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Abstract

Does language comprehension depend, in part, on neural systems for action? In previous studies, motor areas of the brain were activated when people read or listened to action verbs, but it remains unclear whether such activation is functionally relevant for comprehension. In the experiments reported here, we used off-line theta-burst transcranial magnetic stimulation to investigate whether a causal relationship exists between activity in premotor cortex and action-language understanding. Right-handed participants completed a lexical decision task, in which they read verbs describing manual actions typically performed with the dominant hand (e.g., "to throw," "to write") and verbs describing nonmanual actions (e.g., "to earn," "to wander"). Responses to manual-action verbs (but not to nonmanual-action verbs) were faster after stimulation of the hand area in left premotor cortex than after stimulation of the hand area in right premotor cortex. These results suggest that premotor cortex has a functional role in action-language understanding.

Keywords

According to theories of embodied cognition, word meaning is constituted in part by activity in brain areas involved in perception and action (e.g., Barsalou, 2008; Zwaan, 2004). Consistent with this account, studies using functional MRI (fMRI) have demonstrated effector-specific activity in the brain's motor system during action-language processing (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Hauk, Johnsrude, & Pulvermüller, 2004; Tettamanti et al., 2005; Willems, Hagoort, & Casasanto, 2010; but see Kemmerer & Gonzalez-Castillo, 2010; Postle, McMahon, Ashton, Meredith, & de Zubicaray, 2008). According to embodied-cognition accounts, this activity in cortical motor areas is part of a verb's semantics.

Yet these data are also consistent with an alternative proposal (Mahon & Caramazza, 2008). Motor activity cued by action language could be a downstream consequence of "true" semantic processing (see discussion in Willems & Hagoort, 2007). In an effort to demonstrate a functional role for motor areas in the understanding of action language, researchers

have tested how rapidly motor areas are activated in response to language. Differences between the premotor correlates of leg-, arm-, and face-related words emerge around 200 ms after word presentation (Hauk & Pulvermüller, 2004; Pulvermüller, Shtyrov, & Ilmoniemi, 2005). Such rapidity is evidence against the possibility that language-related motor activity is only a consequence of explicit motor imagery (Farah, 1989; Willems, Toni, Hagoort, & Casasanto, 2010). However, these correlational data do not speak to the functional significance of motor activity in the construction of meaning (Mahon & Caramazza, 2008).

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To investigate a possible causal role for the motor system, researchers applied single-pulse transcranial magnetic stimulation (TMS) to motor areas and measured motor evoked potentials (MEPs) in the hands or feet of participants while they processed language about hand or foot actions (Buccino et al., 2005; Papeo, Vallesi, Isaja, & Rumiati, 2009). Reading verbs modulated MEPs in participants' relevant body parts; this modulation demonstrated that language mediates the causal link between activation of motor cortex and excitability of muscles in the limbs. Still, these findings do not imply that the motor system is involved in language processing per se. The contraction of muscles in the limbs in these studies is most easily interpreted as an effect of language comprehension, not as a constituent of language processing.

Does sensorimotor activity contribute to language comprehension? We used theta-burst TMS to test whether modulating activity in the motor system would affect performance on a language-processing task. Right-handed participants performed a lexical decision task (Meyer & Schvaneveldt, 1971) after theta-burst stimulation (TBS) was applied over the hand area of left premotor cortex in one experimental session and over the hand area of right premotor cortex in another session. We compared the effects of stimulation on reaction times to verbs describing actions associated with dominant-hand movements (e.g., "to throw," "to write") with its effects on reaction times to verbs describing nonmanual actions (e.g., "to wander," "to earn").

In right-handers, manual-action verbs preferentially activate the premotor hand area in the left hemisphere, which mainly controls actions performed by the right hand (Tettamanti et al., 2005; Willems, Hagoort, & Casasanto, 2010). We predicted that applying TBS over premotor cortex would modulate reaction times more strongly for manual-action verbs than for nonmanual-action verbs and that the strength of the effect of TBS on reaction times would depend on whether it was applied over left or right premotor cortex.

Method

Participants

Twenty participants took part in the main experiment, but data from 2 participants were discarded because of experimental error. The remaining 18 participants (7 males, 11 females; mean age = 23.5 years, range = 19–35 years) were right-handed, with a mean score of 93 (median = 100, range = 67–100) on the Edinburgh Handedness Inventory (Oldfield, 1971); they had no history of psychiatric or neurological illness and were not taking medication at the time of the test. Eight participants (4 males, 4 females; mean age = 23.6 years, range = 20–35 years; Edinburgh Handedness Inventory score: M = 92, median = 94, range = 82–100) took part in a control experiment (6 of these 8 participants were included in both the main experiment and the control experiment). All participants took part in two sessions: one session in which TBS was applied over left premotor cortex and one in which TBS was applied over right premotor cortex. The institutional review board at the University of California, Berkeley, approved the experiment.

Materials

Stimuli in the main experiment were 192 English verbs describing concrete actions (for a list of the stimuli and their characteristics, see the Supplemental Material available online). Half of the stimuli referred to actions mainly performed with the dominant hand (manual-action verbs; e.g., "to throw," "to write"; Willems, Hagoort, & Casasanto, 2010), whereas the other half referred to actions that are not performed with the dominant hand (nonmanual-action verbs; e.g., "to wander," "to earn"). The stimuli were matched for lexical frequency (Brysbaert & New, 2009; Coltheart, 1981) and word length (Coltheart, 1981; $|t| < 1$). We also created 96 pronounceable pseudoverbs (e.g., "to barst," "to wunger"), which were matched in length to the action verbs.

The manual-action verbs differed from the nonmanual-action verbs not only in their effector-specificity, but also in concreteness and, presumably, imageability. Our previous fMRI study showed selective activation of hand areas in premotor cortex even when manual- and nonmanual-action verbs were equated for imageability (Willems, Hagoort, & Casasanto, 2010). Furthermore, hand-area activation cued by verbs could not be attributed to conscious motor imagery (Willems, Toni, et al., 2010).

We conducted a control experiment to directly assess the effect of concreteness. Stimuli included nouns that referred to nonmanipulable entities with either high or low concreteness (Ms = 557 vs. 313), $t(190) = 45.14$, $p < .0001$, and high or low imageability (Ms = 567 vs. 355), $t(190) = 36.85$, $p < .0001$ (concreteness and imageability were assessed using the database from Coltheart, 1981; for linguistic properties of the stimuli, see the Supplemental Material available online). There were 96 concrete nouns (e.g., "the moon," "the farm"), 96 nonconcrete nouns (e.g., "the topic," "the mercy"), and 96 pseudonouns. Stimuli were matched for lexical frequency (Brysbaert & New, 2009; Coltheart, 1981) and word length, $|t| < 1$.

Procedure

The procedure was the same for the main experiment and the control experiment. Stimuli were presented in 18-point black type in the middle of a computer monitor, on a white background. Participants were seated approximately 25 cm from the screen. They indicated whether letter strings presented onscreen were English words or not (lexical decision task) by pressing a button with their left or right index finger. The response options for a given trial ("yes" or "no") were presented below the verb, and each option was displaced 4.5 cm to the left or right of the middle of the screen. We used a flexible response-mapping scheme so that the left/right position of

the response options varied randomly. Stimuli remained on screen until a response was registered. Participants were instructed to respond as quickly and accurately as possible.

Each trial consisted of the presentation of one stimulus. Stimuli were presented in the infinitive form (e.g., "to scowl") to signal that they were verbs and not nouns. The order of stimulus presentation was randomized, and the intertrial interval was 1 s. There were 48 trials per stimulus type per session, and materials were not repeated over sessions. The order of stimulation site (left premotor cortex, right premotor cortex) was counterbalanced across participants.

Participants completed 18 practice trials. Stimuli used in the practice trials were not presented in the main experiment or in the control experiment.

Data acquisition

A Magstim (Whitland, Wales, United Kingdom) Rapid figure-eight coil was used to generate the TBS (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005). Six hundred pulses were administered in bursts of three pulses at 5 Hz (total stimulation duration was 40 s). Application of TBS over motor cortex following this procedure changes the excitability of cortical tissue for up to 60 min (Huang et al., 2005, 2009). In accordance with safety guidelines, participants remained silent and did not move for 10 min after stimulation, and the two test sessions were separated by at least 1 week (Huang et al., 2005; Rossi, Hallett, Rossini, & Pascual-Leone, 2009).

For each participant, we first determined separately for the two stimulation sites the stimulation level required to elicit MEPs in the first dorsal interosseous muscle of the hand on 5 out of 10 trials, while the participant maintained a contraction level at 20% of maximum force. In the experiment proper, the intensity of the TBS applied was 80% of the threshold determined for each participant (Huang et al., 2005, 2009; Rossi et al., 2009). No difference in stimulation intensity for the two hemispheres was observed (left hemisphere: $M = 40.5\%$ of maximum stimulation output, $SD = 4.94\%$; right hemisphere: $M = 41.7\%$ of maximum stimulation output, $SD = 4.79\%$; $|t| < 1$).

Location of stimulation was determined on the basis of our previous fMRI experiment (Willems, Hagoort, & Casasanto, 2010). Comparing activation during reading of manual- and nonmanual-action verbs, we had observed dorsal premotor cortex activation at the following Montreal Neurological Institute coordinates—left hemisphere: $x = -35$, $y = -1$, $z = 53$; right hemisphere: $x = 34$, $y = 0$, $z = 53$ (see Fig. S1 in the Supplemental Material). In the current experiment, we targeted these areas using a T1-weighted anatomical scan. Brainsight software (Rogue Research, Montreal, Quebec, Canada) was used to determine correspondence between the location at the skull and the site of stimulation on the scan. The normalized regions were taken as a guideline, and stimulation sites were determined in native space on the basis of visual

inspection of landmarks on each individual's MRI. The locations were not normalized to a standardized template.

Data analysis

Incorrect responses were excluded from analysis, and outliers were removed by excluding values 3 standard deviations above or below the overall mean for each participant. We used a repeated measures analysis of variance employing a mixed-effects linear model with hemisphere (left premotor TBS vs. right premotor TBS) and verb type (manual action vs. non-manual action) as fixed effects, and participants and items as random effects.[1] This procedure effectively combines analysis over participants and items, allowing generalization to the general subject and language population (Baayen, Davidson, & Bates, 2008). All main effects and interactions were tested, and post hoc comparisons involved two-tailed t tests.

Analysis of the control-experiment data was conducted similarly using a model with hemisphere (left premotor TBS vs. right premotor TBS) and noun type (concrete vs. nonconcrete) as fixed effects and participants and items as random effects.
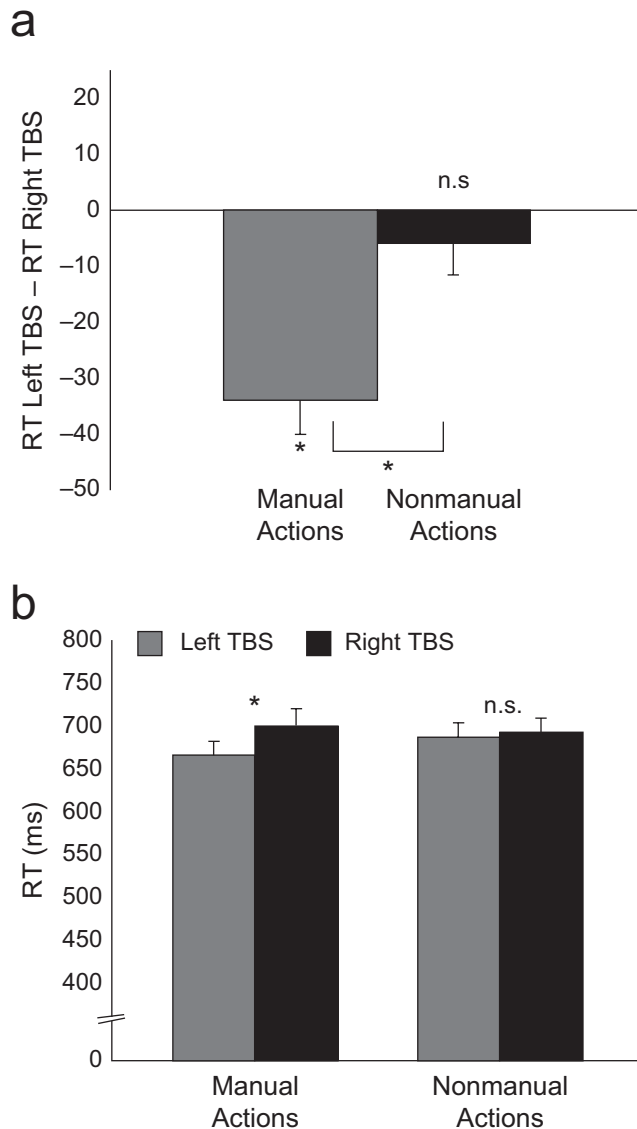
Results

Main experiment

Results for the main experiment showed a Hemisphere × Verb Type interaction, $F(1, 3152) = 5.97$, $r = .09$, $SE = 11.7$, $p = .015$ (see Fig. 1 and Table 1). Responses to manual-action verbs were faster after stimulation of left premotor cortex than after stimulation of right premotor cortex (mean difference = -34.1 ms), $t(3159) = 4.36$, $r = .11$, $SE = 8.2$, $p < .001$. This effect was not observed for the nonmanual-action verbs (mean difference = -5.8 ms), $|t| < 1$. There was a main effect of hemisphere, $F(1, 3152) = 13.46$, $r = .08$, $SE = 8.3$, $p < .001$, but not of verb type ($F < 1$). Reaction times for pseudoverbs showed no effect of hemisphere (Table 1), $F(1, 1393) = 1.72$, $r = .02$, $SE = 8.2$, $p = .19$.

Error rates were low ($M = 4.6\%$, $SE = 0.21\%$). There was no Hemisphere × Verb Type interaction in the error rates (Wald $\chi^2 < 1$) and no statistically significant main effects of verb type (Wald $\chi^2 < 1$) or hemisphere (Wald $\chi^2 = 2.98$, $p = .084$).

Control experiment

There was no Hemisphere × Noun Type interaction in the control experiment, $F < 1$ (see Fig. 2 and Table 1), nor were there statistically significant main effects (all $Fs < 1$). Reaction times to concrete and nonconcrete nouns did not differ depending on whether left or right premotor cortex had been stimulated (concrete nouns: mean difference = -4.2 ms, $|t| < 1$; nonconcrete nouns: mean difference = -7.5 ms, $|t| < 1$). Responses to pseudonouns were influenced by stimulation side (mean difference = -34.6 ms), $t(497) = -2.12$, $r = .01$, $SE = 16.2$, $p = .03$ (see Table 1).

a

b

Fig. 1. Results from the main experiment: (a) mean differences in reaction time (RT) following left- versus right-hemisphere theta-burst stimulation (TBS) as a function of stimulus type (verbs describing manual actions or nonmanual actions) and (b) mean RTs for manual-action and nonmanual-action verbs following left- and right-hemisphere TBS. Error bars show standard errors of the mean (Cousineau, 2005). The asterisks denote statistical significance (*p* < .05).

Comparison of the two experiments

An analysis that directly compared results for the two experiments showed an Experiment (1 vs. 2) × Word Type (manual verb vs. nonmanual verb vs. concrete noun vs. nonconcrete noun) × Hemisphere (left vs. right) interaction, $F(4, 4330) = 3.04$, $SE = 17.89$, $r = .07$, $p = .016$, confirming that the manual-action and nonmanual-action verbs were differentially influenced by left and right premotor TBS, but concrete and nonconcrete nouns were not.

Table 1. Mean Reaction Times (in Milliseconds) in the Main and Control Experiments

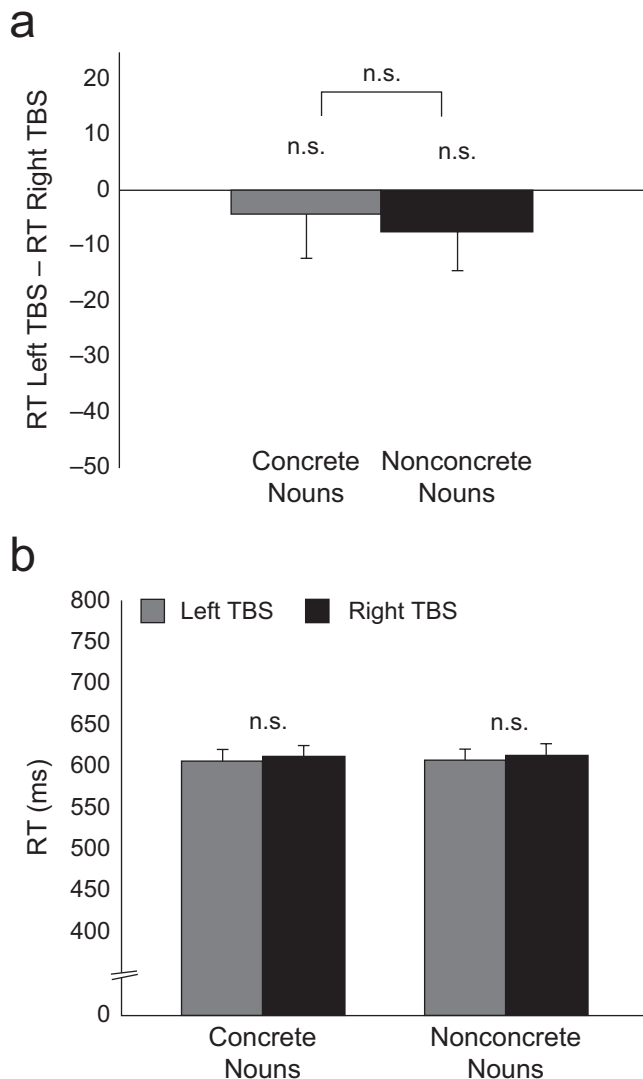| Experiment and stimulus type	Left-hemisphere TBS	Right-hemisphere TBS
Main experiment		
Manual verbs	663.4 (168.8)	697.5 (206.8)
Nonmanual verbs	683.7 (178.9)	689.5 (180.9)
Pseudoverbs	789.3 (175.6)	802.6 (193.0)
Control experiment		
Concrete nouns	606.3 (151.0)	610.5 (172.7)
Nonconcrete nouns	606.4 (153.4)	613.9 (155.1)
Pseudonouns	751.9 (218.6)	787.6 (251.9)

Note: Standard deviations are shown in parentheses. TBS = theta-burst stimulation.

Discussion

We investigated whether the understanding of action language depends in part on activity in the brain's motor system. In a sample of right-handed participants, lexical decisions for manual-action verbs were faster following TBS of left premotor cortex than following TBS of right premotor cortex. In contrast, hemisphere of stimulation did not affect the speed of lexical decisions for nonmanual verbs or, in a control experiment, for concrete or nonconcrete nouns. This dissociation is consistent with fMRI data showing selective activation of left premotor cortex when right-handers read verbs for actions typically performed with the dominant hand (Willems, Hagoort, & Casasanto, 2010). Beyond showing a correlation between brain activation and behavior, our data show that specific changes in premotor activity cause corresponding changes in action-language processing. These data suggest that premotor cortex has a functional role in action-language understanding.

Our TBS experiments provide a more direct test of the motor system's functional contributions to language understanding than have previous single-pulse TMS studies, which used MEPs in limbs as a dependent measure. Unlike a TMS-induced response in hand or foot muscles, which occurs downstream from language processing (Buccino et al., 2005), response to a lexical decision task is a classic index of semantic processing. Pulvermüller, Hauk, Nikulin, and Ilmoniemi (2005) reported modulation of lexical decision reaction times for action verbs following single-pulse TMS. It is crucial to note, however, that their results did not show the predicted specificity of the arm area for processing arm-related verbs. Our results are consistent with the predictions from this earlier study.

Furthermore, our results are consistent with a study by Glenberg, Sato, and Cattaneo (2008) that demonstrated effects of use-induced motor plasticity on comprehension of sentences about concrete and abstract motion. After participants

Fig. 2. Results from the control experiment: (a) mean differences in reaction time (RT) following left- versus right-hemisphere theta-burst stimulation (TBS) as a function of stimulus type (concrete nouns or nonconcrete nouns) and (b) mean RTs for concrete and nonconcrete nouns following left- and right-hemisphere TBS. Error bars show standard errors of the mean (Cousineau, 2005).

an interaction between language comprehension and action production. Glenberg et al. speculated that the effect they observed was due to changes "primarily located in the left inferior frontal and parietal regions" (p. R291). Our results implicate premotor cortex.

The finding that left-hemisphere stimulation resulted in speeded reaction times may seem surprising, as TBS over motor cortex decreases MEPs, an effect that suggests a depression of excitability (Huang et al., 2005). It might be assumed that depression of premotor activity would disrupt action-language processing. Instead, we observed a facilitatory effect at the behavioral level. It is difficult to infer how modulation at the neural level is manifested behaviorally. TBS may have caused inhibition at the neural level that resulted in disinhibition at the behavioral level. Indeed, movement-related cells in premotor cortex exhibit inhibition during observation of action (e.g., Kraskov, Dancause, Quallo, Shepherd, & Lemon, 2009). TBS of left premotor cortex may also facilitate the processing of words referring to actions performed with the right hand by reducing irrelevant background processing within a part of the language-comprehension network (see Landau, Aziz-Zadeh, & Ivry, 2010).

We conclude that processing an action verb depends in part on activity in a motor region that contributes to planning and executing the action named by the verb. Premotor cortex is functionally involved in the understanding of action language. Future research is needed to characterize the neural mechanisms that underlie this functionality, the extent to which premotor representations are necessary for the understanding of everyday language, and how changes in premotor activity are related to changes in a verb's meaning from one instantiation to the next.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

Note

1. Response hand was included as a factor in the initial analyses of the data. Given that this factor was not significant and was not involved in any interactions, we present simplified analyses in which the reaction times were collapsed over response hand. This failure to observe an effect of response hand is in contrast to our previous finding that premotor cortex was preferentially activated contralaterally to the dominant hand when participants read manual-action verbs

moved objects toward or away from their body, they were slower to respond to sentences indicating motion in the same direction. This finding suggests a functional link between language comprehension and motor activity. Our data provide additional information about both the automaticity and the specificity of the link between the motor system and language. First, whereas the study by Glenberg et al. involved sensibility judgments on full sentences, and thus required deep semantic processing, our experiments involved the shallow processing of a lexical decision task, in which the meanings of verbs are activated only incidentally. Thus, our experiments show that modulation of motor system activity can influence even shallow semantic processing. Second, behavioral manipulations of motor activity cannot specify the brain location of

(Willems, Hagoort, & Casasanto, 2010). We note that the current null effect is based on a limited number of trials per stimulus type (< 24 per cell). Future work is required to explore how modulation of the motor system may influence linguistic processing of body-specific actions.

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