CORTEX XXX (2017) 1–15

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research report

Role of medial premotor areas in action language processing in relation to motor skills Q11

Q10 Melody Courson, Joël Macoir and Pascale Tremblay*

Q1 Département de Réadaptation, Université Laval, CERVO Brain Research Center, Québec, Qc., Canada

ARTICLE INFO

Article history:
Received 9 January 2017
Reviewed 06 March, 2017
Revised 4 May 2017
Accepted 2 August 2017
Action editor Alessandro Tavano
Published online xxx

Keywords:
Language embodiment
Supplementary motor area
Pre-supplementary motor area
Fine motor skills
Transcranial magnetic stimulation
Motor imagery

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.

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 (Rueschemeyer, Ekman, van Acheren, & Kilner, 2014; Rueschemeyer, Rooij, Lindemann, Willems, & Bekkering, 2010; Tremblay, & Small, 2011a, 2011b; de Vega et al., 2014; Q3
Wheatley, Weisberg, Beauchamps, & Martin, 2005), and the dorsal premotor cortex (Kana et al., 2015, 2012; de Vega et al., 2014; de Zubicaray, Arciuli, & McMahon, 2013). 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

* *Corresponding author*. Université Laval, Département de Réadaptation, CERVO Brain Research Center, 2601 rue de la Canardière, Office G-2317, Québec, Qc., G1J 2G3, Canada. Q2
E-mail address: Pascale.tremblay@fmed.ulaval.ca (P. Tremblay).

http://dx.doi.org/10.1016/j.cortex.2017.08.002

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; 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; de Vega et al., 2014). 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; van Dam, van Dijk, Bekkering, & Rueschemeyer, 2012; van Dam, Rueschemeyer, & Bekkering, 2010; 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., 2008, 2005; 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., 2009, 2008; Hanakawa, Dimyan, & Hallett, 2008; Hanakawa et al., 2003; Kasess et al., 2008; Lacourse, Orr, Cramer, & Cohen, 2005; Wang, Chen, Gong, Shen, & Gao, 2010; Xu et al., 2014), fist squeezing (Mizuguchi, Nakata, & Kanosue, 2014a; Mizuguchi et al., 2013; Pilgramm et al., 2016), finger or hand extension/flexion (Gerardin et al., 2000; Mizuguchi, Nakata, & Kanosue, 2014b; 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., 2010, 2011, 2009; 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 (Hauk, Davis, Kherif, & Pulvermüller, 2008; Papeo, Rumiati, Cecchetto, & Tomasino, 2012; Tomasino, Fink, Sparing, Dafotakis, & Weiss, 2008; Tomasino, Werner, Weiss, & Fink, 2007; Willems, Hagoort, & Casasanto, 2010; Willems, Toni et al., 2010; Yang & Shu, 2014). 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 (RTs) during a motor imagery task but not during action language reading (Tomasino et al., 2008). Yang and 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, Hagoort et al. (2010); Willems, Toni 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, Hagoort et al. (2010); Willems, Toni 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 (Ferri et al., 2012; de Lange, Helmich, & Toni, 2006; Seurinck, Vingerhoets, De Lange, & Achten, 2004; Vingerhoets, de Lange, Vandemaele, Deblaere, & Achten, 2002; Zapparoli et al., 2014). Results from half of these

Please cite this article in press as: Courson, M., et al., Role of medial premotor areas in action language processing in relation to motor skills, Cortex (2017), http://dx.doi.org/10.1016/j.cortex.2017.08.002

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) (Gerardin 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, repetitive transcranial magnetic stimulation (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 2 × 2 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 behavioral validation of SAT.

Please cite this article in press as: Courson, M., et al., Role of medial premotor areas in action language processing in relation to motor skills, Cortex (2017), http://dx.doi.org/10.1016/j.cortex.2017.08.002

3. Study 1b: behavioral validation of 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 .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, signaling 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 msec, 750 msec, 1000 msec) were randomly assigned to trials in order to prevent a habituation bias. The task was comprised of 256 trials and lasted approximately 20 min. 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 versus 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 RT (for correct responses only) using SPSS (23.0.0.2, IBM). There was no effect of Action on accuracy ($F_{(1,9)} = .00$, $p = 1.00$, $\eta^2 = .00$) or RT ($F_{(1,9)} = .08$, $p = .78$, $\eta^2 = .01$). 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 & Toussaint, 2015; Meugnot, Agbangla, & Toussaint, 2016). Stimuli represented right and left hands, in two different views (i.e., back and palm of the hand), in four different angles: 40°, 80°, 120°, 160°. 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 msec, block 2: 1750 msec, block 3: 1500 msec, block 4: 1250 msec, block 5: 1000 msec, block 6: 750 msec). 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 msec burst of a mean amplitude at least twice that of the preceding 50 msec 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 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 behavioral 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 SAT 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 × 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.

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 msec). 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 msec 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 et al., 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 Fig. 1. The order of stimulation of these two areas was randomized across participants.

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

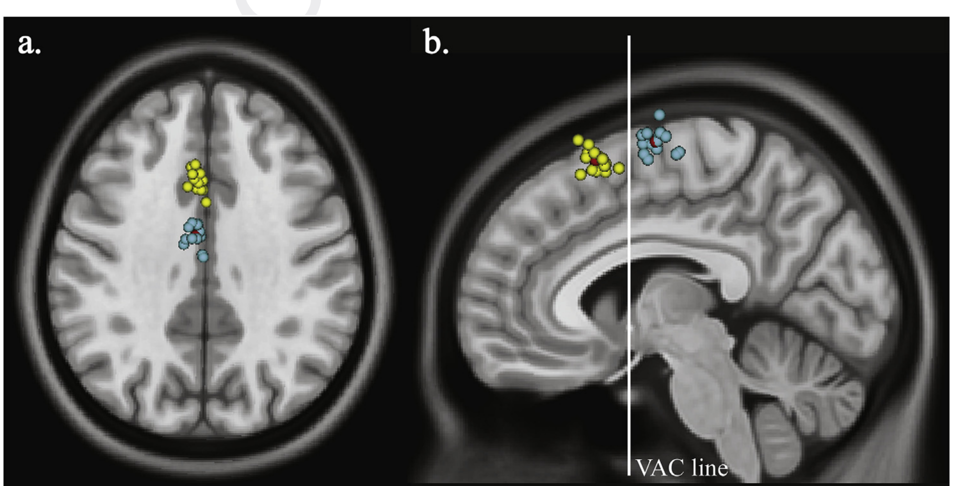

Fig. 1 – rTMS targets. Individual stimulation targets in the SMA (blue) and pre-SMA (yellow), and mean stimulation locations for each site (red). For SMA, the mean location is −3, −8, 66, and for pre-SMA, the mean location is −3, 15, 60.

Please cite this article in press as: Courson, M., et al., Role of medial premotor areas in action language processing in relation to motor skills, Cortex (2017), http://dx.doi.org/10.1016/j.cortex.2017.08.002

of effect sizes are provided in the form of partial eta squared (η_p^2), which are reported for all main effects and interactions. When comparing two means, we report effect sizes in the form of Cohen *d* statistics.

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 × 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 × 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 × Stimulation × Dexterity interaction (see Fig. 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: $f(x) = \left|(x_H - x_{NH})_{TMS} - (x_H - x_{NH})_{NOTMS}\right|$, 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 (Fig. 3). Two additional correlations were performed, using the following formula: $f(x) = |x_{TMS} - x_{NOTMS}|$, 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 Fig. 4.

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 ($r_{(11)} = .01$, $p = .98$, $r^2 = .00$).

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 × motor imagery	1	9	.241	.635	.026
Area × dexterity	1	9	.266	.619	.029
Stimulation	1	9	.801	.394	.082
Stimulation × motor imagery	1	9	.290	.603	.031
Stimulation × dexterity	1	9	.845	.382	.086
Area × stimulation	1	9	1.415	.265	.136
Area × stimulation × motor imagery	1	9	2.777	.130	.236
Area × stimulation × dexterity	1	9	.652	.440	.068
Reaction times					
Area	1	10	8.690	.015	.465
Area × motor imagery	1	10	4.197	.068	.296
Area × dexterity	1	10	8.764	.014	.467
Stimulation	1	10	.641	.442	.060
Stimulation × motor imagery	1	10	.185	.676	.018
Stimulation × Dexterity	1	10	.802	.391	.074
Area × stimulation	1	10	6.661	.027	.400
Area × stimulation × motor imagery	1	10	4732	.055	.321
Area × stimulation × dexterity	1	10	5.956	.035	.373

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,

Please cite this article in press as: Courson, M., et al., Role of medial premotor areas in action language processing in relation to motor skills, Cortex (2017), http://dx.doi.org/10.1016/j.cortex.2017.08.002

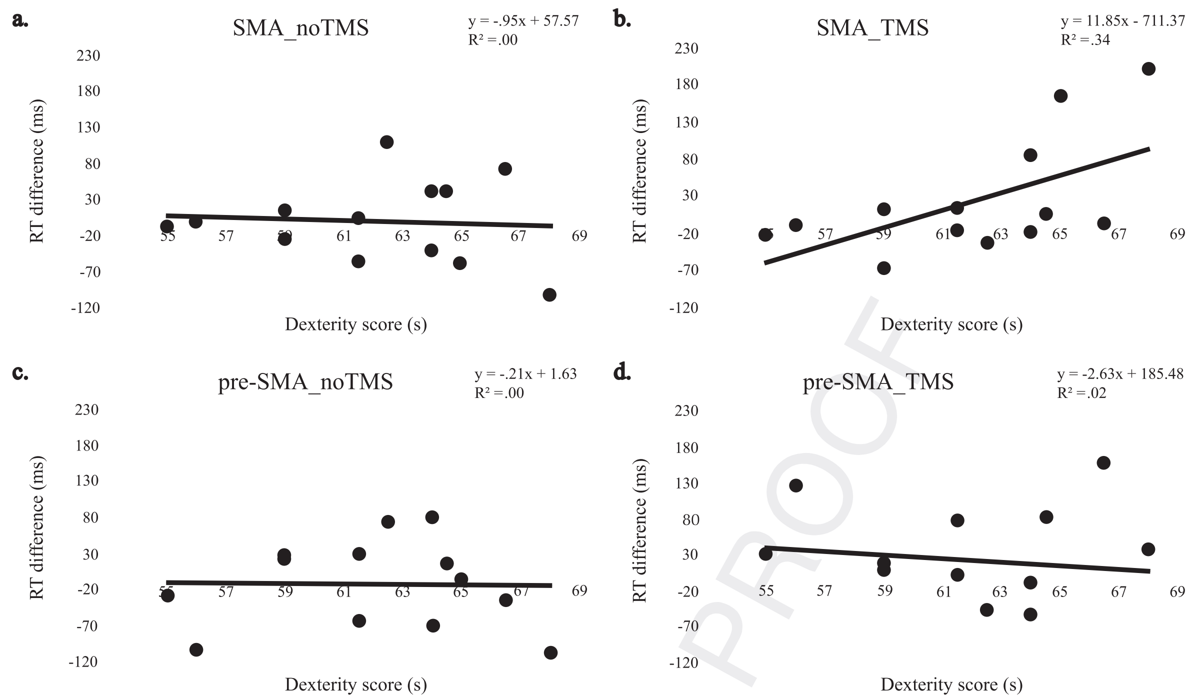

Fig. 2 – Involvement of SMA in action language processing. Relationship between dexterity and RT difference expressed in ms ($[f(x) = x_H - x_{NH}]$ where x_H is the mean RT for human actions and x_{NH} the mean RT for non-human actions), for rTMS administered over the SMA (b), for rTMS administered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

Table 2 – Detailed statistical results for correlation analyses decomposing the Area × Stimulation × Action effect.

Correlations	ddl	r	r^2	*p*
Area × stimulation × dexterity effect				
Dexterity × SMA_nostim	11	−.064	.003	.835
Dexterity × SMA_TMS	11	.586	.343	.035
Dexterity × pre-SMA_nostim	11	−.014	.000	.964
Dexterity × pre-SMA_TMS	11	−.135	.018	.659

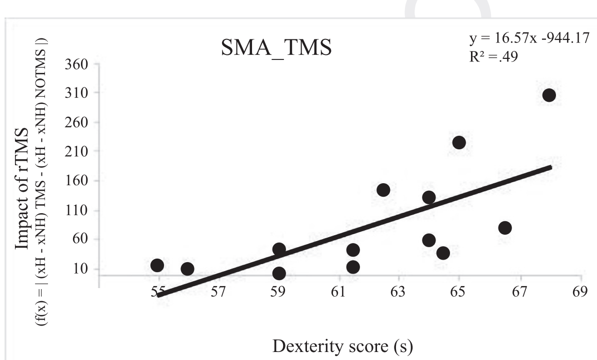

Fig. 3 – General impact of rTMS. Relationship between dexterity and the general impact of rTMS over SMA on the RT difference between human and non-human action trials during the semantic analogy task ($[f(x) = |(x_H - x_{NH})_{TMS} - (x_H - x_{NH})_{NOTMS}|]$ where x_H is the mean RT for human actions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

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

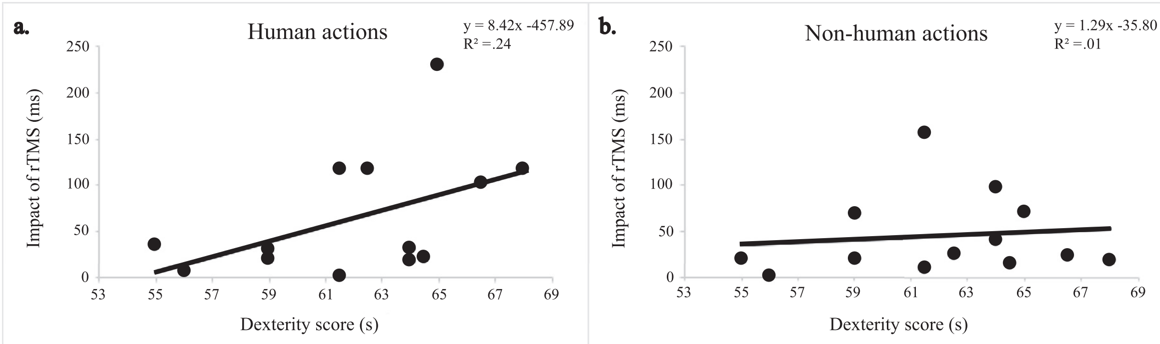

Fig. 4 – Impact of rTMS for human and non-human actions. Relationship between dexterity and the impact of rTMS over SMA [$f(x) = |x_{TMS} - x_{NOTMS}|$], for human action sentences (a), and non-human action sentences (b).

brain dissection (Bozkurt et al., 2016; Catani et al., 2012; Vergani et al., 2014) and diffusion imaging studies (Bozkurt et al., 2016; Catani et al., 2012; Lehéricy et al., 2004; Vergani et al., 2014) 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 et al., 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 behavior 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 & 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.

Uncited reference

Q9 Tomasino et al., 2012, Yang and Shu, 2012, Zwaan, 2016.

Acknowledgments

This study was supported by a Discovery grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) to P.T., from a Leader Opportunity Fund (LOF) from the Canadian Foundation for Innovation (FCI) to P.T. and from an Insight grant from the Social Sciences and Humanities Research Council of Canada (SSHRC) to J.M. P.T. holds a Career Award from the ‘‘Fonds de Recherche du Québec – Santé’’ (FRQS). M.C. is supported by scholarships from the Réseau de Bio-imagerie du Québec (RBIQ) and from the Centre Thématique de Recherche en Neurosciences de l'Université Laval (CTRN). Technical support for data analysis was provided by the “Consortium d'imagerie en neuroscience et santé mentale de Québec” (CINQ) via a platform support grant from the Brain Canada Foundation. The authors thank all the participants. Q6

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2017.08.002.

REFERENCES

Amador, N., & Fried, I. (2004). Single-neuron activity in the human supplementary motor area underlying preparation for action. *Journal of Neurosurgery, 100*, 250–259.

Aravena, P., Delevoye-Turrell, Y., Deprez, V., Cheylus, A., Paulignan, Y., Frak, V., et al. (2012). Grip force reveals the context sensitivity of language-induced motor activity during “action words” processing: Evidence from sentential negation. *PLoS One, 7*(12), e50287. http://dx.doi.org/10.1371/journal.pone.0050287.

Aziz-Zadeh, L., & Damasio, A. (2008). Embodied semantics for actions: Findings from functional brain imaging. *Journal of Physiology, Paris, 102*(1–3), 35–39. http://dx.doi.org/10.1016/j.jphysparis.2008.03.012.

Bedny, M., Caramazza, A., Grossman, E., Pascual-Leone, A., & Saxe, R. (2008). Concepts are more than percepts: The case of action verbs. *The Journal of Neuroscience: the Official Journal of the Society for Neuroscience, 28*(44), 11347–11353. http://dx.doi.org/10.1523/JNEUROSCI.3039-08.2008.

Beilock, S. L., Lyons, I. M., Mattarella-Micke, A., Nusbaum, H. C., & Small, S. L. (2008). Sports experience changes the neural processing of action language. *Proceedings of the National Academy of Sciences of the United States of America, 105*(36), 13269–13273. http://dx.doi.org/10.1073/pnas.0803424105.

Berman, B. D., Horovitz, S. G., Venkataraman, G., & Hallett, M. (2012). Self-modulation of primary motor cortex activity with motor and motor imagery tasks using real-time fMRI-based neurofeedback. *NeuroImage, 59*(2), 917–925. http://dx.doi.org/10.1016/j.neuroimage.2011.07.035.

Binder, J. R., & Desai, H. R. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences, 15*(11), 527–536.

Boulenger, V., Décoppet, N., Roy, A. C., Paulignan, Y., & Nazir, T. A. (2007). Differential effects of age-of-acquisition for concrete nouns and action verbs: Evidence for partly distinct representations? *Cognition, 103*(1), 131–146. http://dx.doi.org/10.1016/j.cognition.2006.03.001.

Boulenger, V., Hauk, O., & Pulvermüller, F. (2009). Grasping ideas with the motor system: Semantic somatotopy in idiom comprehension. *Cerebral Cortex, 19*(8), 1905–1914. http://dx.doi.org/10.1093/cercor/bhn217.

Bozkurt, B., Yagmurlu, K., Middlebrooks, E. H., Karadag, A., Ovalioglu, T. C., Jagadeesan, B., et al. (2016). Microsurgical and tractographic anatomy of the supplementary motor area complex in humans. *World Neurosurgery, 95*, 99–107. http://dx.doi.org/10.1016/j.wneu.2016.07.072.

Burianová, H., Lee, Y., Grady, C. L., & Moscovitch, M. (2013). Age-related dedifferentiation and compensatory changes in the functional network underlying face processing. *Neurobiology of Aging, 34*(12), 2759–2767. http://dx.doi.org/10.1016/j.neurobiolaging.2013.06.016.

Butson, M. L., Hyde, C., Steenbergen, B., & Williams, J. (2014). Assessing motor imagery using the hand rotation task: Does performance change across childhood? *Human Movement Science, 35*, 50–65. http://dx.doi.org/10.1016/j.humov.2014.03.013.

Carota, F., Moseley, R., & Pulvermüller, F. (2012). Body-part-specific representations of semantic noun categories. *Journal of Cognitive Neuroscience, 24*(6), 1492–1509. http://dx.doi.org/10.1162/jocn_a_00219.

Catani, M., Dell'Acqua, F., Vergani, F., Malik, F., Hodge, H., Roy, P., et al. (2012). Short frontal lobe connections of the human brain. *Cortex; a Journal Devoted To the Study of the Nervous System and Behavior, 48*(2), 273–291. http://dx.doi.org/10.1016/j.cortex.2011.12.001.

Chen, X., Scangos, K. W., & Stuphorn, V. (2010). Supplementary motor area exerts proactive and reactive control of arm movements. *Journal of Neuroscience, 30*(44), 14657–14675. http://dx.doi.org/10.1523/JNEUROSCI.2669-10.2010.

Conson, M., Mazzarella, E., Frolli, A., Esposito, D., Marino, N., Trojano, L., et al. (2013). Motor imagery in asperger syndrome: Testing action simulation by the hand laterality task. *PLoS One, 8*(7), 1–7. http://dx.doi.org/10.1371/journal.pone.0070734.

van Dam, W. O., Rueschemeyer, S. A., & Bekkering, H. (2010). How specifically are action verbs represented in the neural motor system: An fMRI study. *NeuroImage, 53*(4), 1318–1325. http://dx.doi.org/10.1016/j.neuroimage.2010.06.071.

van Dam, W. O., van Dijk, M., Bekkering, H., & Rueschemeyer, S.-A. (2012). Flexibility in embodied lexical-semantic representations. *Human Brain Mapping, 33*(10), 2322–2333. http://dx.doi.org/10.1002/hbm.21365.

Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., et al. (1994). Mapping motor representations with positron emission tomography. *Nature, 371*, 600–602.

Dechent, P., Merboldt, K.-D., & Frahm, J. (2004). Is the human primary motor cortex involved in motor imagery? *Cognitive Brain Research, 19*(2), 138–144. http://dx.doi.org/10.1016/j.cogbrainres.2003.11.012.

Desai, R. H., Binder, J. R., Conant, L. L., Mano, Q. R., & Seidenberg, M. S. (2011). The neural career of sensory-motor metaphors. *Journal of Cognitive Neuroscience, 23*(9), 2376–2386. http://dx.doi.org/10.1162/jocn.2010.21596.

Desai, R. H., Conant, L. L., Binder, J. R., Park, H., & Seidenberg, M. S. (2013). A piece of the action: Modulation of sensory-motor regions by action idioms and metaphors. *NeuroImage, 83*, 862–869. http://dx.doi.org/10.1016/j.neuroimage.2013.07.044.

Desai, R. H., Herter, T., Riccardi, N., Rorden, C., & Fridriksson, J. (2015). Concepts within reach: Action performance predicts action language processing in stroke. *Neuropsychologia, 71*, 217–224. http://dx.doi.org/10.1016/j.neuropsychologia.2015.04.006.

van Elk, M., van Schie, H. T., Zwaan, R. A., & Bekkering, H. (2010). The functional role of motor activation in language processing: Motor cortical oscillations support lexical-semantic retrieval. *NeuroImage, 50*(2), 665–677. http://dx.doi.org/10.1016/j.neuroimage.2009.12.123.

Fargier, R., & Laganaro, M. (2015). Neural dynamics of object noun, action verb and action noun production in picture naming. *Brain and Language, 150*, 129–142. http://dx.doi.org/10.1016/j.bandl.2015.09.004.

Ferri, F., Frassinetti, F., Ardizzi, M., Costantini, M., & Gallese, V. (2012). A sensorimotor network for the bodily self. *Journal of Cognitive Neuroscience, 24*(7), 1584–1595. http://dx.doi.org/10.1162/jocn_a_00230.

Formaggio, E., Storti, S. F., Cerini, R., Fiaschi, A., & Manganotti, P. (2010). Brain oscillatory activity during motor imagery in EEG-fMRI coregistration. *Magnetic Resonance Imaging, 28*(10), 1403–1412. http://dx.doi.org/10.1016/j.mri.2010.06.030.

Forstmann, B. U., Dutilh, G., Brown, S., Neumann, J., von Cramon, D. Y., Ridderinkhof, K. R., et al. (2008). Striatum and pre-SMA facilitate decision-making under time pressure. *Proceedings of the National Academy of Sciences of the United States of America, 105*(45), 17538–17542. http://dx.doi.org/10.1073/pnas.0805903105.

Frak, V., Paulignan, Y., & Jeannerod, M. (2001). Orientation of the opposition axis in mentally simulated grasping. *Experimental Brain Research, 136*(1), 120–127. http://dx.doi.org/10.1007/s002210000583.

Gerardin, E., Sirigu, A., Lehéricy, S., Poline, J. B., Gaymard, B., Marsault, C., et al. (2000). Partially overlapping neural networks for real and imagined hand movements. *Cerebral Cortex (New York, N.Y. : 1991), 10*(11), 1093–1104. Retrieved from: http://www.ncbi.nlm.nih.gov/pubmed/11053230.

Ghio, M., & Tettamanti, M. (2010). Semantic domain-specific functional integration for action-related vs. abstract concepts. *Brain and Language, 112*(3), 223–232. http://dx.doi.org/10.1016/j.bandl.2008.11.002.

Ghio, M., Vaghi, M. M. S., Perani, D., & Tettamanti, M. (2016). Decoding the neural representation of fine-grained conceptual categories. *NeuroImage, 132*, 93–103. http://dx.doi.org/10.1016/j.neuroimage.2016.02.009.

Glenberg, A. M., Sato, M., Cattaneo, L., Riggio, L., Palumbo, D., & Buccino, G. (2008). Processing abstract language modulates motor system activity (2006) *Quarterly Journal of Experimental Psychology, 61*(6), 905–919. http://dx.doi.org/10.1080/17470210701625550.

Glenberg, A. M., Witt, J. K., & Metcalfe, J. (2013). From the revolution to embodiment: 25 years of cognitive psychology. *Perspectives on Psychological Science, 8*(5), 573–585. http://dx.doi.org/10.1177/1745691613498098.

Grafton, S. T., Arbib, M. A., Fadiga, L., & Rissolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. *Experimental Brain Research, 112*, 103–111.

Guillot, A., Collet, C., Nguyen, V. A., Malouin, F., Richards, C., & Doyon, J. (2008). Functional neuroanatomical networks associated with expertise in motor imagery. *NeuroImage, 41*(4), 1471–1483. http://dx.doi.org/10.1016/j.neuroimage.2008.03.042.

Guillot, A., Collet, C., Nguyen, V. A., Malouin, F., Richards, C., & Doyon, J. (2009). Brain activity during visual versus kinesthetic imagery: An fMRI study. *Human Brain Mapping, 30*(7), 2157–2172. http://dx.doi.org/10.1002/hbm.20658.

Hagoort, P. (2014). Nodes and networks in the neural architecture for language: Broca's region and beyond. *Current Opinion in Neurobiology, 28*, 136–141.

Hanakawa, T., Dimyan, M. A., & Hallett, M. (2008). Motor planning, imagery, and execution in the distributed motor network: A time-course study with functional MRI. *Cerebral Cortex, 18*(12), 2775–2788. http://dx.doi.org/10.1093/cercor/bhn036.

Hanakawa, T., Immisch, I., Toma, K., Dimyan, M. A., Van Gelderen, P., & Hallett, M. (2003). Functional properties of brain areas associated with motor execution and imagery. *Journal of Neurophysiology, 89*(2), 989–1002. http://dx.doi.org/10.1152/jn.00132.2002.

Hauk, O., Davis, M. H., Kherif, F., & Pulvermüller, F. (2008). Imagery or meaning? Evidence for a semantic origin of category-specific brain activity in metabolic imaging. *The European Journal of Neuroscience, 27*(7), 1856–1866. http://dx.doi.org/10.1111/j.1460-9568.2008.06143.x.

Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron, 41*(2), 301–307. Retrieved from: http://www.ncbi.nlm.nih.gov/pubmed/14741110.

Hauk, O., & Pulvermüller, F. (2011). The lateralization of motor cortex activation to action-words. *Frontiers in Human Neuroscience, 5*, 1–10. http://dx.doi.org/10.3389/fnhum.2011.00149.

Hoenig, K., Sim, E.-J., Bochev, V., Herrnberger, B., & Kiefer, M. (2008). Conceptual flexibility in the human brain: Dynamic recruitment of semantic maps from visual, motor, and motion-related areas. *Journal of Cognitive Neuroscience, 20*(10), 1799–1814. http://dx.doi.org/10.1162/jocn.2008.20123.

Holt, L. E., & Beilock, S. L. (2006). Expertise and its embodiment: Examining the impact of sensorimotor skill expertise on the representation of action-related text. *Psychonomic Bulletin & Review, 13*(4), 694–701. http://dx.doi.org/10.3758/BF03193983.

Hoshi, E., & Tanji, J. (2004). Differential roles of neuronal activity in the supplementary and presupplementary motor areas : From information retrieval to motor planning and execution.

Journal of Neurophysiology, 92, 3482–3499. http://dx.doi.org/10.1152/jn.00547.2004.
Jeannerod, M., & Frak, V. (1999). Mental imaging of motor activity in humans. *Current Opinion in Neurobiology, 9*(6), 735–739. http://dx.doi.org/10.1016/S0959-4388(99)00038-0.
Johnson, S. H. (2000). Thinking ahead: The case for motor imagery in prospective judgements of prehension. *Cognition, 74*(1), 33–70. http://dx.doi.org/10.1016/S0010-0277(99)00063-3.
Johnson, S. (2002). Selective activation of a parietofrontal circuit during implicitly imagined prehension. *NeuroImage, 17*(4), 1693–1704. http://dx.doi.org/10.1006/nimg.2002.1265.
Kana, R. K., Ammons, C. J., Doss, C. F., Waite, M. E., Kana, B., Herringshaw, A. J., et al. (2015). Language and motor cortex response to comprehending accidental and intentional action sentences. *Neuropsychologia, 77*, 158–164. http://dx.doi.org/10.1016/j.neuropsychologia.2015.08.020.
Kana, R. K., Blum, E. R., Ladden, S. L., & Ver Hoef, L. W. (2012). "How to do things with words": Role of motor cortex in semantic representation of action words. *Neuropsychologia, 50*(14), 3403–3409. http://dx.doi.org/10.1016/j.neuropsychologia.2012.09.006.
Kasess, C. H., Windischberger, C., Cunnington, R., Lanzenberger, R., Pezawas, L., & Moser, E. (2008). The suppressive influence of SMA on M1 in motor imagery revealed by fMRI and dynamic causal modeling. *NeuroImage, 40*(2), 828–837. http://dx.doi.org/10.1016/j.neuroimage.2007.11.040.
Kemmerer, D., Castillo, J. G., Talavage, T., Patterson, S., & Wiley, C. (2008). Neuroanatomical distribution of five semantic components of verbs: Evidence from fMRI. *Brain and Language, 107*(1), 16–43. http://dx.doi.org/10.1016/j.bandl.2007.09.003.
King, A. (2016). Rise of resilience. *Nature, 351*, 818–819.
Lacourse, M. G., Orr, E. L. R., Cramer, S. C., & Cohen, M. J. (2005). Brain activation during execution and motor imagery of novel and skilled sequential hand movements. *NeuroImage, 27*(3), 505–519. http://dx.doi.org/10.1016/j.neuroimage.2005.04.025.
de Lange, F. P., Helmich, R. C., & Toni, I. (2006). Posture influences motor imagery: An fMRI study. *NeuroImage, 33*(2), 609–617. http://dx.doi.org/10.1016/j.neuroimage.2006.07.017.
Lau, H. C., Rogers, R. D., Ramnani, N., & Passingham, R. E. (2004). Willed action and attention to the selection of action. *NeuroImage, 21*(4), 1407–1415. http://dx.doi.org/10.1016/j.neuroimage.2003.10.034.
Lehéricy, S., Ducros, M., Krainik, A., Francois, C., Van De Moortele, P. F., Ugurbil, K., et al. (2004). 3-D diffusion tensor axonal tracking shows distinct SMA and pre-SMA projections to the human striatum. *Cerebral Cortex, 14*(12), 1302–1309. http://dx.doi.org/10.1093/cercor/bhh091.
Lorey, B., Bischoff, M., Pilgramm, S., Stark, R., Munzert, J., & Zentgraf, K. (2009). The embodied nature of motor imagery: The influence of posture and perspective. *Experimental Brain Research, 194*(2), 233–243. http://dx.doi.org/10.1007/s00221-008-1693-1.
Lorey, B., Naumann, T., Pilgramm, S., Petermann, C., Bischoff, M., Zentgraf, K., et al. (2013). How equivalent are the action execution, imagery, and observation of intransitive movements? Revisiting the concept of somatotopy during action simulation. *Brain and Cognition, 81*(1), 139–150. http://dx.doi.org/10.1016/j.bandc.2012.09.011.
Lorey, B., Pilgramm, S., Bischoff, M., Stark, R., Vaitl, D., Kindermann, S., et al. (2011). Activation of the parieto-premotor network is associated with vivid motor imagery-A parametric fMRI study. *PLoS One, 6*(5), 1–10. http://dx.doi.org/10.1371/journal.pone.0020368.
Lorey, B., Pilgramm, S., Walter, B., Stark, R., Munzert, J., & Zentgraf, K. (2010). Your mind's hand: Motor imagery of pointing movements with different accuracy. *NeuroImage, 49*(4), 3239–3247. http://dx.doi.org/10.1016/j.neuroimage.2009.11.038.
Lowe, C. J., Staines, W. R., & Hall, P. A. (2017). Effects of moderate exercise on cortical resilience: A transcranial magnetic stimulation study targeting the dorsolateral prefrontal cortex. *Psychosomatic Medicine, 79*(2), 43–52. http://dx.doi.org/10.1097/PSY.0000000000000361.
Luppino, G., Matelli, M., Camarda, R., & Rizzolatti, G. (1993). Corticocortical connections of area F3 (SMA-proper) and area F6 (pre-SMA) in the Macaque monkey. *Journal of Comparative Neurology, 338*(1), 114–140. http://dx.doi.org/10.1002/cne.903380109.
Lyons, I. M., Mattarella-Micke, A., Cieslak, M., Nusbaum, H. C., Small, S. L., & Beilock, S. L. (2010). The role of personal experience in the neural processing of action-related language. *Brain and Language, 112*(3), 214–222. http://dx.doi.org/10.1016/j.bandl.2009.05.006.
Macuga, K. L., & Frey, S. H. (2012). Neural representations involved in observed, imagined, and imitated actions are dissociable and hierarchically organized. *NeuroImage, 59*(3), 2798–2807. http://dx.doi.org/10.1016/j.neuroimage.2011.09.083.
Mahon, B. Z. (2015). What is embodied about cognition? *Language, Cognition and Neuroscience, 30*(4), 420–429. http://dx.doi.org/10.1080/23273798.2014.987791.
Mahon, B. Z., & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of Physiology, Paris, 102*, 59–70. http://dx.doi.org/10.1016/j.jphysparis.2008.03.004.
Meugnot, A., Agbangla, N. F., & Toussaint, L. (2016). Selective impairment of sensorimotor representations following short-term upper-limb immobilisation. *The Quarterly Journal of Experimental Psychology, 218*, 1–23. http://dx.doi.org/10.1080/17470218.2015.1125376.
Meugnot, A., & Toussaint, L. (2015). Functional plasticity of sensorimotor representations following short-term immobilization of the dominant versus non-dominant hands. *Acta Psychologica, 155*, 51–56. http://dx.doi.org/10.1016/j.actpsy.2014.11.013.
Mizuguchi, N., Nakata, H., Hayashi, T., Sakamoto, M., Muraoka, T., Uchida, Y., et al. (2013). Brain activity during motor imagery of an action with an object: A functional magnetic resonance imaging study. *Neuroscience Research, 76*(3), 150–155. http://dx.doi.org/10.1016/j.neures.2013.03.012.
Mizuguchi, N., Nakata, H., & Kanosue, K. (2014a). Activity of right premotor-parietal regions dependent upon imagined force level: An fMRI study. *Frontiers in Human Neuroscience, 8*, 810. http://dx.doi.org/10.3389/fnhum.2014.00810.
Mizuguchi, N., Nakata, H., & Kanosue, K. (2014b). Effector-independent brain activity during motor imagery of the upper and lower limbs: An fMRI study. *Neuroscience Letters, 581*, 69–74. http://dx.doi.org/10.1016/j.neulet.2014.08.025.
Moody-Triantis, C., Humphreys, G. F., & Gennari, S. P. (2014). Hand specific representations in language comprehension. *Frontiers in Human Neuroscience, 8*, 1–10. http://dx.doi.org/10.3389/fnhum.2014.00360.
Moody, C. L., & Gennari, S. P. (2010). Effects of implied physical effort in sensory-motor and pre-frontal cortex during language comprehension. *NeuroImage, 49*(1), 782–793. http://dx.doi.org/10.1016/j.neuroimage.2009.07.065.
Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S., Whitehead, V., Collin, I., et al. (2005). The montreal cognitive assessment, MoCA : A brief screening tool for mild cognitive impairment. *Journal of the American Geriatric Society, 53*, 695–699.
Obeso, I., Robles, N., Marrón, E. M., & Redolar-Ripoll, D. (2013). Dissociating the role of the pre-SMA in response inhibition and switching: A combined online and offline TMS approach.

Frontiers in Human Neuroscience, 7, 150. http://dx.doi.org/10.3389/fnhum.2013.00150.
Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia, 9(1), 97–113. http://dx.doi.org/10.1016/0028-3932(71)90067-4.
Oosterhof, N. N., Tipper, S. P., & Downing, P. E. (2012). Visuo-motor imagery of specific manual actions: A multi-variate pattern analysis fMRI study. NeuroImage, 63(1), 262–271. http://dx.doi.org/10.1016/j.neuroimage.2012.06.045.
Papeo, L., Rumiati, R. I., Cecchetto, C., & Tomasino, B. (2012). On-line changing of thinking about words: The effect of cognitive context on neural responses to verb reading. Journal of Cognitive Neuroscience, 24(12), 2348–2362. http://dx.doi.org/10.1162/jocn_a_00291.
Peck, K. K., Bradbury, M., Psaty, E. L., Brennan, N. P., & Holodny, A. I. (2009). Joint activation of the supplementary motor area and presupplementary motor area during simultaneous motor and language functional MRI. NeuroReport, 20(5), 487–491. http://dx.doi.org/10.1097/WNR.0b013e3283297d71.
Pilgramm, S., de Haas, B., Helm, F., Zentgraf, K., Stark, R., Munzert, J., et al. (2016). Motor imagery of hand actions: Decoding the content of motor imagery from brain activity in frontal and parietal motor areas. Human Brain Mapping, 37(1), 81–93. http://dx.doi.org/10.1002/hbm.23015.
Postle, N., McMahon, K. L., Ashton, R., Meredith, M., & de Zubicaray, G. I. (2008). Action word meaning representations in cytoarchitectonically defined primary and premotor cortices. NeuroImage, 43(3), 634–644. http://dx.doi.org/10.1016/j.neuroimage.2008.08.006.
Pulvermüller, F. (2005). Brain mechanisms linking language and action. Nature, 6, 576–582.
Pulvermüller, F., Cook, C., & Hauk, O. (2012). Inflection in action: Semantic motor system activation to noun- and verb-containing phrases is modulated by the presence of overt grammatical markers. NeuroImage, 60(2), 1367–1379. http://dx.doi.org/10.1016/j.neuroimage.2011.12.020.
Pulvermüller, F., Shtyrov, Y., Ilmoniemi, R. J., & Marslen-Wilson, W. D. (2006). Tracking speech comprehension in space and time. NeuroImage, 31(3), 1297–1305. http://dx.doi.org/10.1016/j.neuroimage.2006.01.030.
Raposo, A., Moss, H. E., Stamatakis, E. a, & Tyler, L. K. (2009). Modulation of motor and premotor cortices by actions, action words and action sentences. Neuropsychologia, 47(2), 388–396. http://dx.doi.org/10.1016/j.neuropsychologia.2008.09.017.
Rossi, S., Hallett, M., Rossini, P. M., & Pascual-Leone, A. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. Clinical Neurophysiology, 120(12), 2008–2039. http://dx.doi.org/10.1016/j.clinph.2009.08.016.
Roth, M., Decety, J., Raybaudi, M., Massarelli, R., Delon-Martin, C., Segebarth, C., et al. (1996). Possible involvement of primary motor cortex in mentally simulated movement: A functional magnetic resonance imaging study. Cognitive Neuroscience, 7, 1280–1284.
Rueschemeyer, S.-A., Ekman, M., van Acheren, M., & Kilner, J. (2014). Observing, performing, and understanding actions: Revisiting the role of cortical motor areas in processing of action words. Journal of Cognitive Neuroscience, 26(8), 1644–1653. http://dx.doi.org/10.1162/jocn.
Rueschemeyer, S., Rooij, D. Van, Lindemann, O., Willems, R. M., & Bekkering, H. (2010). The function of words : Distinct neural correlates for words denoting differently manipulable objects. Journal of Cognitive Neuroscience, 22(8), 1844–1851. Q7
Rushworth, M. F. S., Hadland, K. A., Paus, T., & Sipila, P. K. (2002). Role of the human medial frontal cortex in task switching: A combined fMRI and TMS study. Journal of Neurophysiology, 87, 2577–2592. http://dx.doi.org/10.1152/jn.00812.2001.
Sakreida, K., Scorolli, C., Menz, M. M., Heim, S., Borghi, A. M., & Binkofski, F. (2013). Are abstract action words embodied? An fMRI investigation at the interface between language and motor cognition. Frontiers in Human Neuroscience, 7, 125. http://dx.doi.org/10.3389/fnhum.2013.00125.
Samur, D., Lai, V. T., Hagoort, P., & Willems, R. M. (2015). Emotional context modulates embodied metaphor comprehension. Neuropsychologia, 78, 108–114. http://dx.doi.org/10.1016/j.neuropsychologia.2015.10.003.
Sauvage, C., Poirriez, S., Manto, M., Jissendi, P., & Habas, C. (2011). Reevaluating brain networks activated during mental imagery of finger movements using probabilistic Tensorial Independent Component Analysis (TICA). Brain Imaging and Behavior, 5(2), 137–148. http://dx.doi.org/10.1007/s11682-011-9118-3.
Schuil, K. D. I., Smits, M., & Zwaan, R. A. (2013). Sentential context modulates the involvement of the motor cortex in action language processing: An FMRI study. Frontiers in Human Neuroscience, 7, 100. http://dx.doi.org/10.3389/fnhum.2013.00100.
Seurinck, R., Vingerhoets, G., De Lange, F. P., & Achten, E. (2004). Does egocentric mental rotation elicit sex differences? NeuroImage, 23(4), 1440–1449. http://dx.doi.org/10.1016/j.neuroimage.2004.08.010.
Sharma, N., & Baron, J. (2013). Does motor imagery share neural networks with executed movement : A multivariate fMRI analysis. Frontiers in Human Neuroscience, 7, 1–8. http://dx.doi.org/10.3389/fnhum.2013.00564.
Solodkin, A., Hlustik, P., Chen, E. E., & Small, S. L. (2004). Fine modulation in network activation during motor execution and motor imagery. Cerebral Cortex, 14(11), 1246–1255. http://dx.doi.org/10.1093/cercor/bhh086.
Stippich, C., Ochmann, H., & Sartor, K. (2002). Somatotopic mapping of the human primary sensorimotor cortex during motor imagery and motor execution by functional magnetic resonance imaging. Neuroscience Letters, 331(1), 50–54. http://www.ncbi.nlm.nih.gov/pubmed/12359321.
Strack, G., Kaufmann, C., Kherer, S., Brandt, S., & Stürmer, B. (2013). Anticipatory regulation of action control in a simon task: Behavioral, electrophysiological, amd fMRI correlates. Frontiers in Psychology, 4, 47. http://dx.doi.org/10.3389/fpsyg.2013.00047.
Szameitat, A. J., McNamara, A., Shen, S., & Sterr, A. (2012). Neural activation and functional connectivity during motor imagery of bimanual everyday actions. PLoS One, 7(6), e38506. http://dx.doi.org/10.1371/journal.pone.0038506.
Tankus, A., Yeshurun, Y., Flash, T., & Fried, I. (2009). Encoding of speed and direction of movement in the human supplementary motor area. Journal of Neurosurgery, 110(6), 1304–1316. http://dx.doi.org/10.3171/2008.10.JNS08466.
Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., et al. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. Journal of Cognitive Neuroscience, 17(2), 273–281. http://dx.doi.org/10.1162/0898929053124965.
Tomasino, B., Budai, R., Mondani, M., Skrap, M., & Rumiati, R. I. (2005). Mental rotation in a patient with an implanted electrode grid in the motor cortex. NeuroReport, 16(16), 1795–1800. http://dx.doi.org/10.1097/01.wnr.0000185957.65723.52.
Tomasino, B., Fabbro, F., & Brambilla, P. (2014). How do conceptual representations interact with processing demands: An fMRI study on action- and abstract-related words. Brain Research, 1591, 38–52. http://dx.doi.org/10.1016/j.brainres.2014.10.008.
Tomasino, B., Fink, G. R., Sparing, R., Dafotakis, M., & Weiss, P. H. (2008). Action verbs and the primary motor cortex: A comparative TMS study of silent reading, frequency judgments, and motor imagery. Neuropsychologia, 46(7),

1915–1926. http://dx.doi.org/10.1016/j.neuropsychologia.2008.01.015.
Tomasino, B., Guatto, E., Rumiati, R. I., & Fabbro, F. (2012). The role of volleyball expertise in motor simulation. *Acta Psychologica, 139*(1), 1–6. http://dx.doi.org/10.1016/j.actpsy.2011.11.006.
Tomasino, B., Maieron, M., Guatto, E., Fabbro, F., & Rumiati, R. I. (2013). How are the motor system activity and functional connectivity between the cognitive and sensorimotor systems modulated by athletic expertise? *Brain Research, 1540*, 21–41. http://dx.doi.org/10.1016/j.brainres.2013.09.048.
Tomasino, B., Weiss, P. H., & Fink, G. R. (2010). To move or not to move: Imperatives modulate action-related verb processing in the motor system. *Neuroscience, 169*(1), 246–258. http://dx.doi.org/10.1016/j.neuroscience.2010.04.039.
Tomasino, B., Werner, C. J., Weiss, P. H., & Fink, G. R. (2007). Stimulus properties matter more than perspective: An fMRI study of mental imagery and silent reading of action phrases. *NeuroImage, 36*(Suppl. 2), T128–T141. http://dx.doi.org/10.1016/j.neuroimage.2007.03.035.
Tremblay, P., & Dick, A. S. (2016). Broca and Wernicke are dead, or moving past the classic model of language neurobiology. *Brain and Language, 162*, 60–71. http://dx.doi.org/10.1016/j.bandl.2016.08.004.
Tremblay, P., & Gracco, V. (2009). Contribution of the pre-SMA to the production of words and non-speech oral motor gestures, as revealed by repetitive transcranial magnetic stimulation (rTMS). *Brain Research, 1268*, 112–124.
Tremblay, P., & Small, S. L. (2010). From language comprehension to action understanding and back again. *Cerebral Cortex (New York, N.Y. : 1991), 21*(5), 1166–1177. http://dx.doi.org/10.1093/cercor/bhq189.
Tremblay, P., & Small, S. L. (2011a). From language comprehension to action understanding and back again. *Cerebral Cortex, 21*(5), 1166–1177. http://dx.doi.org/10.1093/cercor/bhq189.
Q8
Tremblay, P., & Small, S. L. (2011b). On the context-dependent nature of the contribution of the ventral premotor cortex to speech perception. *NeuroImage, 57*(4), 1561–1571. http://dx.doi.org/10.1016/j.neuroimage.2011.05.067.
Troyer, M., Curley, L. B., Miller, L. E., Saygin, A. P., & Bergen, B. K. (2014). Action verbs are processed differently in metaphorical and literal sentences depending on the semantic match of visual primes. *Frontiers in Human Neuroscience, 8*, 982. http://dx.doi.org/10.3389/fnhum.2014.00982.
Urrutia, M., Gennari, S. P., & de Vega, M. (2012). Counterfactuals in action: An fMRI study of counterfactual sentences describing physical effort. *Neuropsychologia, 50*(14), 3663–3672. http://dx.doi.org/10.1016/j.neuropsychologia.2012.09.004.
de Vega, M., León, I., Hernández, J., Valdés, M., Padrón, I., & Ferstl, E. (2014). Action sentences activate sensory motor regions in the brain independently of their status of reality. *Journal of Cognitive Neuroscience*, 1–10. http://dx.doi.org/10.1162/jocn.
Vergani, F., Lacerda, L., Martino, J., Attems, J., Morris, C., Mitchell, P., et al. (2014). White matter connections of the supplementary motor area in humans. *Journal of Neurology, Neurosurgery, and Psychiatry*. http://dx.doi.org/10.1136/jnnp-2013-307492.
Vingerhoets, G., de Lange, F. P., Vandemaele, P., Deblaere, K., & Achten, E. (2002). Motor imagery in mental rotation: An fMRI study. *NeuroImage, 17*(3), 1623–1633. http://dx.doi.org/10.1006/nimg.2002.1290.
Vromen, A., Verbunt, J. a, Rasquin, S., & Wade, D. T. (2011). Motor imagery in patients with a right hemisphere stroke and unilateral neglect. *Brain Injury, 25*(4), 387–393. http://dx.doi.org/10.3109/02699052.2011.558041.
Wang, Y., Chen, H., Gong, Q., Shen, S., & Gao, Q. (2010). Analysis of functional networks involved in motor execution and motor imagery using combined hierarchical clustering analysis and independent component analysis. *Magnetic Resonance Imaging, 28*(5), 653–660. http://dx.doi.org/10.1016/j.mri.2010.02.008.
Wassermann, E. M. (1998). Risk and safety of repetitive transcranial magnetic stimulation : Report and suggested guidelines from the international workshop on the safety of repetitive transcranial magnetic stimulation. *Electroencephalography and Clinical Neurophysiology, 108*, 1–16. http://dx.doi.org/10.1016/S0168-5597(97)00096-8.
Wheatley, T., Weisberg, J., Beauchamps, M. S., & Martin, A. (2005). Automatic priming of semantically related words reduces activity in the fusiform gyrus. *Journal of Cognitive Neuroscience, 17*(12), 1871–1885.
Willems, R. M., Hagoort, P., & Casasanto, D. (2010). Body-specific representations of action verbs: Neural evidence from right- and left-handers. *Psychological Science, 21*(1), 67–74.
Willems, R. M., Toni, I., Hagoort, P., & Casasanto, D. (2010). Neural dissociations between action verb understanding and motor imagery. *Journal of Cognitive Neuroscience, 22*(10), 2387–2400. http://dx.doi.org/10.1162/jocn.2009.21386.
Xu, L., Zhang, H., Hui, M., Long, Z., Jin, Z., Liu, Y., et al. (2014). Motor execution and motor imagery: a comparison of functional connectivity patterns based on graph theory. *261*, 184–194. http://dx.doi.org/10.1016/j.neuroscience.2013.12.005.
Yang, J., & Shu, H. (2012). The role of the premotor cortex and the primary motor cortex in action verb comprehension: Evidence from granger causality analysis. *Brain Research Bulletin, 88*(5), 460–466. http://dx.doi.org/10.1016/j.brainresbull.2012.04.006.
Yang, J., & Shu, H. (2014). Passive reading and motor imagery about hand actions and tool-use actions: An fMRI study. *Experimental Brain Research, 232*(2), 453–467. http://dx.doi.org/10.1007/s00221-013-3753-4.
Zapparoli, L., Invernizzi, P., Gandola, M., Berlingeri, M., De Santis, A., Zerbi, A., et al. (2014). Like the back of the (right) hand? A new fMRI look on the hand laterality task. *Experimental Brain Research, 232*(12), 3873–3895. http://dx.doi.org/10.1007/s00221-014-4065-z.
de Zubicaray, G., Arciuli, J., & McMahon, K. (2013). Putting an "end" to the motor cortex representations of action words. *Journla of Cognitive Neuroscience, 25*(11), 1957–1974. http://dx.doi.org/10.1162/jocn.
Zwaan, R. A. (2014). Embodiment and language comprehension: Reframing the discussion. *Trends in Cognitive Sciences, 18*(5), 229–234. http://dx.doi.org/10.1016/j.tics.2014.02.008.
Zwaan, R. A. (2016). Situation models, mental simulations, and abstract concepts in discourse comprehension. *Psychonomic Bulletin & Review, 23*, 1028–1034. http://dx.doi.org/10.3758/s13423-015-0864-x.