RESEARCH ARTICLE

# Modulation of the motor system during visual and auditory language processing

**Ludovica Labruna · Miguel Fernández-del-Olmo ·
Ayelet Landau · Julie Duqué · Richard B. Ivry**

**Abstract** Studies of embodied cognition have demonstrated the engagement of the motor system when people process action-related words and concepts. However, research using transcranial magnetic stimulation (TMS) to examine linguistic modulation in primary motor cortex has produced inconsistent results. Some studies report that action words produce an increase in corticospinal excitability; others, a decrease. Given the differences in methodology and modality, we re-examined this issue, comparing conditions in which participants either read or listened to the same set of action words. In separate blocks of trials, participants were presented with lists of words in the visual and auditory modality, and a TMS pulse was applied over left motor cortex, either 150 or 300 ms after the word onset. Motor evoked potentials (MEPs) elicited were larger following the presentation of action words compared with control words. However, this effect was only observed when the words were presented visually; no changes in MEPs were found when the words were presented auditorily. A review of the TMS literature on action word processing reveals a similar modality effect on corticospinal excitability. We discuss different hypotheses that might account for this differential modulation of action semantics by vision and audition.

**Keywords** TMS · Language · Embodiment · Action · Reading · Listening · Visual · Auditory

L. Labruna (✉)
Health Science Department, University of Molise, Molise, Italy
e-mail: lulabrun@gmail.com

L. Labruna · A. Landau · R. B. Ivry
Department of Psychology,
University of California, Berkeley, CA, USA

M. Fernández-del-Olmo
Departamento de Educación Física e Deportiva,
Facultade de Ciencias do Deporte e a Educación Física,
INEF, Galicia, Spain

J. Duqué
Institute of Neuroscience, Université catholique de Louvain,
Louvain-la-Neuve, Belgium

## Introduction

Action comprehension involves the engagement of neural regions traditionally associated with action production. The mirror neuron system (MNS), identified in physiological studies in non-human primates and fMRI studies with humans, spans premotor and parietal cortex (reviewed in Buccino et al. 2004; Morin and Grezes 2008). It has been shown that action representations within the MNS, examined at either the single neuron or network level, can be activated through different modalities. For example, cells in premotor cortex which are activated when a monkey reaches to pick up a peanut are also activated when the animal observes the peanut being picked up by another agent (e.g., the experimenter) or when listening to the sound of a peanut shell being cracked (Kohler et al. 2002). Similarly, the MNS is not only activated when observing pictures or videos of actions, but also when participants listen to sounds related to these actions (Lahav et al. 2007; Pizzamiglio et al. 2005).

This work suggests that units within the MNS represent the semantics of actions, and are not constrained by a specific sensory context. Indeed, the functional domain of the MNS is thought to extend beyond action observation. Much of the excitement concerning these seminal observations

centers on the idea that these representations may provide the basis for the emergence of more abstract representations, and in particular serve as the biological foundation for symbolic representation required for language. Theories of embodied semantics (Glenberg and Kaschak 2002; Feldman and Narayanan 2004) posit that language comprehension of action-based concepts emerges from, and depends on, the grounding of these concepts in sensorimotor representations. Consistent with this view, fMRI studies have shown that the MNS is activated when people process action-based words, with similar patterns of activation during reading and listening. For example, using movement-defined ROIs, somatotopic patterns of activation were observed in premotor cortex when people listened to action words (Tettamanti et al. 2005) or read action words (Hauk et al. 2004).

The overlap between action production, observation, and action-based language becomes less clear when the focus shifts to primary motor cortex. As assessed by tests of action observation, neurons in M1 generally do not have mirror properties (Rizzolatti and Craighero 2004). Indeed, a recent fMRI study reported a reduction in the BOLD signal in motor cortex during hand action observation, an effect hypothesized to relate to the prevention of unwanted imitative movements (Gazzola and Keysers 2009). In contrast, studies using transcranial magnetic stimulation (TMS) have consistently observed increases in corticospinal excitability during action observation, and this activation is frequently effector specific (Fadiga et al. 1995; Gangitano et al. 2001; Strafella and Paus 2000; Aziz-Zadeh et al. 2002). The difference between the fMRI and TMS studies may reflect the differential sensitivity of the two measures. TMS, producing a relatively large perturbation of a restricted region, may provide a more sensitive probe on changes in M1 excitability (Fadiga et al. 2005).

Measures of motor evoked potentials (MEPs) following TMS stimulation have also been used to probe changes in M1 excitability during linguistic processing. A series of studies have reported somatotopic-specific MEP increases when people are processing action words. For example, Papeo et al. (2009) reported larger MEPs when the TMS pulses were applied while participants read verbs related to actions (e.g., I chew) compared with verbs describing mental states (e.g., I adore). However, effector-specific decreases in MEPs during word comprehension have also been reported (Buccino et al. 2005). That is, MEPs in the hand area were lower when people listened to words describing hand actions compared with when they listened to words describing foot actions. Moreover, a subsequent behavioral study showed that reaction times (RTs) were slower when the responses were made with the effector referred to in the sentences. These results led Buccino et al.

(2005) to conclude that the motor cortex may be actively inhibited by the MNS during linguistic processing.[1]

There are numerous methodological differences between the two representative TMS studies reviewed above. First, the studies differ in terms of the modality used to present the linguistic stimuli. Notably, two studies (Papeo et al. 2009; Glenberg et al. 2008) showing an increase in MEPs during word processing used visual stimuli. Similarly, studies showing that TMS stimulation over primary motor cortex facilitates RT in making linguistic judgments also involve reading (Pulvermuller et al. 2005; Tomasino et al. 2008). In contrast, in the study showing a decrease in MEPs and behavioral cost from motor cortex TMS increase of RT, the stimuli were presented auditorily (Buccino et al. 2005).

Second, the studies do not consistently relate changes in MEPs to the type of action conveyed by the stimulus words. For example, in the study by Papeo et al. (2009), the participants had to read hand and other body effector action words (e.g., "mastico", I chew) while MEPs were recorded in a hand muscle (FDI). Monitoring the relationship between the probed effector and words is important if we consider that embodied semantics would lead us to expect some form of somatotopically based organization for action understanding (Aziz-Zadeh et al. 2006; Boulenger et al. 2009).

Third, the timing of the TMS stimulation varied across the studies. Timing is obviously critical when probing excitability changes in a dynamic system, and may have important consequences in terms of function (Papeo et al. 2009). Because the different studies used different times of stimulation, they might have probed the underlying processes at different time points. In a review of studies using TMS to probe excitability changes in motor cortex, Hauk et al. (2008) suggest that the optimal window for observing the effects of action observation and action word comprehension requires the stimulation to occur within 200–300 ms of stimulus presentation.

The aim of the present study was to re-examine excitability changes in the corticospinal system during the comprehension of action words, directly comparing reading and listening with identical experimental procedures. To this end, we applied single-pulse TMS over the left M1 and

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[1] Pulvermuller et al. (2005) applied single-pulse TMS to motor cortex while participants performed a lexical decision task. RTs were influenced in an effector-specific manner. For example, the time to judge that "kick" was a word was faster following TMS directed at the foot area of motor cortex. The authors interpreted this result as indicating that the TMS primed neural activity in the foot area and facilitated the access of an embodied representation. However, the results are also consistent with the hypothesis that the TMS disrupted activity in effector-specific areas that are potential sources of interference for reading comprehension, consistent with the work of Buccino et al. (2005).
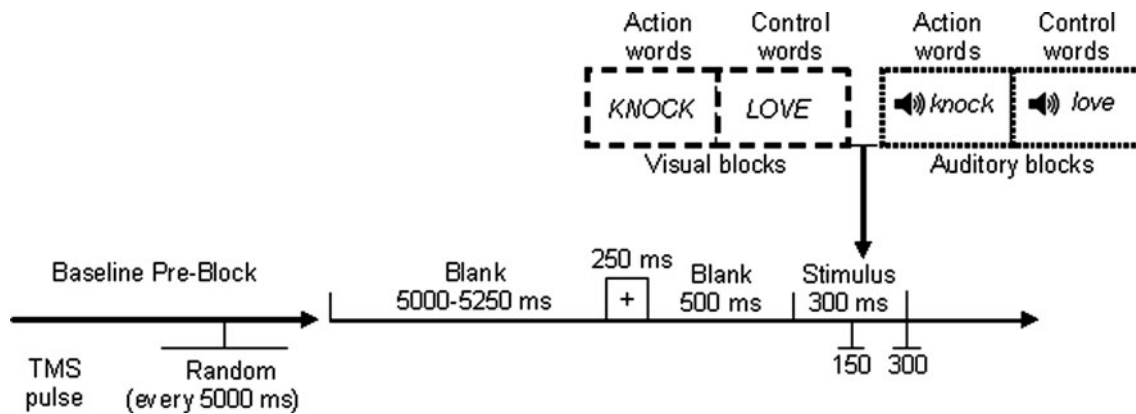
**Fig. 1** Schematic of trial structure and conditions in Experiment 1. On each trial, a fixation cross was followed by a stimulus word. In the visual condition, the word appeared in the center of the monitor. In the auditory condition, the stimulus was played over a speaker. The stim- ulus lasted for 300 ms and a TMS pulse was applied, either 150 ms or 300 ms after stimulus onset. At the beginning of each block of 40 trials, baseline MEP measurements were obtained by applying single-pulse TMS stimulation at random intervals

recorded MEPs from the contralateral right hand while participants read or heard words. For the action-related stimuli, the words were associated with hand movements (e.g., grasp). As controls, we included words about nature (e.g., rain) or feelings (e.g., aspire). We predicted that the MEP amplitudes would be differentially modulated following the action and control words. Of particular interest was whether the direction of the effect was dependent on stimulus modality, stimulus timing, or some combination of these factors.

**Methods**

Participants

Nineteen participants were recruited for the study (age: 21.6, SD = 3.6; 10 women, 9 men). All were native English speakers and were right handed as measured by the Edinburgh Handedness Inventory (Oldfield 1971). The participants were naive to the purpose of the study and financially compensated for their time. The protocol was approved by the institutional review board at UC Berkeley. As part of the informed consent, participants completed a TMS safety checklist prior to the start of the experiment.

Stimuli

A total of 80 words were selected, consisting of 40 hand action words (e.g., applaud) and 40 control words. The control words included nouns that referred to nature (e.g., forest) and verbs that referred to abstract concepts (e.g., believe). Given that our main point of comparison was a within-set comparison of the visual and auditory versions of the stimuli, we focused on matching the action and control words in terms of word length. Post-hoc comparisons of a number of

word properties were performed using two on-line databases, the MRC Psycholinguistic Database (psy.uwa.edu.au/ MRCDataBase/mrc2.html) and SubtlexUS (subtlexus.lexi- que.org). For the MRC database (used for familiarity, image- ability and concreteness), data were available for 71% of the words. For the SubtlexUS database (frequency), data were available for 100% of the words. The action and control words did not differ in word length (4.7 vs. 4.6, respectively, $P = 0.71$), familiarity (548.4 vs. 560.1, $P = 0.27$), imageabil- ity (503.9 vs. 522.1, $P = 0.50$), and concreteness (481.9 vs. 479.5, $P = 0.94$). The action words contained fewer syllables (1.18 vs. 1.38, $P = 0.04$) and occurred with a higher fre- quency (403 vs. 2,851 occurrences per million, $P = 0.02$).

We generated a visual and auditory version of each stim- ulus. For the visual version, words were presented in a black font on a white background. For the auditory version, digital recordings (705 kbps; 16 bit; 22 kHz) were made of a male speaker. The speaker was trained to articulate each word in approximately 300 ms. Post-production editing was performed to standardize the duration and intensity of the sound files. All of the edited stimuli were easily com- prehended by the participants.

Procedure

The stimuli formed four conditions, based on the factorial combination of Modality (vision vs. audition) and Stimulus type (action vs. non-action). The conditions were tested in separate blocks of 40 trials each. A trial started with the appearance of a fixation cross at the center of the screen for 250 ms (Fig. 1), followed by a blank screen for 500 ms. The stimulus was then presented. In the visual condition, the stim- ulus appeared at the center of the screen for 300 ms; in the auditory condition, a sound file of the stimulus word was played over a speaker and lasted 300 ms. The screen remained blank for an extended inter-trial interval (5,000–5,250 ms).

The participant was seated in front of the computer screen with her elbows flexed at 90° and hands prone in a totally relaxed position. A single TMS pulse was applied either 150 or 300 ms after stimulus onset. The participants were instructed to focus on the words (silently read or listen), because they would be asked to recall as many of the words as they could in a memory test at the end of the block. They were informed that they would earn a monetary bonus if they were able to recall at least ten of the 40 words at the end of the block.

## TMS protocol

A single-pulse TMS protocol was employed, with the stimulation applied over the left hemisphere. Using surface electrodes, we measured the size of motor-evoked potentials (MEPs) from the first dorsal interosseous muscle (FDI) of the right hand, the primary abductor of the index finger. The EMG signal was bandpass filtered (50–2,000 Hz; Delsys Inc., Boston, USA) and digitized at 2,000 Hz for offline analysis.

To locate the optimal stimulation site, the participant was fitted with an EEG cap. TMS was applied using a figure-eight magnetic coil (diameter = 70 mm) connected to a rapid Magstim 200 stimulator (Magstim, Whitland, Dyfed, UK). The coil was placed tangentially on the scalp with the handle pointing backward and laterally at a 45° angle from midline, a position that is approximately perpendicular to the central sulcus. The coil position was adjusted to identify the optimal location for eliciting MEPs in right FDI.

Once this position was identified, we determined the stimulation intensity for the experiment. The resting motor threshold (rMT) was defined as the minimal stimulator intensity required to elicit MEPs on five out of 10 consecutive trials. To be scored as an MEP, the peak-to-peak change in amplitude had to exceed 50 µV in the relaxed FDI. Across participants, the stimulator intensity required for the rMT was 44% (±10) of maximum stimulator output.

The test intensity for the experiment was set to 120% of the rMT. During the test blocks, a single TMS pulse at this intensity was applied in each trial, either 150 or 300 ms after stimulus onset. Forty MEPs were recorded for each condition, half at each of the two timings, with the timing randomized from trial to trial. The EMG data were sampled for a 4-s interval, starting at fixation onset. Trials associated with elevated background EMG activity in right FDI were excluded from the analysis.

Baseline measures of right FDI MEPs were obtained at the start of each block. For these measurements, participants were instructed to passively stare at a blank screen for approximately 2 min. During this time, 12 TMS pulses were applied at random intervals with a minimum inter-stimulus interval of 5 s. We opted to obtain pre-block measurements because pilot work indicated that the baseline level varied within a block across the four conditions (see also Labruna et al. in press).

## Results

Single-pulse TMS was used to probe changes in corticospinal excitability 150 or 300 ms following the onset of action words that were either read or heard. To normalize the data, we calculated the mean MEP for each block and divided each of these four values by the mean baseline MEP. We averaged the MEPs over the four baseline phases since a preliminary analysis revealed that these values remained relatively stable.

A three-way, repeated measure ANOVA was performed on the normalized MEP values with the factors Modality (auditory vs. visual), Stimulus Type (hand vs. control) and TMS Time (150 ms vs. 300 ms). No differences were found between the two TMS timings, nor did this factor interact with any of the other factors. The ANOVA revealed main effects of Modality ($F(1,18) = 5.65$, $P = 0.029$) and Stimulus Type ($F(1,18) = 3.52$, $P = 0.048$). Moreover, the interaction of these two variables was significant (Modality × Stimulus Type: $F(1,18) = 4.29$, $P = 0.044$).

As can be seen in Fig. 2, MEPs elicited following the words were always larger than the MEPs elicited in the baseline measurements (obtained just before the start of the test block). This increase was larger for the action words compared with the control words, but only when the words were presented visually. Using a set of planned post-hoc comparisons (two-tailed, Bonferroni corrected for multiple comparisons), the normalized MEPs were larger following action words compared with non-action words in the visual condition ($t_{18} = 2.12$, $P = 0.048$). The same comparison for the auditory condition did not approach significance ($t_{18} = 0.35$, $P = 0.72$). Thus, comprehension of action words produced an increase in the excitability of motor cortex as inferred from MEPs, but only when the action words were read.

A secondary analysis was performed to evaluate the effects of stimulus repetition on MEPs. A two-way, repeated measure ANOVA was performed on the normalized MEP values averaged over the two TMS timings with the factors Order (first vs. second block) and Stimulus Type (hand vs. control). Neither main effect was significant, nor was the 2-way interaction.

In the free recall memory tests that followed each block, participants correctly recalled, on average, 19.4 of the 40 words (±3.7, essentially no false alarms). These data were analyzed with a two-way, repeated measures ANOVA with the factors Modality (auditory vs. visual) and Stimulus
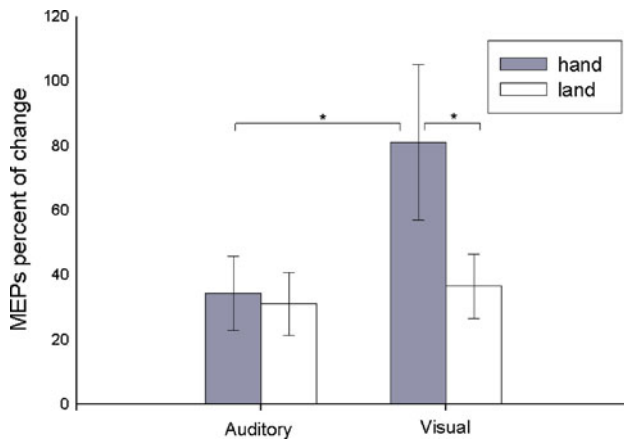
**Fig. 2** Percent increase in the amplitude of the motor-evoked potentials during word processing compared with the mean baseline MEP amplitude. The words were either action words or non-action, control words, presented auditorily or visually. MEPs were recorded from the FDI muscle of the right hand. *Error bars* refer to standard error of the means

Type (hand vs. control). There was a main effect for Stimulus Type ($F(1,18) = 6.30$, $P = 0.022$). Participants recalled more of the control words compared with the action words (20.3 vs. 18.5), perhaps due to the fact that the control words had a higher frequency rate ("Methods"). Importantly, there was no effect of Modality ($F(1,18) = 9.22$, $P = 0.35$) nor was the interaction reliable ($F(1,18) = 1.47$, $P = 0.24$). Thus, participants appeared to attend to the stimuli equally well in the auditory and visual conditions.

## Discussion

The goal of the present study was to systematically examine the modulation of M1 excitability during the comprehension of action words. Previous work had yielded inconsistent results, and comparisons across these studies were limited by substantial methodological differences. Given this, we measured MEPs elicited by stimulation over the hand area of left hemisphere M1 while participants read or listened to action and non-action words.

The MEP data showed an overall increase in excitability during word comprehension compared to baseline. We assume this effect reflects some overall change in set between the baseline and task phases of the experiment, even though the participants were not required to make any overt responses during the presentation of the stimuli (i.e., they were only required to memorize the stimuli presented).

Of central interest, we observed a differential modulation of corticospinal excitability in the reading and auditory conditions. MEPs were larger when participants read the action words compared with the non-action words. In contrast, action and non-action words produced similar

changes on the MEPs when participants listened to the words. While this modality effect may seem puzzling, it is consistent with previous reports. Papeo et al. (2009) and Glenberg et al. (2008) had observed increases in MEPs when participants read action words compared with non-action words. In contrast, Buccino et al. (2005) observed a decrease in MEPs elicited in a hand muscle when people heard sentences describing hand actions compared with sentences describing foot actions or abstract actions. Here, we demonstrated a similar modality effect (vision > audition) in a single experiment in which the methods were identical for the two modalities.

To further explore modality effects, we performed a simple meta-analysis of studies that have used TMS to measure changes in M1 excitability during action comprehension. We included studies in which MEPs were elicited while people observed videos of actions, imagined actions, or listened or read actions words (see Table 1). MEPs were measured in right FDI following stimulation of left hemisphere motor cortex, similar to the procedure employed in the current study. While different control conditions were used across the studies, they all met the requirement that the control stimuli were presented in the same modality as the action-based stimuli. To allow a comparison of effect size across papers despite the differences in dependent variables, we restricted this analysis to studies in which the results were either presented in terms of z-scores or in which we could calculate the z-score. By using this normalized measure, it is not possible to infer if the effects indicate a facilitation or inhibition on the motor system; rather, they indicate the relative modulation of M1 excitability between the experimental and control conditions.

The results of this review are presented in Fig. 3. An increase in M1 excitability is consistently observed when people observe actions or imagine actions. The normalized effects become attenuated for action language. While the data set is small, the pattern also confirms that, across studies, reading and listening may have different effects on M1 excitability. Reading action words either produces a small increase in MEPs or no change, relative to a control condition; in contrast, listening to action words produces either no change or a reduction in MEPs.

Why might reading be more effective in engaging the motor system compared to listening? One hypothesis centers on the dynamics of reading and listening. We opted to use identical procedures for reading and listening, but this may not be appropriate, given the differential time course for visual and auditory language processes. It is possible that the stimulation times used in the current study were optimal for assessing the modulation of M1 during reading but not for assessing modulation during listening. A priori, one would expect auditory comprehension processes to occur more rapidly, given the more rapid dynamics of the

**Table 1** Studies that have examined MEP modulation during action observation, action imagery, reading of action words, and listening to action words

| Ref. | Papers | TMS pulse (ms) | Modality | Experimental cond. | I control cond. | II control cond. | III control cond. |
|---|---|---|---|---|---|---|---|
| A | Fadiga et al. (1995) | ? end of action | Watch video | Hand grasping an object | Object movement | Arm movement | Light detection |
| B1 | Patuzzo et al. (2003) | ? Flexing finger—Random | Watch video | Flexio-extension finger (hand facing out) | Object movement | | |
| B2 | Patuzzo et al. (2003) | Random | Imagery | Flexio-extension finger movement (I person imagery) | Object movement | | |
| C1 | Fourkas et al. (2006) | 3,000–3,500 | Imagery | Abduction–adduction of the index (I person imagery) | Static hand | | |
| C2 | Fourkas et al. (2006) | 3,000–3,500 | Imagery | Abduction–adduction of the index (III person imagery) | Static hand | | |
| D | Glenberg et al. (2008) | 200 after verb | Read words | Transfer sentences | No transfer sentences | | |
| E | Papeo et al. (2009) | 875 | Read words | Hand action words | Non hand action words | Non action words | |
| F1 | Our experiment | 150–300 | Read words | Hand action words | Non action words | | |
| G | Oliveri et al. (2004) | 500 | Read words | Action verbs | Non action verbs | | |
| F2 | Our experiment | 150–300 | Hear words | Hand action words | Non action words | | |
| H | Buccino et al. (2005) | 500–700 | Hear words | Sentence of hand actions | Abstract content sentences | Foot action sentences | |

For comparison purposes, the set is limited to those in which an estimate can be made of the normalized difference between the experimental and control conditions
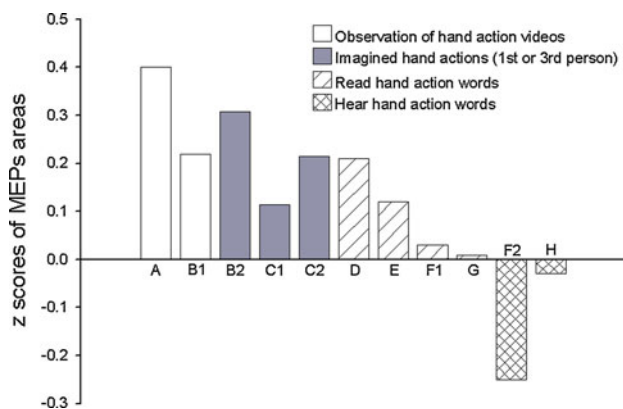


**Fig. 3** Modulation of MEPs elicited in the right hand during action observation, action imagery, reading of action words, and listening of action words. For the latter two, the words were either presented individually or in sentences. To facilitate comparison across the studies, the data are expressed in terms of a difference in z-scores with respect to a baseline condition. The data depicted here are adapted from: A: Fadiga et al. (1995); B: Patuzzo et al. (2003); C: Fourkas et al. (2006); D: Glenberg et al. (2008), E: Papeo et al. (2009); F: current experiments; G: Oliveri et al. (2004); H: Buccino et al. (2005)

auditory sensory system (Recanzone 2009), as well as the fact that language is, as a human universal, built on auditory-motoric pathways (Pulvermuller and Fadiga 2010). Nonetheless, we did not observe a difference between the

MEPs elicited at 150 and 300 ms, and there was no indication of a larger effect for the listening condition at the shorter stimulation time.

The stimulation times used in the present study are relatively early, at least compared with the other studies listed in Table 1. For example, Papeo et al. (2009) observed increased MEPs when people read action words, but only when the TMS pulses were applied 875 ms after stimulus onset. In fact, when the stimulation was applied earlier (545 ms after stimulus onset), there was no reliable increase in MEPs. We opted to use a shorter time, given our interest in the engagement of motor cortex during word comprehension. We assume this is relatively advanced, if not complete by 300 ms (e.g., Shtyrov et al. 2010). Consistent with our findings, Glenberg et al. (2008) also observed MEP increases in a sentence comprehension task when the stimulation was applied 200 ms after the onset of the verb. Stimulating at later times would provide a less direct probe, potentially "contaminating" the excitability by imagery processes as participants generate a schema based on semantics. As for listening, both our study and that of Buccino et al. (2005) have failed to observe any indication of an increase in MEPs during an initial processing stage. Indeed, Buccino et al. (2005) report a reliable decrease 500–700 ms after stimulus onset.

If we assume that the modality differences are not related to timing, then we must consider alternative hypotheses that might underlie the differential engagement of the motor system during reading and listening. The observation that MEPs may be enhanced when reading action words and suppressed when listening to action words suggests a qualitative difference. Indeed, such an effect presents a challenge to embodied theories of cognition (see Mahon and Caramazza 2008). If, at some level in the system, similar representations are activated for action concepts conveyed through reading or speech, then the present results suggest that this shared representation is not manifest in the activity of motor cortex. It seems problematic to provide a parsimonious account of how understanding a given concept through reading (or action observation) could produce an increase in cortical excitability, while either producing no change or a decrease in excitability through listening.

A different possibility is that there is a quantitative difference in the recruitment of motor cortex during visual and auditory comprehension of action words. One hypothesis builds on the idea that language comprehension involves some sort of internal simulation, or retrieval of motoric associations to the linguistic message (Liberman and Mattingly 1989). While this idea is generally considered with respect to item-specific semantics, it may also be relevant at a more global level with respect to modality differences. Speech comprehension is hypothesized to require reference to underlying articulatory processes (Liberman and Mattingly 1989). Perhaps reading printed text involves reference to underlying manual gestures that would be required to produce the text (writing or typing). By this view, the engagement of the hand area in motor cortex might be more strongly associated with visual language in a generic manner compared with auditory language (where we might have seen greater modulation in articulatory muscles). However, this hypothesis cannot account for why this effect was limited to the action words; that is, this hypothesis would predict similar modality effects for the control words.

An alternative hypothesis centers on the idea that, unlike oral language, reading is an acquired skill. Our participants were, of course, advanced readers. Nonetheless, there remain significant differences, both cognitively and neurally, in language comprehension for reading and listening. Whereas an infant will develop the capacity to understand and produce oral language automatically during the first 2 years of life, learning to read is a laborious process that challenges most 6-year-olds. Biologically grounded models of language acquisition (Feldman 2006) have emphasized the importance of embodied cognition for learning, the idea that our linguistic and conceptual knowledge arise from sensorimotor experience. While this notion has been applied to language acquisition in general, it is possible that the links between sensorimotor systems and action language might be stronger in a linguistic system that has a protracted learning period.

Modality effects have received minimal attention in research on the mirror network system and embodied cognition. Indeed, the emphasis has generally been on the similar response within this system across modalities, highlighting the conceptual nature of action representation (e.g., Gazzola et al. 2006). Accumulating evidence suggests that dynamic interactions between language and sensorimotor representations may be constrained by the manner in which language is perceived. Understanding these dynamics remains a challenge for future research.

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