The literature on the link between action language processing and motor imagery has mainly focused on explicit motor imagery (Tomasino, et al., 2008; Barbara Tomasino et al., 2007; Willems et al., 2009; Yang & Shu, 2014), which is less likely to be involved in action language processing than implicit motor imagery (Willems et al., 2009). Further research is therefore needed to confirm the extent and nature of the relationship between *implicit* motor imagery and action language processing. The comparison of action language tasks with different implicit motor imagery tasks would provide insights regarding which elements of implicit motor imagery may be involved in action language processing. For instance, action language processing could be investigated in relation to a prospective action judgment task, where participants decide, for each visually presented tool image, whether they would use an overhand or underhand grip to grasp the tool (Johnson, 2000), or a feasibility task, where participants determine whether an action is feasible on the basis of a tool picture showing suggested finger positions (Frak, Paulignan, & Jeannerod, 2001).

The finding of a lack of a correlation between the involvement of the pre-SMA in action language processing and motor imagery in the present study could also mean that the involvement of pre-SMA in action language is related to functions of the pre-SMA other than motor imagery. For instance, pre-SMA is also involved in decision-making (*e.g.*, Rushworth, Hadland, Paus, & Sipila, 2002) and anticipation of action (e.g. Strack, Kaufmann, Kehrer, Brandt, & Stürmer, 2013). Further research is needed to determine which functions of the pre-SMA could be involved in action language processing.

6.3. Resilience of SMA

The novelty of this study resides in the investigation of the link between the involvement of SMA and fine manual motor skills. The link between action execution and action language processing has mostly been studied in the context of diminished or enhanced motor abilities including for example the study of stroke patients (Desai, Herter, Riccardi, Rorden, & Fridriksson, 2015) and the study of athletes (Beilock, Lyons, Mattarella-Micke, Nusbaum, & Small, 2008; Holt & Beilock, 2006; Lyons et al., 2010; Tomasino, Maieron, Guatto, Fabbro, & Rumiati, 2013). However, inter-individual differences in a healthy non-expert population have scarcely been considered in the investigation of the neurobiological correlates of action language processing, despite the importance of studying the general population to draw generalizable conclusions.

In the present study, we showed inter-individual variability in the impact of rTMS over SMA during SAT as a function of manual dexterity, in a healthy non-expert population. A new and important finding is that the degree of involvement of the SMA during SAT was not identical for all participants. The performance of individuals with greater dexterity was not affected by rTMS, suggesting that high levels of dexterity allowed for a faster recovery (or protection against interference) of SMA after rTMS. The ability to recover from a temporary perturbation has been called "*cortical resilience*" (Lowe, Staines, & Hall, 2017) in a study where continuous theta burst stimulation (cTBS) administered over M1 had a shorter impact on behaviour after physical exercise in comparison to no exercise. According to Lowe et al. (2017), this resilience was linked to neurophysiological mechanisms such as increased cerebral blood oxygenation immediately following physical training. The resilience observed in our study was not the result of dexterity training and must therefore be related to mechanisms other than neurophysiological changes, such as neuroplasticity. In neurobiology, resilience is defined as a "reactive response" (King, 2016) and is mostly studied in the context of adaptive neurobiological changes in response to environmental stress. The aim of studies in that field is to uncover the neurobiological mechanisms, such as the number of cells and brain networks (King, 2016), that explain the considerable inter-individual differences in resilience. Here we examined the impact of rTMS on the SMA on language processing performance and observed a dexterity-related inter-individual difference in resilience. Thus, high levels of dexterity could be linked to neuroplasticity in SMA, which could be accountable for its degree of resilience. More generally, our study shows, for the first time, that, even in a healthy non-expert population, inter-individual differences in fine motor skills may modulate the involvement of motor areas during action language processing.

6.4. Limitations

The current study has several potential limitations, including the motor imagery task, the possible spreading of activation from SMA to M1, and the absence of a sham condition with noise. First, the motor imagery task is a limit in our study. Although the task of mental rotation of hands has been used to assess motor imagery abilities for the past twenty years (*e.g.*, Kosslyn, DiGirolamo, Thompson, & Alpert, 1998), the essence of motor imagery leads to the methodological difficulty of objectively measuring it, and the mental rotation of hands task might not have measured motor imagery abilities but possibly other cognitive processes such as visual imagery (Bläsing, Brugger, Weigelt, & Schack, 2013). Future studies using different motor imagery tasks are needed to further current understanding of the potential role of implicit motor imagery in action language processing.

A second limitation is the impossibility to determine whether participants were engaging in motor imagery or motor planning processes during SAT. SAT was conducted prior to the motor imagery task, thus avoiding motor imagery priming during SAT. Therefore, if motor imagery was executed during SAT, it was spontaneous and ecological. Furthermore, the correlation between dexterity and the involvement of SMA in action language processing suggests that motor-related skills and action language processing are linked. It is thus conceivable that motor-related processes occurred during SAT. Further studies are needed to determine the nature of the motor processes involved *during* action language processing (*e.g.* motor planning, motor imagery). Thirdly, the possible spreading of activation from SMA to M1 is a limitation in our study. This type of spreading has been shown in previous research (Arai et al., 2012; Shirota et al., 2012; Matsunaga et al., 2005; Oliveri et al, 2003). However, no MEPs were recorded during the stimulation of SMA in the motor imagery study that was conducted with the same parameters as the present study (whose results are not reported here). Since the stimulation site was identical in both studies, it is likely that stimulation of SMA during SAT did not induce MEPs.

Finally, we cannot discard the possibility that rTMS noise affected behavior during the TMS conditions. Though the lack of a sham condition prevents us from discarding this interpretation completely, the dissociation that was observed between rTMS to the SMA and pre-SMA suggests that there was no general effect of rTMS noise on RTs during SAT. Moreover, given that participants were wearing insert earphones throughout the procedure, which provided a 30 dB external noise reduction, and given the absence of a global impact of TMS on behavior, we believe that the observed effects are not related to the presence of noise.

7. CONCLUSION

During SAT, a novel task involving deep semantic processing, SMA was causally involved in the processing of human action language, consistent with the notion of an embodiment of action language. This study thus contributes to furthering current neurobiological theories of language processing (Binder & Desai, 2011; Hagoort, 2014) by clarifying the role of the two premotor areas, regions that have historically not been involved in models of language (for a discussion, see Tremblay and Dick 2016). Understanding the networks involved in language processing is key to understand underlying neurobiological mechanisms. Importantly, the involvement of the SMA was associated with motor dexterity but not with motor imagery abilities. Specifically, a high level of dexterity was associated with a form of resilience against neuromodulation to the SMA during the processing of human action language. Our results show that inter-individual differences in manual motor skills may play an important part in the degree of involvement of premotor areas during action language processing. Whether manual motor training could optimize the involvement of motor areas during action language processing needs to be explored, in healthy populations, younger and older, as well as in populations demonstrating semantic deficits in language processing as this may open up new avenues of treatments.

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Figures

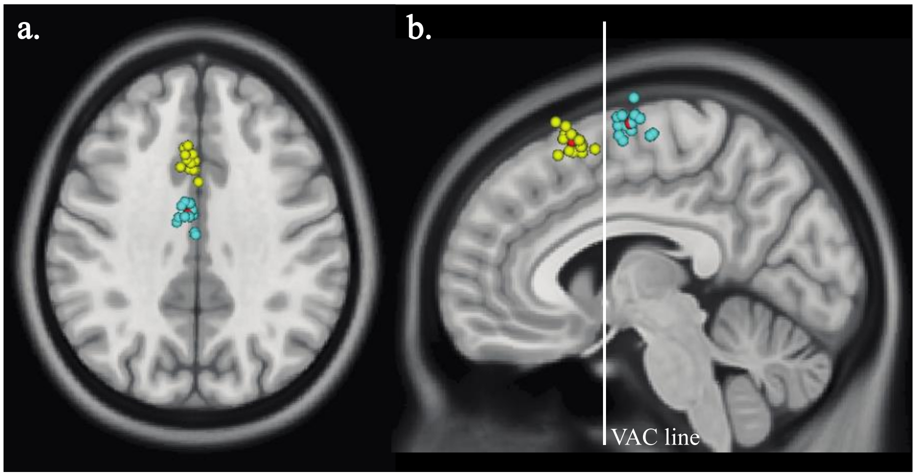

Figure 1: rTMS targets. Individual stimulation targets in the SMA (blue) and pre-SMA (yellow), and mean stimulation locations for each site (red). For SMA, the mean location is -3, -8, 66, and for pre-SMA, the mean location is -3, 15, 60.

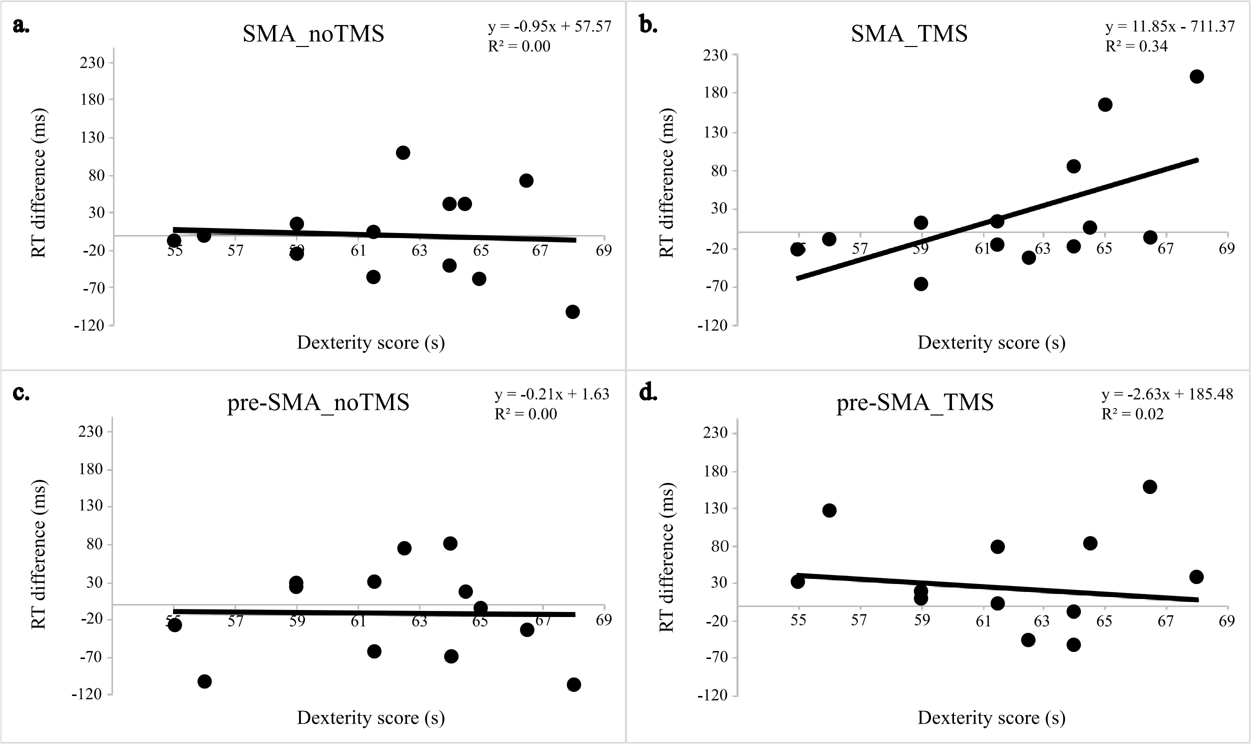

Figure 2: involvement of SMA in action language processing. Relationship between dexterity and RT difference expressed in ms ([$f(x) = x_H - x_{NH}$] where x_H is the mean RT for human actions and x_{NH} the mean RT for non-human actions), for rTMS administered over the SMA (b), for rTMS administered over pre-SMA (d), and for NOTMS over SMA (a) and pre-SMA (c).

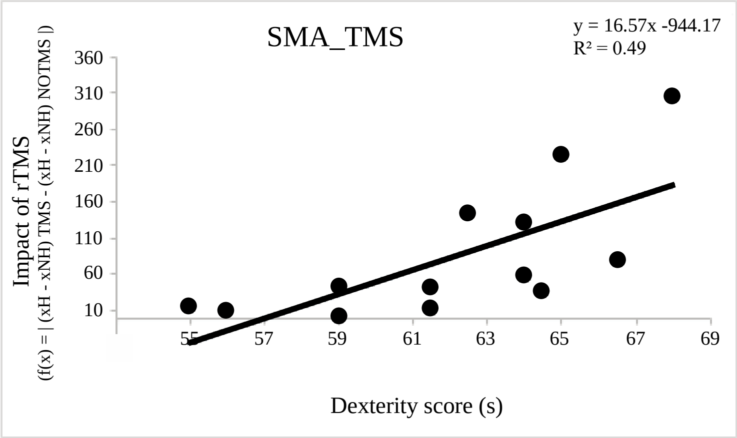

Figure 3: general impact of rTMS. Relationship between dexterity and the general impact of rTMS over SMA on the RT difference between human and non-human action trials during the semantic analogy task ($[f(x) = |(x_{\mathrm{H}}-x_{\mathrm{NH}})_{\mathrm{TMS}} - (x_{\mathrm{H}} - x_{\mathrm{NH}})_{\mathrm{NOTMS}}|]$ where x_{H} is the mean RT for human actions and x_{NH} the mean RT for non-human actions).

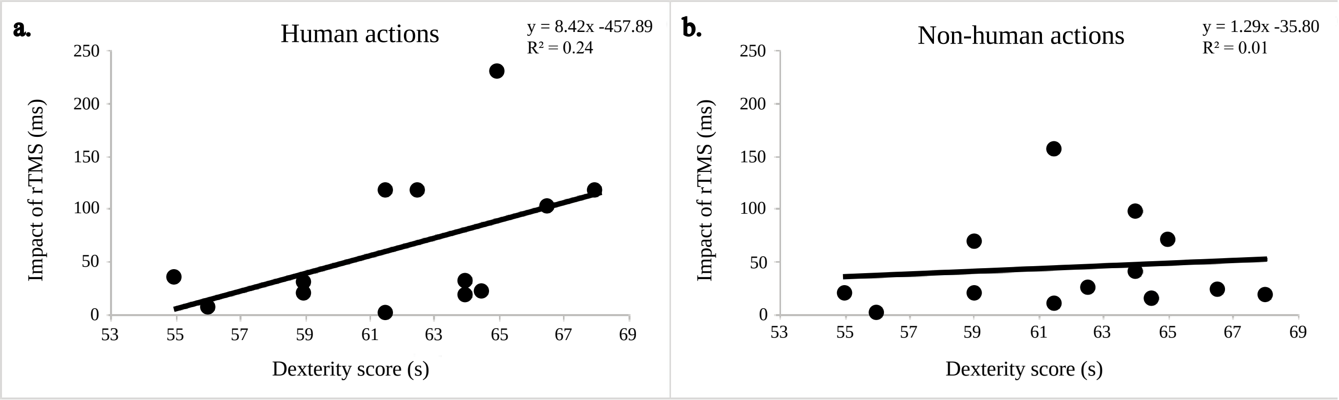

Figure 4: impact of rTMS for human and non-human actions. Relationship between dexterity and the impact of rTMS over SMA $[f(x) = |x_{\mathrm{TMS}} - x_{\mathrm{NOTMS}}|]$, for human action sentences (a), and non-human action sentences (b).

Tables

Table 1.

Detailed statistical results from the ANCOVA for correct responses and reaction times.

ANCOVAs	ddl	ddl (error)	F	p	η^2
Percentage of correct responses					
Area	1	9	,328	,581	,035
Area x Motor Imagery	1	9	,241	,635	,026
Area x Dexterity	1	9	,266	,619	,029
Stimulation	1	9	,801	,394	,082
Stimulation x Motor Imagery	1	9	,290	,603	,031
Stimulation x Dexterity	1	9	,845	,382	,086
Area x Stimulation	1	9	1,415	,265	,136
Area x Stimulation x Motor Imagery	1	9	2,777	,130	,236
Area x Stimulation x Dexterity	1	9	,652	,440	,068
Reaction Times					
Area	1	10	8,690	,015	,465
Area x Motor Imagery	1	10	4,197	,068	,296
Area x Dexterity	1	10	8,764	,014	,467
Stimulation	1	10	,641	,442	,060
Stimulation x Motor Imagery	1	10	,185	,676	,018
Stimulation x Dexterity	1	10	,802	,391	,074
Area x Stimulation	1	10	6,661	,027	,400
Area x Stimulation x Motor Imagery	1	10	4,732	,055	,321
Area x Stimulation x Dexterity	1	10	5,956	,035	,373

Table 2.

Detailed statistical results for correlation analyses decomposing the Area x Stimulation x Action effect.

Correlations	ddl	r	r^2	p
Area x Stimulation x Dexterity effect				
Dexterity x SMA_nostim	11	-,064	,003	,835
Dexterity x SMA_TMS	11	,586	,343	,035
Dexterity x pre-SMA_nostim	11	-,014	,000	,964
Dexterity x pre-SMA_TMS	11	-,135	,018	,659

Supplementary Material 1

The stimuli for SAT are presented in two different formats. In table 1, we present all the word pairs. Below we present the two lists of sentences (*i.e.* List A and List B), that were randomized across participants.

Table 1.
Verb/noun pairs used in SAT

	Verb	**Strongly associated noun 1**	**Strongly associated noun 2**	**Poorly associated noun 1**	**Poorly associated noun 2**
Human Actions	cuisiner	spatule	casserole	savon	crayon
	barrer	clé	cadenas	cisailles	couteau
	réparer	tournevis	clé anglaise	bâton	pioche
	brûler	briquette	chalumeau	filet	règle
	peinturer	pinceau	rouleau	pince	hachette
	épiler	pince	cire	cadenas	pinceau
	attacher	corde	ficelle	revolver	levier
	creuser	pelle	pioche	plumeau	compas
	frapper	masse	raquette	ruban	ciseaux
	pêcher	hameçon	épuisette	clé anglaise	cric
	verser	pichet	carafe	pinceau	hameçon
	découper	ciseaux	hachette	clé	clavier
	tracer	équerre	règle	pistolet	brosse
	manger	cuillère	fourchette	masse	stylo
	coiffer	brosse	peigne	chalumeau	raquette
	chasser	arc	fusil	ficelle	casserole
	attraper	cage	filet	lingette	troueuse
	assommer	massue	bâton	clou	plume
	suspendre	clou	crochet	briquet	râteau
	percer	aiguille	troueuse	équerre	rouleau
	clouer	marteau	maillet	éponge	peigne
	dessiner	crayon	stylo	épuisette	guenille
	épousseter	plumeau	lingette	pelle	carafe
	mesurer	ruban	compas	fourchette	porte-poussière
	ramasser	râteau	porte-poussière	tournevis	éponge
	couper	scie	cisailles	fusil	cage
	trancher	couteau	hâche	balai	marteau
	tirer	revolver	pistolet	hâche	massue
	laver	savon	éponge	aiguille	Scie
	écrire	plume	clavier	crochet	Spatule
Non-Human Actions	pétiller	liqueur	champagne	rosier	poire
	atterrir	avion	fusée	radeau	maison
	piquer	hérisson	oursin	tortue	œuf
	fleurir	tulipe	rosier	diamant	orage
	pondre	poule	tortue	planète	bourgeon
	rouiller	fer	acier	soupe	soleil
	abriter	toit	maison	poire	brasier
	éclore	œuf	bourgeon	avion	pluie
	refléter	miroir	vitre	fève	alarme
	contaminer	virus	bactéries	abeille	lampe

bouillir	eau	soupe	sirène	navire
butiner	guêpe	abeille	bombe	virus
éclairer	lanterne	lampe	champagne	barque
éblouir	soleil	phares	glaçon	fromage
bourgeonner	orchidée	géranium	aigle	abeille
faner	jonquille	rose	toit	moineau
germer	graine	fève	rivière	fusée
crépiter	feu	brasier	miroir	tulipe
briller	diamant	paillettes	bactéries	oursin
dériver	paquebot	navire	fer	paillettes
voler	aigle	moineau	géranium	villes
chavirer	bateau	barque	acier	phares
exploser	bombe	grenade	graine	fleuve
couler	rivière	fleuve	planète	satellite
tourner	satellite	planète	jonquille	feu
fondre	fromage	glaçon	rose	bateau
mouiller	pluie	orage	grenade	guêpe
fusionner	villes	entreprises	orchidée	pomme
pourrir	pomme	poire	poule	lanterne
sonner	sirène	alarme	bulle	guêpe

Part II : Sentences

List A stimuli :

Congruent human actions

Couper est à scie ce que brûler est à chalumeau.
Cuisiner est à casserole ce que laver est à éponge.
Rouleau est à peinturer ce que plume est à écrire.
Couteau est à trancher ce que rouleau est à peinturer.
Attacher est à ficelle ce que ramasser est à râteau.
Découper est à ciseaux ce que cuisiner est à spatule.
Brûler est à briquet ce que suspendre est à crochet.
Assommer est à massue ce que brûler est à chalumeau.
Pistolet est à tirer ce que fourchette est à manger.
Plume est à écrire ce que pichet est à verser.
Attraper est à cage ce que cuisiner est à spatule.
Aiguille est à percer ce que tournevis est à réparer.
Savon est à laver ce que crochet est à suspendre.
Carafe est à verser ce que hache est à trancher.
Aiguille est à percer ce que cadenas est à barrer.
Dessiner est à stylo ce que épiler est à pince.
Réparer est à clé anglaise ce que assommer est à bâton.
Assommer est à massue ce que barrer est à cadenas.

Arc est à chasser ce que ciseaux est à découper.
Masse est à frapper ce que lingette est à épousseter.
Clou est à suspendre ce que ruban est à mesurer.
Peinturer est à pinceau ce que percer est à troueuse.
Attraper est à cage ce que coiffer est à brosse.
Cuillère est à manger ce que revolver est à tirer.
Clouer est à maillet ce que creuser est à pelle.
Brûler est à briquet ce que dessiner est à crayon.
Règle est à tracer ce que hache est à trancher.
Pistolet est à tirer ce que fourchette est à manger.
Masse est à frapper ce que fusil est à chasser.
Couteau est à trancher ce que pichet est à verser.
Barrer est à clé ce que écrire est à clavier.
Dessiner est à stylo ce que réparer est à tournevis.
Règle est à tracer ce que râteau est à ramasser.
Hameçon est à pêcher ce que ruban est à mesurer.
Couper est à scie ce que pêcher est à épuisette.
Brosse est à coiffer ce que compas est à mesurer.
Barrer est à couteau ce que couper est à cisailles.
Peigne est à coiffer ce que éponge est à laver.
Creuser est à pioche ce que clouer est à marteau.
Compas est à mesurer ce que pelle est à creuser.
Peinturer est à pinceau ce que tirer est à revolver.
Épiler est à cire ce que attraper est à filet.
Hachette est à découper ce que lingette est à épousseter.
Épiler est à cire ce que clouer est à marteau.
Épousseter est à plumeau ce que attacher est à corde.
Arc est à chasser ce que crochet est à suspendre.
Savon est à laver ce que raquette est à frapper.
Carafe est à verser ce que clavier est à écrire.
Barrer est à clé ce que attraper est à filet.
Creuser est à pioche ce que dessiner est à crayon.
Épousseter est à plumeau ce que pêcher est à épuisette.
Cuisiner est à casserole ce que chasser est à fusil.
Clouer est à maillet ce que tracer est à équerre.
Ramasser est à porte-poussière ce que frapper est à raquette.
Ramasser est à porte-poussière ce que attacher est à corde.
Hameçon est à pêcher ce que cisailles est à couper.
Cuillère est à manger ce que bâton est à assommer.
Hachette est à découper ce que cisailles est à couper.

Incongruent human actions

Ramasser est à porte-poussière ce que creuser est à plumeau.
Clé est à découper ce que revolver est à tirer.
Chalumeau est à coiffer ce que marteau est à clouer.
Corde est à attacher ce que clé anglaise est à pêcher.
Hameçon est à verser ce que revolver est à tirer.
Peinturer est à pince ce que trancher est à hache.
Assommer est à massue ce que barrer est à cisailles.
Briquet est à suspendre ce que râteau est à ramasser.
Savon est à laver ce que corde est à épiler.
Clouer est à maillet ce que suspendre est à briquet.
Couper est à scie ce que brûler est à filet.
Épousseter est à plumeau ce que barrer est à couteau.
Cuisiner est à savon ce que clouer est à marteau.
Peinturer est à hachette ce que percer est à troueuse.
Couper est à scie ce que découper est à clavier.
Plume est à écrire ce que ruban est à frapper.
Ruban est à frapper ce que crayon est à dessiner.
Dessiner est à stylo ce que réparer est à bâton.
Assommer est à massue ce que découper est à clé.
Couteau est à trancher ce que crayon est à cuisiner.
Réparer est à bâton ce que ramasser est à râteau.
Ramasser est à porte-poussière ce que manger est à stylo.
Chalumeau est à coiffer ce que filet est à attraper.
Attraper est à cage ce que manger est à masse.
Dessiner est à stylo ce que verser est à hameçon.
Arc est à chasser ce que pinceau est à verser.
Équerre est à tracer ce que pinceau est à épiler.
Aiguille est à percer ce que pistolet est à tracer.
Frapper est à raquette ce que brûler est à règle.
Pinceau est à verser ce que lingette est à épousseter.
Attacher est à revolver ce que écrire est à clavier.
Masse est à manger ce que raquette est à frapper.
Brûler est à règle ce que dessiner est à crayon.
Brosse est à tracer ce que troueuse est à percer.
Épiler est à cadenas ce que couper est à cisailles.
Clouer est à maillet ce que peinturer est à pince.
Clé anglaise est à pêcher ce que éponge est à laver.

Épousseter est à plumeau ce que coiffer est à raquette.
Réparer est à pioche ce que laver est à éponge.
Pistolet est à tirer ce que chalumeau est à coiffer.
Barrer est à cisailles ce que chasser est à fusil.
Brûler est à filet ce que écrire est à clavier.
Clavier est à découper ce que bâton est à assommer.
Arc est à chasser ce que levier est à attacher.
Attraper est à cage ce que creuser est à compas.
Cuisiner est à crayon ce que assommer est à bâton.
Savon est à laver ce que pioche est à réparer.
Creuser est à compas ce que attraper est à filet.
Compas est à mesurer ce que savon est à cuisiner.
Creuser est à plumeau ce que épousseter est à lingette.
Couteau est à trancher ce que hachette est à peinturer.
Râteau est à suspendre ce que fusil est à chasser.
Aiguille est à percer ce que clé anglaise est à pêcher.
Équerre est à tracer ce que revolver est à attacher.
Pistolet est à tracer ce que ruban est à mesurer.
Pistolet est à tirer ce que cadenas est à épiler.
Compas est à mesurer ce que râteau est à suspendre.
Clé anglaise est à pêcher ce que hache est à trancher.
Stylo est à manger ce que ruban est à mesurer.
Plume est à écrire ce que revolver est à attacher.

Congruent non-human actions

Mouiller est à pluie ce que atterrir est à fusée.
Tortue est à pondre ce que aigle est à voler.
Exploser est à bombe ce que refléter est à vitre.
Miroir est à refléter ce que villes est à fusionner.
Mouiller est à pluie ce que pétiller est à champagne.
Bourgeonner est à orchidée ce que briller est à diamant.
Liqueur est à pétiller ce que diamant est à briller.
Fleurir est à tulipe ce que dériver est à paquebot.
Paillettes est à briller ce que rosier est à fleurir.
Moineau est à voler ce que bourgeon est à éclore.
Hérisson est à piquer ce que aigle est à voler.
Germer est à graine ce que piquer est à oursin.
Feu est à crépiter ce que soleil est à éblouir.
Navire est à dériver ce que oursin est à piquer.

Butiner est à guêpe ce que couler est à fleuve.
Miroir est à refléter ce que brasier est à crépiter.
Eau est à bouillir ce que poire est à pourrir.
Jonquille est à faner ce que maison est à abriter.
Entreprises est à fusionner ce que poule est à pondre.
Pomme est à pourrir ce que vitre est à refléter.
Butiner est à guêpe ce que sonner est à sirène.
Couler est à rivière ce que pétiller est à champagne.
Atterrir est à avion ce que faner est à rose.
Contaminer est à virus ce que chavirer est à bateau.
Toit est à abriter ce que fèves est à germer.
Rouiller est à fer ce que crépiter est à brasier.
Feu est à crépiter ce que fusée est à atterrir.
Germer est à graine ce que butiner est à abeille.
Fondre est à glaçon ce que éclairer est à lanterne.
Hérisson est à piquer ce que grenade est à exploser.
Éblouir est à phares ce que pourrir est à poire.
Tourner est à satellite ce que butiner est à abeille.
Exploser est à bombe ce que abriter est à maison.
Fondre est à glaçon ce que éblouir est à soleil.
Atterrir est à avion ce que couler est à fleuve.
Éclore est à œuf ce que fondre est à fromage.
Paillettes est à briller ce que soupe est à bouillir.
Bourgeonner est à orchidée ce que mouiller est à orage.
Toit est à abriter ce que planète est à tourner.
Fleurir est à tulipe ce que germer est à fève.
Sonner est à alarme ce que contaminer est à bactéries.
Couler est à rivière ce que éclore est à bourgeon.
Entreprises est à fusionner ce que acier est à rouiller.
Barque est à chavirer ce que bactéries est à contaminer.
Lampe est à éclairer ce que orage est à mouiller.
Navire est à dériver ce que géranium est à bourgeonner.
Éclore est à œuf ce que dériver est à paquebot.
Jonquille est à faner ce que rosier est à fleurir.
Éblouir est à phares ce que fondre est à fromage.
Moineau est à voler ce que lanterne est à éclairer.
Barque est à chavirer ce que acier est à rouiller.
Tourner est à satellite ce que bouillir est à soupe.
Liqueur est à pétiller ce que villes est à fusionner.
Contaminer est à virus ce que tourner est à planète.

Lampe est à éclairer ce que sirène est à sonner.
Rouiller est à fer ce que chavirer est à bateau.
Eau est à bouillir ce que rose est à faner.
Pomme est à pourrir ce que géranium est à bourgeonner.
Sonner est à alarme ce que pondre est à poule.
Tortue est à pondre ce que grenade est à exploser.

Incongruent non-human actions

Rouiller est à soleil ce que crépiter est à brasier.
Butiner est à virus ce que faner est à rose.
Barque est à chavirer ce que sirène est à bouillir.
Couler est à rivière ce que bourgeonner est à abeille.
Germer est à graine ce que abriter est à brasier.
Éblouir est à glaçon ce que exploser est à grenade.
Sonner est à alarme ce que atterrir est à radeau.
Éblouir est à fromage ce que sonner est à sirène.
Moineau est à voler ce que aigle est à bourgeonner.
Rosier est à pétiller ce que villes est à fusionner.
Mouiller est à pluie ce que piquer est à tortue.
Brasier est à abriter ce que orage est à mouiller.
Germer est à graine ce que refléter est à alarme.
Sonner est à alarme ce que voler est à géranium.
Pomme est à pourrir ce que bombe est à butiner.
Bourgeonner est à aigle ce que faner est à rose.
Navire est à bouillir ce que paquebot est à dériver.
Tourner est à satellite ce que atterrir est à maison.
Alarme est à refléter ce que planète est à tourner.
Couler est à rivière ce que éblouir est à glaçon.
Tortue est à piquer ce que aigle est à voler.
Navire est à dériver ce que diamant est à fleurir.
Atterrir est à maison ce que mouiller est à orage.
Fleurir est à diamant ce que tourner est à planète.
Poire est à abriter ce que paquebot est à dériver.
Fondre est à glaçon ce que éblouir est à fromage.
Œuf est à piquer ce que aigle est à voler.
Planète est à pondre ce que poire est à pourrir.
Poire est à pourrir ce que rosier est à pétiller.
Fèves est à refléter ce que fromage est à fondre.
Feu est à crépiter ce que barque est à éclairer.

Tourner est à satellite ce que refléter est à fève.
Éclore est à avion ce que chavirer est à bateau.
Exploser est à bombe ce que rouiller est à soupe.
Pomme est à pourrir ce que virus est à butiner.
Moineau est à voler ce que rosier est à pétiller.
Contaminer est à abeille ce que chavirer est à bateau.
Paillettes est à briller ce que abeille est à contaminer.
Éclore est à pluie ce que sonner est à sirène.
Barque est à chavirer ce que champagne est à éclairer.
Paillettes est à briller ce que lampe est à contaminer.
Rouiller est à soupe ce que couler est à fleuve.
Bourgeonner est à abeille ce que couler est à fleuve.
Butiner est à bombe ce que briller est à diamant.
Fondre est à glaçon ce que éclore est à pluie.
Jonquille est à faner ce que poire est à abriter.
Navire est à dériver ce que planète est à pondre.
Jonquille est à faner ce que soleil est à rouiller.
Contaminer est à lampe ce que exploser est à grenade.
Barque est à éclairer ce que fève est à germer.
Sirène est à bouillir ce que fromage est à fondre.
Bourgeon est à pondre ce que fèves est à germer.
Rosier est à pétiller ce que brasier est à crépiter.
Grenade est à mouiller ce que entreprises est à fusionner.
Champagne est à éclairer ce que hérisson est à piquer.
Fleurir est à orage ce que fusionner est à villes.
Atterrir est à radeau ce que briller est à diamant.
Feu est à crépiter ce que avion est à éclore.
Exploser est à bombe ce que bouillir est à navire.
Entreprises est à fusionner ce que bourgeons est à pondre.

List B stimuli :

Congruent human actions

Scie est à couper ce que fusil est à chasser.
Barrer est à clé ce que manger est à cuillère.
Découper est à hachette ce que brûler est à brique.t
Ramasser est à porte-poussière ce que percer est à troueuse.
Maillet est à clouer ce que pince est à épiler.
Mesurer est à ruban ce que suspendre est à crochet.

Spatule est à cuisiner ce que stylo est à dessiner.
Rouleau est à peinturer ce que peigne est à coiffer.
Manger est à cuillère ce que cuisiner est à casserole.
Barrer est à cadenas ce que coiffer est à brosse.
Peigne est à coiffer ce que pioche est à creuser.
Brûler est à briquet ce que verser est à carafe.
Pêcher est à hameçon ce que percer est à aiguille.
Massue est à assommer ce que corde est à attacher.
Clou est à suspendre ce que pistolet est à tirer.
Plumeau est à épousseter ce que hache est à trancher.
Corde est à attacher ce que porte-poussière est à ramasser.
Troueuse est à percer ce que marteau est à clouer.
Fusil est à chasser ce que scie est à couper.
Lingette est à épousseter ce que savon est à laver.
Bâton est à assommer ce que compas est à mesurer.
Règle est à tracer ce que clé anglaise est à réparer.
Découper est à ciseaux ce que cuisiner est à spatule.
Ramasser est à râteau ce que peinturer est à pinceau.
Pichet est à verser ce que clavier est à écrire.
Dessiner est à stylo ce que tirer est à revolver.
Attraper est à cage ce que brûler est à chalumeau.
Troueuse est à percer ce que équerre est à tracer.
Hache est à trancher ce que maillet est à clouer.
Corde est à attacher ce que filet est à attraper.
Rouleau est à peinturer ce que masse est à frapper.
Brûler est à chalumeau ce que attraper est à cage.
Tirer est à revolver ce que manger est à fourchette.
Écrire est à plume ce que ramasser est à râteau.
Tournevis est à réparer ce que crayon est à dessiner.
Spatule est à cuisiner ce que règle est à tracer.
Hache est à trancher ce que cisailles est à couper.
Manger est à fourchette ce que barrer est à cadenas.
Attraper est à filet ce que trancher est à couteau.
Marteau est à clouer ce que plume est à écrire.
Tirer est à pistolet ce que assommer est à bâton.
Frapper est à masse ce que mesurer est à ruban.
Mesurer est à compas ce que frapper est à raquette.
Entreprises est à fusionner ce que oursin est à piquer.
Pêcher est à épuisette ce que réparer est à tournevis.
Éponge est à laver ce que plumeau est à épousseter.

Creuser est à pelle ce que découper est à ciseaux.
Creuser est à pioche ce que découper est à hachette.
Fusil est à chasser ce que clou est à suspendre.
Brosse est à coiffer ce que pelle est à creuser.
Épiler est à cire ce que pêcher est à hameçon.
Pêcher est à épuisette ce que réparer est à tournevis.
Carafe est à verser ce que ficelle est à attacher.
Dessiner est à crayon ce que épiler est à cire.
Crochet est à suspendre ce que rouleau est à peinturer.
Épiler est à pince ce que verser est à pichet.
Pioche est à réparer ce que équerre est à tracer.
Éponge est à laver ce que lingette est à épousseter.
Frapper est à raquette ce que barrer est à clé.
Écrire est à clavier ce que assommer est à massue.

Incongruent human actions

Règle est à tracer ce que casserole est à chasser.
Brûler est à règle ce que épousseter est à plumeau.
Cisailles est à couper ce que chalumeau est à creuser.
Clou est à suspendre ce que revolver est à attacher.
Rouleau est à percer ce que scie est à couper.
Lingette est à épousseter ce que cadenas est à épiler.
Revolver est à attacher ce que règle est à tracer.
Bâton est à réparer ce que cuillère est à manger.
Brûler est à filet ce que découper est à hachette.
Carafe est à verser ce que règle est à brûler.
Pêcher est à hameçon ce que attacher est à levier.
Attraper est à filet ce que cuisiner est à savon.
Épiler est à cadenas ce que suspendre est à crochet.
Peigne est à coiffer ce que pince est à peinturer.
Marteau est à trancher ce que crayon est à dessiner.
Tirer est à massue ce que attraper est à filer.
Barrer est à cisailles ce que coiffer est à brosse.
Ramasser est à râteau ce que mesurer est à fourchette.
Creuser est à chalumeau ce que coiffer est à brosse.
Épiler est à corde ce que pêcher est à hameçon.
Hachette est à peinturer ce que fourchette est à manger.
Mesurer est à porte-poussière ce que attraper est à cage.
Savon est à cuisiner ce que masse est à frapper.

Couper est à scie ce que mesurer est à porte-poussière.
Ficelle est à chasser ce que marteau est à clouer.
Crayon est à cuisiner ce que bâton est à assommer.
Ramasser est à râteau ce que tirer est à hache.
Lingette est à épousseter ce que aiguille est à laver.
Découper est à hachette ce que trancher est à balai.
Écrire est à spatule ce que pêcher est à épuisette.
Bâton est à assommer ce que cisailles est à barrer.
Marteau est à clouer ce que massue est à tirer.
Règle est à tracer ce que crayon est à cuisiner.
Aiguille est à laver ce que clou est à suspendre.
Frapper est à raquette ce que trancher est à marteau.
Scie est à laver ce que stylo est à dessiner.
Casserole est à chasser ce que cadenas est à barrer.
Stylo est à manger ce que maillet est à clouer.
Attraper est à filet ce que écrire est à crochet.
Manger est à cuillère ce que écrire est à spatule.
Dessiner est à crayon ce que laver est à scie.
Clou est à suspendre ce que pioche est à réparer.
Équerre est à tracer ce que éponge est à ramasser.
Frapper est à raquette ce que percer est à rouleau.
Bâton est à assommer ce que équerre est à percer.
Peigne est à coiffer ce que hachette est à peinturer.
Barrer est à couteau ce que épousseter est à lingette.
Découper est à hachette ce que épiler est à corde.
Balai est à trancher ce que massue est à assommer.
Équerre est à percer ce que râteau est à ramasser.
pêcher est à hameçon ce que réparer est à bâton.
Mesurer est à fourchette ce que couper est à cisailles.
Creuser est à compas ce que découper est à ciseaux.
Écrire est à crochet ce que verser est à carafe.
Dessiner est à crayon ce que brûler est à filet.
Marteau est à clouer ce que compas est à creuser.
Carafe est à verser ce que ficelle est à chasser.
Revolver est à attacher ce que pichet est à verser.
Tirer est à hache ce que ramasser est à porte-poussière.
Pince est à peinturer ce que raquette est à frapper.

Congruent non-human actions

Germer est à graine ce que abriter est à toit.
Poire est à pourrir ce que œuf est à éclore.
Pomme est à pourrir ce que maison est à abriter.
Rouiller est à acier ce que mouiller est à orage.
Pétiller est à champagne ce que sonner est à sirène.
Pondre est à poule ce que crépiter est à feu.
Orage est à mouiller ce que soleil est à éblouir.
Exploser est à grenade ce que refléter est à vitre.
Œuf est à éclore ce que alarme est à sonner.
Éblouir est à soleil ce que fondre est à fromage.
Éclairer est à lanterne ce que tourner est à planète.
Rosier est à fleurir ce que fleuve est à couler.
Toit est à abriter ce que villes est à fusionner.
Pondre est à tortue ce que faner est à rose.
Grenade est à mouiller ce que miroir est à refléter.
Bourgeon est à éclore ce que moineau est à voler.
Sonner est à sirène ce que éclore est à bourgeon.
Liqueur est à pétiller ce que glaçon est à fondre.
Rose est à faner ce que tulipe est à fleurir.
Glaçon est à fondre ce que phares est à éblouir.
Éclairer est à lampe ce que briller est à diamant.
Briller est à paillettes ce que contaminer est à bactéries.
Éblouir est à phares ce que germer est à graine.
Planète est à tourner ce que rosier est à fleurir.
Oursin est à piquer ce que jonquille est à faner.
Exploser est à bombe ce que refléter est à miroir.
Briller est à diamant ce que pétiller est à liqueur.
Sonner est à alarme ce que bouillir est à eau.
Soupe est à bouillir ce que entreprises est à fusionner.
Rouiller est à fer ce que voler est à aigle.
Contaminer est à virus ce que dériver est à paquebot.
Dériver est à navire ce que butiner est à abeille.
Maison est à abriter ce que fèves est à germer.
Fromage est à fondre ce que champagne est à pétiller.
Dériver est à paquebot ce que atterrir est à avion.
Jonquille est à faner ce que acier est à rouiller.
Eau est à bouillir ce que rivière est à couler.
Barque est à chavirer ce que lanterne est à éclairer.
Hérisson est à piquer ce que bateau est à chavirer.
Abeille est à butiner ce que paillettes est à briller.

Germer est à fève ce que pondre est à poule.
Villes est à fusionner ce que orchidée est à bourgeonner.
Voler est à aigle ce que pondre est à tortue.
Crépiter est à brasier ce que contaminer est à virus.
Pluie est à mouiller ce que hérisson est à piquer.
Couler est à rivière ce que rouiller est à fer.
Satellite est à tourner ce que lampe est à éclairer.
Voler est à moineau ce que atterrir est à fusée.
Orchidée est à bourgeonner ce que satellite est à tourner.
Tulipe est à fleurir ce que pluie est à mouiller.
Couler est à fleuve ce que bouillir est à soupe.
Géranium est à bourgeonner ce que navire est à dériver.
Refléter est à miroir ce que exploser est à bombe.
Refléter est à vitre ce que pourrir est à pomme.
Contaminer est à bactéries ce que chavirer est à barque.
Crépiter est à feu ce que bourgeonner est à géranium.
Atterrir est à fusée ce que exploser est à grenade.
Atterrir est à avion ce que pourrir est à poire.
Bateau est à chavirer ce que guêpe est à butiner.
Guêpe est à butiner ce que brasier est à crépiter.

Incongruent non-human actions

Sonner est à bulle ce que abriter est à maison.
Pétiller est à liqueur ce que voler est à villes.
Acier est à chavirer ce que grenade est à exploser.
Bourgeon est à éclore ce que géranium est à voler.
Éblouir est à phares ce que dériver est à fer.
Œuf est à éclore ce que acier est à chavirer.
Lanterne est à pourrir ce que contaminer est à bactéries.
Germer est à rivière ce que abriter est à toit.
Pétiller est à liqueur ce que germer est à fusée.
Phares est à chavirer ce que lampe est à éclairer.
Tulipe est à fleurir ce que grenade est à mouiller.
Contaminer est à virus ce que tourner est à jonquille.
Exploser est à graine ce que butiner est à abeille.
Toit est à abriter ce que guêpe est à sonner.
Orchidée est à fusionner ce que tulipe est à fleurir.
Jonquille est à tourner ce que poule est à pondre.
Rouiller est à fer ce que exploser est à graine.

Poule est à pourrir ce que virus est à contaminer.
Bateau est à fondre ce que guêpe est à butiner.
Exploser est à fleuve ce que rouiller est à fer.
Grenade est à mouiller ce que miroir est à refléter.
Pondre est à tortue ce que fusionner est à pomme.
Sonner est à guêpe ce que éclore est à œuf .
Moineau est à faner ce que tortue est à pondre.
Toit est à faner ce que lanterne est à éclairer.
Atterrir est à avion ce que crépiter est à miroir.
Feu est à tourner ce que orchidée est à bourgeonner.
Briller est à oursin ce que bouillir est à eau.
Orchidée est à bourgeonner ce que tulipe est à crépiter.
Eau est à bouillir ce que bateau est à fondre.
Dériver est à fer ce que atterrir est à fusée.
Germer est à fusée ce que bourgeonner est à géranium.
Voler est à ville ce que pétiller est à liqueur.
Orchidée est à bourgeonner ce que satellite est à couler.
Refléter est à miroir ce que fusionner est à orchidée.
Rose est à fondre ce que rosier est à fleurir.
Crépiter est à miroir ce que éblouir est à phares.
Rosier est à pétiller ce que vitre est à refléter.
Éblouir est à soleil ce que briller est à bactéries.
Hérisson est à piquer ce que rivière est à germer.
Contaminer est à lampe ce que rouiller est à fer.
Refléter est à miroir ce que pourrir est à lanterne.
Grenade est à mouiller ce que acier est à rouiller.
Couler est à satellite ce que atterrir est à avion.
Œuf est à éclore ce que phares est à chavirer.
Hérisson est à piquer ce que grenade est à mouiller.
Pomme est à fusionner ce que soupe est à bouillir.
Éclairer est à lampe ce que fondre est à rose.
Guêpe est à butiner ce que planète est à couler.
Eau est à bouillir ce que bactéries est à briller.
Guêpe est à butiner ce que moineau est à faner.
Tulipe est à fleurir ce que toit est à faner.
Dériver est à paillettes ce que piquer est à hérisson.
Couler est à planète ce que piquer est à oursin.
Éblouir est à phares ce que briller est à oursin.
Toit est à abriter ce que géranium est à voler.
Éclairer est à lampe ce que dériver est à paillettes.

Pondre est à tortue ce que pourrir est à poule.
Atterrir est à avion ce que sonner est à bulle.
Crépiter est à tulipe ce que tourner est à planète.

Supplementary Material S2: coordinates of SMA and pre-SMA in previous fMRI studies

First author	**Year of publication**	**SMA**		**Pre-SMA**	
		MNI	**Talairach**	**MNI**	**Talairach**
Studies on motor imagery					
Mizuguchi	2016	-18, -6, 66	-18, -2, 59		
Pilgramm	2016	-6, -10, 56	-5, -7, 51		
Sauvage	2015			-2, 6, 56	-1, 9, 51
Taube	2015	-5, -15, 69	-4, -10, 62		
Lorey	2014	-6, -4, 64	-5, 0, 57		
Mizuguchi	2014a			-9, 1, 61	-8, 5, 55
Mizuguchi	2014b			-10, 4, 68	-9, 8, 61
van der Meulen	2014	0, -6, 69	0, -1, 62		
Zhang	2014	-12, -6, 60	-12, -2, 54		
Lorey	2013	-3, -4, 55	-2, -1, 50		
Oosterhof	2012			-8, 2, 65	-7, 6, 58
Szameitat	2012	-4, -8, 64	-3, -4, 57		
Formaggio	2010	-3, -11, 62	-2.2, -7.4, 56		
Guillot	2009	-5, -11, 72	-4, -5, 64	-10, 5, 68	-9, 9, 61
Lorey	2009	-9, -6, 60	-8, -2, 54		
Lui	2008			-8, 6, 44	-7, 7, 40
Orr	2008	-4, -6, 68	-3, -1, 61		
Kasess	2008	0, -5, 60	0, -1, 54		
Szameitat	2007			-5, 7, 52	-4, 10, 47
Kuhtz-Buschbeck	2003	-1, -13, 72	0, -8, 64		
Hanakawa	2003	-3, -7, 50	-2, -4, 46	-3, 5, 54	-2, 8, 49
Johnson	2002	-1, -10, 59	0, -6, 53	3, 10, 50	0, 13, 46
Gérardin	2000			-7, 13, 70	-6, 18, 63
Studies on action language					
Moody-Triantis	2014	-2, -2, 70	-1, 2, 63		
de Vega	2014	-4, -6, 64	-3, -2, 57	-8, 6, 66	-7, 10, 59
Tomasino	2014			-8, 12, 48	-7, 14, 44
Schuil	2013			-4, 18, 48	-3, 20, 44
Sakreida	2013			-3, 0, 62	-2, 4, 56
Tremblay	2011			-7, 1, 74	-6, 6, 66
Tomasino	2010			0, 4, 68	0, 8, 61
Boulenger	2009	-6, -14, 70	-5, -9, 63	-4, 10, 54	-3, 13, 49
Postle	2008			-1, 8, 63	0, 12, 57
Hauk	2008			-12, 14, 48	-11, 16, 44
Tomasino	2007			-4, 12, 50	-3, 14, 45
General mean		-5, -8, 64	-4, -4, 57	-5, 8, 58	-5, 11, 53
Language papers mean		-4, -7, 68	-3, -3, 61	-5, 9, 58	-4, 12, 53
Current study		**-3, -8, 66**	**-2, -3, 59**	**-3, 15, 60**	**-2, 19, 54**

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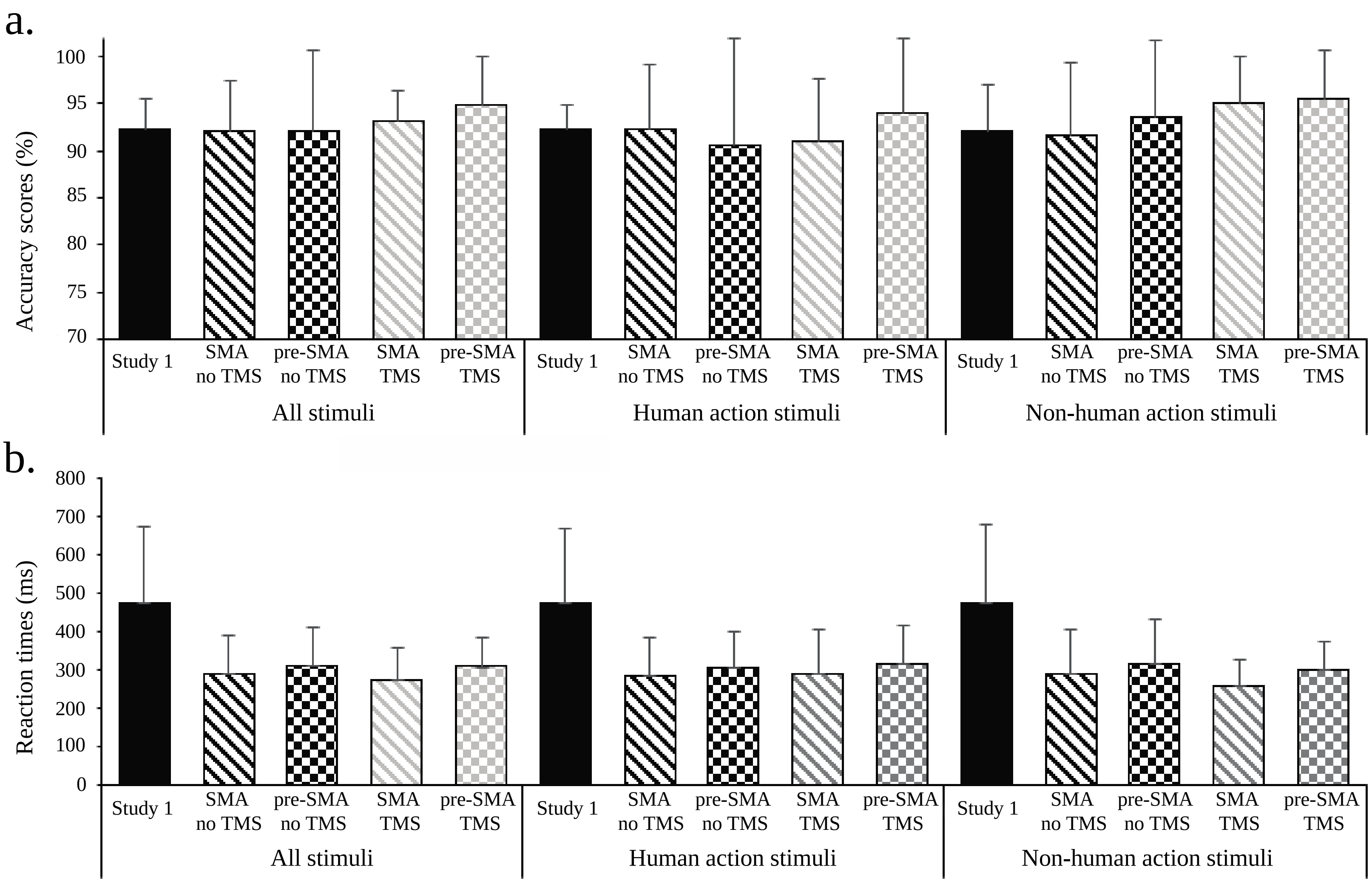

Supplementary Material S3: performance in Studies 1 and 2. Accuracy (Panel a) and reaction time (Panel b) averages for all stimuli, human and non-human stimuli, for the behavioral data of Study 1, and the no TMS and the TMS data of Study 2.