tDCS to premotor cortex changes action verb understanding: Complementary effects of inhibitory and excitatory stimulation

Tom Gijssels[1,2]
(tomgijssels@uchicago.edu)

Daniel Casasanto[1,3]
(casasanto@uchicago.edu)

[1]Department of Psychology, University of Chicago, IL
[2]Department of Linguistics, Vrije Universiteit Brussel, Belgium
[3]Grossman Institute for Neuroscience, University of Chicago, IL

Abstract

Do neural systems for planning motor actions play a functional role in understanding action language? Across multiple neuroimaging studies, processing action verbs correlates with somatotopic activity in premotor cortex (PMC). Yet, only one neurostimulation study supports a functional role for PMC in action verb understanding: paradoxically, inhibiting PMC made people respond *faster* to action verbs. Here we investigated effects of PMC excitation and inhibition on action verb understanding using tDCS. Right-handers received excitatory or inhibitory stimulation to left PMC hand areas, then made lexical decisions on unimanual action verbs and abstract verbs. tDCS polarity selectively affected how accurately participants responded to unimanual action verbs. Inhibitory stimulation to left PMC caused a relative improvement in performance for right-hand responses, whereas excitatory left PMC stimulation caused a relative impairment. tDCS polarity did not differentially affect responses to abstract verbs. Premotor areas that subserve planning actions also support understanding language about these actions.

Keywords: action; language; embodiment; premotor cortex; tDCS

Introduction

How do people understand the meaning of words? According to theories of embodied cognition, word meaning relies, in part, on neural systems for perceiving and acting on the world (Barsalou, 1999). For instance, to understand the sentence *I am petting a cat*, modality-specific brain areas may simulate the visual experience of seeing a cat, the tactile experience of feeling its fur, and the motor programs for petting it. So far, most of the empirical support for embodied semantics comes from neuroimaging studies of action language understanding. When people read action verbs like *kick*, *pick*, and *lick*, frontal motor areas tend to show somatotopic activation (i.e. *kick*, *pick* and *lick* preferentially activate leg-, hand-, and mouth-areas; Hauk, Johnsrude, & Pulvermüller, 2004, Pulvermüller, 2005, for review).

What could the motor system be contributing to the meanings of action verbs? On one view, motor simulations recapitulate previous action experiences by re-activating some of the neural circuits that were used to perform those actions (Barsalou, 1999). On an alternative view, motor simulations may not recapitulate past actions, but rather partially prepare the motor system for future actions – thus simulations are "pre-enactments" rather than reenactments (Willems, Toni, Hagoort, & Casasanto, 2010; Zwaan & Kaschak, 2008). One advantage of the "simulation as pre-enactment" view is it clarifies the computational-level motivation for simulation (Marr, 1982): partially preparing for actions should allow people to perform these actions more efficiently, if overt actions are needed (Willems, Toni, et al., 2010). If this view is correct, motor simulations should be implemented primarily in neural systems that support action planning. The available fMRI data support this proposal: processing action verbs correlates mainly with activity in motor planning areas (e.g., premotor cortex; PMC), rather than activity in motor execution areas (e.g., primary motor cortex; M1) (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Tettamanti et al., 2005; Willems, Hagoort, & Casasanto, 2010; Willems, Toni, et al., 2010, but see Pulvermüller, 2005).

To date, only one neurostimulation study has tested for a functional relationship between PMC activity and action verb understanding. Willems and colleagues (2011) used continuous theta-burst stimulation (cTBS) to change neural activity in either left or right PMC areas involved in planning right and left hand actions, respectively (Willems, Labruna, D'Esposito, Ivry, & Casasanto, 2011). The right-handed participants then performed a lexical decision task on unimanual and nonmanual action verbs. Right-handers responded faster to unimanual action verbs after cTBS to dominant hand areas (in left PMC) than after cTBS to non-dominant hand areas (in right PMC) (Willems et al., 2011). By contrast, responses to nonmanual action verbs were not differentially affected by cTBS to left vs. right PMC. The predicted interaction suggests that left PMC circuits that plan dominant hand actions play a causal role in understanding language about those actions.

Yet, the direction of Willems et al.'s (2011) reaction time (RT) pattern was unexpected. CTBS has been shown to suppress neural excitability (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005). Therefore, on the simplest prediction, left PMC stimulation might be expected to cause a *impairment* in performance instead of an improvement. Willems et al's data, therefore, appear to be an instance of "paradoxical functional facilitation," (Kapur, 1996) which arises because normal brain functioning relies on a complex interaction of excitation and inhibition. Patients with brain lesions sometimes show enhanced behavioral performance, relative to controls. Presumably, their lesions selectively affect inhibitory circuits, thus the behavior supported by these circuits becomes facilitated (Kapur, 1996; Papeo, Pascual-Leone, & Caramazza, 2013). Similarly, cTBS could have facilitated

action verb processing either by reducing interference from background noise, or by modulating the activity of inhibitory PMC circuits: inhibition may be necessary to prevent people from overtly performing the actions named by verbs, rather than covertly simulating them (Willems et al., 2011). This post-hoc explanation for Willems et al.'s findings generates testable predictions regarding the effects of excitatory vs. inhibitory stimulation of left PMC.

The current study tested for the complementary effects of excitatory and inhibitory stimulation of left PMC hand area (and surrounding tissues) on behavioral responses to manual action verbs. Right-handers received transcranial Direct Current Stimulation (tDCS) over hand areas in left and right PMC. tDCS passes a weak direct current between two scalp electrodes, causing neural excitation under the anodal electrode and, when applied to motor areas, neural inhibition under the cathodal electrode (Nitsche et al., 2008; Jacobson, Koslowsky, & Lavidor, 2012). After receiving tDCS, participants performed a lexical decision task on unimanual and abstract verbs, making responses with their left and right hand. Since the polarity of the tDCS montage determines whether its neural effects are inhibitory or excitatory, we predicted the following patterns. First, inhibitory stimulation to left PMC hand areas should cause an *improvement* in processing unimanual action verbs, as was found by Willems et al. By contrast, excitatory stimulation to the same areas should cause a behavioral *impairment* in processing unimanual action verbs; this finding would complement the pattern found by Willems et al. Second, if the meaning of unimanual action verbs relies on the same premotor circuits for preparing hand actions, then the effects of tDCS polarity should depend critically on which hand is used to make a response.

Method

Participants

73 participants from the University of Chicago community took part in the experiment. Data from 1 participant were replaced for not following task instructions and data from 1 other participant were lost due to a script error. The remaining 71 participants were monolingual native English speakers and were right-handed as established by the Edinburgh Handedness Inventory (EHI: M = 78; range = 47-100; Oldfield, 1971). Participants were healthy adults who did not report being pregnant, having sustained a stroke or brain injury, being on psychoactive medication, or having any electronic implants. All participants provided informed consent and received course credit or $30 for their participation.

Materials

198 verbs were used in this experiment: 66 unimanual verbs (e.g. *to write*), 66 abstract verbs (e.g. *to tempt*), and 66 phonotactically legal nonce words (e.g. *to frinckle*). The unimanual verbs were selected from a set of manual action verbs that elicited dominant hand responses in a pantomime elicitation study (Gijssels & Casasanto, unpublished data). Al-

though we used a within-item design, all three verb types were matched in word length (unimanual vs. abstract: $t(130)$ = 1.48, p = .14; unimanual vs. nonce: $t(130)$ = -.74, p = .46; abstract vs. nonce: $t(130)$ = -.74, p = .46). Unimanual and abstract verbs were matched in word frequency ($t(96)$ = .20; p = .85; Coltheart, 1981).

Procedure

Transcranial Direct Current Stimulation tDCS was performed using a battery-powered Soterix Medical 1x1 (Soterix Medical, New York) with two 5x7cm saline-soaked sponges covering the electrodes. Each participants received 20 minutes of stimulation at 2 mA, which was slowly ramped up from 0 mA at stimulation onset, and ramped down to 0 mA at stimulation offset. The electrodes were placed over premotor hand areas, at FC3 and FC4 in the 10-20 electrode system (Koessler et al., 2009; Nitsche et al., 2010). In the left PMC inhibition condition (N=35), the cathode was placed at FC3 and the anode at FC4, inhibiting left PMC and simultaneously exciting right PMC. In the left PMC excitation condition (N=36) this placement was reversed, with the anode placed at FC3 and the cathode at FC4, exciting left PMC and inhibiting right PMC.

Behavioral Procedure After receiving tDCS participants performed a lexical decision task. Verbs appeared one at a time in the center of a computer screen. Participants indicated whether each stimulus was an existing English word by pressing a button corresponding to "yes" or "no" with their left or right index finger. The response mappings for each button were presented below the verb, on the left or right side of the screen. For each verb type, the "yes" response was mapped to the right button for half of the stimuli and to the left button for the other half (mapping counterbalanced across participants). The stimuli appeared in a random order, and the placement of the response labels varied unpredictably from one trial to the next.

Every trial had the following structure. First, participants saw a "Ready?" sign prompting them to push and hold down the two white "home" buttons with their left and right index finger (mapped to the 'd' and 'k' keys). Once the buttons were held down, a fixation cross appeared for a duration randomly selected between 750 and 1250 ms. Then, the stimulus and response prompts appeared. As soon as the participant had decided the correct response, they released the home button held down by the response hand and used the same hand to push the correct pink response button, after which a new trial started. Response buttons were mapped to the 'z' and 'period' keys. If participants released either of the home buttons before the stimulus was presented, the trial was restarted.

Accuracy and RTs were collected. All trials in which participants released or pressed the wrong button were classified as incorrect. Participants performed 16 practice trials and received feedback about errors during both the practice and the experimental trials.
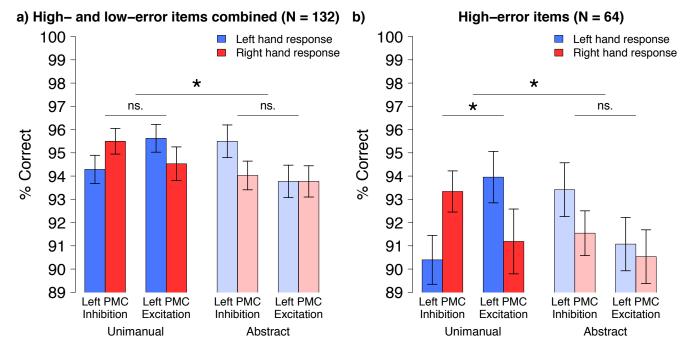
Figure 1: Mean accuracy on the lexical decision task for **a)** all items and **b)** items with a high error rate. Left PMC Inhibition = cathode left PMC, anode right PMC; Left PMC Excitation = anode left PMC, cathode right PMC. Unimanual and Abstract refer to the Verb type of the stimuli. Error bars reflect within- subject *SEM*. * indicates $p < .05$

Results

The accuracy data and RTs for target trials were analyzed with maximal mixed effects models. Both models included three two-level independent variables: tDCS polarity (left inhibitory vs. left excitatory); Verb type (unimanual vs. abstract), and Response hand for the required response (left vs. right). We used the maximal random effects structure. Nonce trials were excluded before the analyses. Accuracy data were analyzed using a general linear model with a binomial linking function. The dependent variable for this model was whether the response for each trial was correct or incorrect. For the RT model, we discarded all the incorrect trials and log-transformed RTs to reduce skew in the residuals.

Accuracy The accuracy results showed the predicted 3-way interaction of tDCS polarity x Verb type x Response hand ($\beta = -.82$, *SE* = .40, $z = -2.07$, $p = .04$; Fig. 1a). The polarity of tDCS to left PMC differentially affected the accuracy of participants' responses to unimanual and abstract verbs. In addition to the significant 3-way interaction, we also found the predicted *qualitative* pattern of results for the constituent 2-way interactions, suggesting that the predicted relationship between tDCS polarity and response hand was present, selectively for unimanual verbs. Yet, neither of the 2-way interactions was statistically significant (unimanual verbs: $\beta = -.32$, *SE* = .32, $z = -.98$, $p = .33$; abstract verbs: $\beta = .33$, *SE* = .31, $z = 1.06$, $p = .29$).

One possible reason why the predicted 2-way interaction in the unimanual verb condition did not reach significance is that accuracy approached 100%, in all conditions: a ceiling effect.

To determine whether the predicted effects were masked by this ceiling effect, we performed a second analysis on a subset of items that were not near ceiling. We calculated the number of errors for each verb (Range = 0 - 16 errors, *Median* = 3) and then performed a median split to identify items that led to more errors (High-error items: n = 31 unimanual verbs, n = 33 abstract verbs; Low-error items: n = 35 unimanual verbs, n = 33 abstract verbs). Unimanual and abstract high-error items did not differ in word frequency or word length (p's >.38).

The accuracy analysis of high-error items again showed the predicted 3-way interaction of tDCS polarity x Verb type x Response hand ($\beta = -1.07$, *SE* = .47, $z = -2.29$, $p = .02$; Fig. 1b). As expected, this 3-way interaction was driven selectively by responses to unimanual verbs, as shown by a significant 2-way interaction of tDCS polarity x Response hand ($\beta = .80$, *SE* = .35, $z = -2.32$, $p = .02$; Fig. 1b). After inhibitory stimulation to left PMC, participants tended to respond more accurately to unimanual verbs with their right hand than with their left hand ($\beta = -.41$, *SE* = .26, $z = -1.58$, $p = .11$; Fig. 1b). After excitatory stimulation to left PMC, we found a trend in the opposite direction: participants tended to respond less accurately with their right hand than with their left hand ($\beta = .62$, *SE* = .37, $z = 1.67$, $p = .10$; Fig. 1b). As expected, there was no statistically significant 2-way interaction of tDCS polarity and Response hand for abstract verbs ($\beta = .20$, *SE* = .36, $z = .56$, $p = .58$; Fig. 1b).

Although not of interest, for completeness we report that analysis of the low-error (near-ceiling) items showed no evidence for a 3-way interaction of tDCS polarity x Verb type x

Response hand (β = -.18, *SE* = .74, *z* = -.25, *p* = .80) nor for either of the 2-way interactions of tDCS polarity x Response hand (unimanual verbs: β =.08, *SE* = 0.68, *z* = .11, *p* = 0.91; abstract verbs: β =.43, *SE* = 0.65, *z* = .66, *p* = 0.51).

Reaction Times RTs were defined as the latency from stimulus onset to release of the "home" button. There were no statistically significant effects for the 3-way interaction of tDCS polarity x Verb type x Response hand (Wald $\chi^2(1)$ = .68, *p* = .41), nor for the constituent 2-way interactions of tDCS polarity x Response hand for either verb type (unimanual: Wald $\chi^2(1)$ = .10, *p* = .75; abstract: Wald $\chi^2(1)$ = .31, *p* = .58). As with the accuracy data, we analyzed the release RTs separately for the high- and low-error items. There were no statistically significant 3-way or 2-way interactions in either model (all Wald χ^2s < 1.94; all *p*s > .15).

General Discussion

This study tested whether motor circuits involved in action preparation play a causal role in action verb understanding. In right-handers, inhibitory and excitatory tDCS to hand areas in left PMC differentially affected the accuracy of responses to unimanual action verbs, but not to abstract verbs. After left-PMC inhibition, right-handers tended to make *fewer* errors to unimanual verbs with their right hand than with their left hand. After left-PMC excitation, right-handers tended to make *more* errors to unimanual verbs with their right hand than with their left hand. By contrast, the polarity of tDCS did not differentially influence how accurately participants responded to abstract verbs. These results are the first to demonstrate complementary effects of exciting and inhibiting left PMC activity on action verb processing, thus clarifying the functional contribution of PMC to understanding action language.

Some researchers have been hesitant to accept previous neurostimulation data as evidence for a functional link between motor system activity and action language understanding because there was "no evidence yet that sensory-motor cortex stimulation disrupts semantic processing," (Hauk & Tschentscher, 2013: p. 6, see also Mahon & Caramazza, 2005, 2008). Here we find both a relative improvement and a relative impairment in accuracy for lexical decisions (a task known to show semantic priming effects; Neely, Keefe, & Ross, 1989), depending on the polarity of tDCS to the motor system and on the response hand. Furthermore, the finding that response hand interacts with tDCS polarity to predict accuracy, selectively for unimanual verbs, suggests that processing these verbs not only relies on "motor circuits," but also relies on the *same* motor circuits that plan and execute unimanual hand actions (see Bedny & Caramazza, 2011).

Complementary effects of excitatory and inhibitory tDCS

Why do inhibition and excitation of left PMC lead to behavioral improvements and impairments, respectively? Across two studies, using two different neurostimulation methods, we now find a complementary pattern of results. Inhibitory

tDCS to left PMC produced a conceptual replication of Willems et al.'s (2011) study that showed "paradoxical facilitation" of lexical decision after (presumably inhibitory) cTBS to left PMC hand area. Excitatory tDCS produced the complementary finding: what we could call "paradoxical impairment" of lexical decision. One potential explanation for these complementary effects of excitatory and inhibitory neurostimulation is that the mental simulation processes that contribute to action language understanding do not depend on an all-or-nothing activation of premotor circuits, but rather rely on a complex balance of neural excitation and inhibition. Left-inhibitory stimulation could facilitate performance by reducing activation of competing motor plans (see Willems et al., 2011). On another, non-mutually exclusive account, PMC inhibition may ensure that simulations do not result in the actual execution of the action named by a verb. For instance, reading the verb *throw* should not always lead to actual throwing, just like reading the word *blue* does not automatically cause the percept of blue. Left-inhibitory stimulation may have improved behavioral performance by increasing inhibition of contextually inappropriate motor plans (since our participants were asked to recognize the verbs, not to perform the actions the refer to). Left-excitatory stimulation may have impaired performance by boosting activation of all potentially relevant motor plans, thus increasing competition among them.

PMC activity affects quality of understanding

The current data also provide some of the first evidence that motor system activity not only affects how fast people understand action verbs, but also how well. Previous neurostimulation results showed that changing motor system activity affects the speed with which people process action verbs (Willems et al., 2011; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005, though see below). Yet, as Willems and Casasanto (2011) point out, these data do not address how motor activity changes the quality with which people understand these verbs. Here we show that stimulation of hand areas affects how accurately participants process manual action verbs. In combination with previous findings, these results suggest that motor simulations contribute to both *how fast* and *how well* people construct the meaning of action language.

Why did we observe the predicted pattern in the accuracy data but not in the RT data? Since we did not speed participants (e.g., with a trial timeout), it may not be surprising that we observed the predicted interactions in the accuracy data, alone. Furthermore, the absence of an RT effect allows us to rule out the presence of a speed-accuracy trade-off. In general, it is often unclear a priori whether studies investigating motor-system contributions to action language understanding will show the predicted effect in RTs, accuracy, or both (see Mahon & Caramazza, 2008). Across our cTBS and tDCS studies, we find the predicted effects in *both* reaction times and accuracy. Since finding the predicted effect in either accuracy or RT could be interpreted as support for our

experimental hypothesis, a reasonable (though non-standard) precaution to take would be to double our *p*-values (i.e. Bonferroni correction). Even if we do so, the critical 3-way and 2-way interactions remain significant in our high-error data set.

We found the predicted 3-way interaction of tDCS, verb type, and response hand in the full data set, but the predicted lower-order interaction was not significant due to a ceiling effect. Overall, these results should be interpreted with some caution given that we had to perform an unplanned median split in order to observe the predicted 2-way interaction of tDCS by response hand. Our confidence in the data is increased, however, by the fact that (a) inhibitory left PMC stimulation produced a close conceptual replication of our previous cTBS study, and (b) excitatory left PMC stimulation produced a mirror image of these results, providing convergent evidence that inhibitory left PMC activity plays a functional role in processing unimanual action verbs.

Stimulation to M1 and action language

In contrast to PMC stimulation, stimulation of primary motor cortex (M1) has not shown consistent effects on action verb understanding. Several studies applied transcranial magnetic stimulation (TMS) to M1 but did not show the predicted behavioral effects on an action verb task (Papeo, Vallesi, Isaja, & Rumiati, 2009; Tomasino, Fink, Sparing, Dafotakis, & Weiss, 2008; Lo Gerfo et al., 2008[1]). One other study applied single pulse TMS to M1 hand and leg areas, and reported that TMS modulated lexical decision times to hand and leg action verbs differentially. However, the data do not show the predicted somatotopic specificity; the predicted effect was only found for leg verbs with no clear effect of TMS on hand verb processing(Pulvermüller et al., 2005).

The inconsistent results of M1 stimulation are problematic for the view that language-driven simulations are reenactments of previous actions, but may be compatible with the view that simulations are pre-enactments. If verb-driven motor simulations are partial preparations to perform the action named by the verb, then they should mainly rely on neural systems for action preparation (PMC), and not necessarily on systems for action execution (M1). In an fMRI test of this proposal, both motor simulations and motor imagery activated PMC, but only motor imagery activated M1 (Willems, Toni, et al., 2010). Consistent with M1 being involved selectively in imagery, the only study that showed the predicted somatotopic effects of TMS to M1 asked participants to judge the concreteness of action verbs, a task that is likely to induce imagery (Repetto, Colombo, Cipresso, & Riva, 2013, see also Tomasino et al., 2008).

Why tDCS?

Across hundreds of studies of embodied cognition, only a few have used true experimental methods to test the functional relationship between the motor system and action verb representation. Two of these studies used tDCS to test the role of M1 in action language processing, but did not find the predicted differences among the anodal, cathodal, and sham conditions (Liuzzi et al., 2010; Vicario & Rumiati, 2012). Our results, however, show that tDCS can be a useful alternative to TMS for testing theories of language-driven motor simulation. tDCS does not lead to any noticeable muscle twitches, which might inadvertently draw participants attention to the stimulated body part (Papeo et al., 2013). tDCS is also safer, less unpleasant, and less expensive than TMS. One potential shortcoming is that excitatory tDCS to one area is often paired with inhibitory stimulation of another area. Yet, this complementary montage can also be an advantage: in the current study, we were able to simultaneously induce complementary stimulation to left and right PMC. Presumably, this montage enhanced the *relative* excitation or inhibition of the target left-hemisphere regions compared to their right-hemisphere homologues.

Conclusions

These results suggest a functional relationship between the neural systems for preparing hand actions and understanding language about those actions. tDCS to left PMC affected how accurately people processed action language, in a predictable way: inhibitory stimulation caused a relative improvement in performance (consistent with our previous cTBS results), and excitatory stimulation caused a relative impairment. These complementary effects of excitatory and inhibitory tDCS were specific to unimanual action verbs, and depended critically on the hand that participants used to respond. Previous neurostimulation results have shown that modulating PMC activity can influence how fast people can respond to action verbs. The present results show that modulating PMC activity in the hemisphere that controls the dominant hand can also affect *how well* people process verbs that name dominant-hand actions, strengthening the evidence that motor simulations contribute to the meanings of action words.

Acknowledgments

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[1]Parenthetically, we note that Lo Gerfo et al. (2008) reported that RTs for action-related verbs and nouns were slower after rTMS to left M1 compared to sham, according to a one-tailed test. However, this effect is not well supported by the data: not only was the use of a one-tailed test unlicensed, the comparison of interest was not licensed by the necessary higher-order interaction, nor was there any correction for multiple comparisons in their 2x2x2x2 design.

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