



HAL
open science

Does the Motor Cortex Want the Full Story? The Influence of Sentence Context on Corticospinal Excitability in Action Language Processing

W. Dupont, C. Papaxanthis, Florent Lebon, Carol Madden-Lombardi

► **To cite this version:**

W. Dupont, C. Papaxanthis, Florent Lebon, Carol Madden-Lombardi. Does the Motor Cortex Want the Full Story? The Influence of Sentence Context on Corticospinal Excitability in Action Language Processing. *Neuroscience*, 2022, 506, pp.58-67. 10.1016/j.neuroscience.2022.10.022 . hal-04185286

HAL Id: hal-04185286

<https://u-bourgogne.hal.science/hal-04185286v1>

Submitted on 10 Nov 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

1 **Does the motor cortex want the full story? The influence of sentence context**
2 **on corticospinal excitability in action language processing**

3
4
5 Dupont W ^{1*}, Papaxanthis C ¹, Lebon F ^{1#}, Madden-Lombardi C ^{12#}

6 ¹*INSERM UMR1093-CAPS, Université Bourgogne Franche-Comté, UFR des*
7 *Sciences du Sport, F-21000, Dijon.*²*Centre National de la Recherche Scientifique*
8 *(CNRS), France*

9
10
11 # F.L. and C. M-L. equally contributed to this work

12 * Corresponding author: william.dupont@u-bourgogne.fr

13

14 **Highlights**

- 15 • We studied the effects of action words and sentence context on motor activity.
- 16 • Corticospinal excitability is modulated by the presence of manual action verbs.
- 17 • Context helps eliminate residual motor activation when no manual action is present.

18 **Abstract**

19 The reading of action verbs has been shown to activate motor areas, whereby
20 sentence context may serve to either globally strengthen this activation or to
21 selectively sharpen it. To investigate this issue, we manipulated the presence of
22 manual actions and sentence context, assessing the level of corticospinal excitability
23 by means of transcranial magnetic stimulation. We hypothesized that context would
24 serve to sharpen the neural representation of the described actions in the motor
25 cortex, reflected in context-specific modulation of corticospinal excitability.

26 Participants silently read manual action verbs and non-manual verbs, preceded by a
27 full sentence (rich context) or not (minimal context). Transcranial magnetic
28 stimulation pulses were delivered at rest or shortly after verb presentation. The coil
29 was positioned over the cortical representation of the right first dorsal interosseous
30 (pointer finger).

31 We observed a general increase of corticospinal excitability while reading both
32 manual action and non-manual verbs in minimal context, whereas the modulation
33 was action-specific in rich context: corticospinal excitability increased while reading
34 manual verbs, but did not differ from baseline for non-manual verbs. These findings
35 suggest that sentence context sharpens motor representations, activating the motor
36 cortex when relevant and eliminating any residual motor activation when no action is
37 present.

38 **Keywords:** Action language, motor representation, transcranial magnetic stimulation.

39 **Introduction**

40 Over the past couple of decades, researchers have established a link between
41 language processes and perceptual-motor processes (Barsalou, 1999, 2008;
42 Barsalou et al., 2003; Gallese and Lakoff, 2005; Decety and Grèzes, 2006; Zwaan
43 and Taylor, 2006; Fischer and Zwaan, 2008; Jeannerod, 2008; Glenberg and
44 Gallese, 2012). More precisely, these authors suggest that the information described
45 by language would lead to activation in the brain areas that are concerned with the
46 concept itself; if the concept concerns sight, this will lead to activation in the visual
47 areas. The same applies to action language, such that semantic information referring
48 to an action would engage the sensory motor system. While there exist
49 inconsistencies in the literature suggesting that this distributed activation may be
50 epiphenomenal at most (Rogers et al., 2006; Patterson et al., 2007; Mahon and
51 Caramazza, 2008; Lambon Ralph et al., 2009, 2010; Pobric et al., 2010; Mahon,
52 2015), many researchers would postulate that such activation contributes to
53 language comprehension.

54 To better understand this link, researchers have probed the involvement of the
55 motor system during action language processing using various methodologies, such
56 as functional Magnetic Resonance Imaging (fMRI) (Hauk et al., 2004; Pulvermüller et
57 al., 2005; Aziz-Zadeh et al., 2006; Van Dam et al., 2010; although for critical views
58 see: de Zubicaray et al., 2013; Wurm and Caramazza, 2019),
59 electroencephalography (EEG) (Pulvermüller et al., 2001; Kellenbach et al., 2002; Xu
60 et al., 2016), behavioral measures (Pulvermüller et al., 2001; Rabahi et al., 2012,
61 2013; Andres et al., 2015; Klepp et al., 2019) and Transcranial Magnetic Stimulation
62 (TMS) (Papeo et al., 2009, 2015; Labruna et al., 2011; Scorolli et al., 2012; Innocenti
63 et al., 2014; Franklin et al., 2020; see review: Papeo et al. 2013). Specifically, Hauk

64 et al. (2004) using fMRI reported that silent reading of action words leads to
65 somatotopic activation of the effector-related representation within the primary motor
66 cortex. Papeo et al. (2009) used TMS to observe an increase in MEP amplitude for
67 hand action verbs vs. non-action verbs 500 ms after verb presentation. These cortical
68 activations could explain behavioral modulation during language processing, such as
69 improvement in squat jump (Rabahi et al., 2012, 2013), and facilitation of motor
70 response time (Andres et al., 2015; Klepp et al., 2019).

71 Such behavioral facilitations are present only if the linguistic content is
72 compatible with the movement performed (Gentilucci et al., 2000; Taylor and Zwaan,
73 2008; Dalla Volta et al., 2009; Glenberg and Gallese, 2012; Zwaan et al., 2012; Van
74 Dam and Desai, 2017). Furthermore, some studies report decreases in motor
75 activation for action verbs compared to non-action verbs at very early latencies (TMS
76 before end of verb: Buccino et al., 2005), or fail to observe activation of the motor
77 cortex (lexical decision tasks: Perani et al., 1999; Longe et al., 2007; motion word
78 comprehension: Grossman et al., 2002; passive reading: Gianelli et al., 2020). While
79 some of the discrepancies in these findings may be attributable to the timing of these
80 studies (see early interference explanation proposed by Buccino et al., 2005), such
81 results generally undermine the idea that action verbs systematically/automatically
82 activate the motor cortex (see also Rüschemeyer et al., 2007; Raposo et al., 2009).
83 Instead, this activation seems to be, as Kemmerer (2015, page 4) states, “sensitive
84 to attentional and situational factors that we are only beginning to understand.”

85 In our view, context is one of these factors that plays an important role in
86 language processing, allowing a more effective and precise understanding of the
87 action described in the sentence. Indeed, studies using fMRI and behavioral
88 measures demonstrate how context can modulate the degree of motor activation and

89 performance (Raposo et al., 2009; Van Dam et al., 2010; van Dam et al., 2010;
90 Zwaan et al., 2010; Papeo et al., 2012; Van Dam et al., 2012; van Dam et al., 2012;
91 Gilead et al., 2013; Van Dam et al., 2014; Kemmerer, 2015; Beauprez et al., 2018).
92 For instance, Raposo and colleagues (2009) observed activation of motor areas for
93 action verbs in isolation (e.g., *kick*) and in literal phrases (e.g., *kick the ball*), but not
94 in idiomatic phrases (e.g., *kick the bucket*). Likewise, Van Dam et colleagues (2010)
95 observed greater activation in motor-related brain areas for highly specific action
96 verbs (to wave, to wipe) than for less specific action verbs (to greet, to clean).

97 Given these results, it is possible that specifying actions by increasing the
98 sentence context may lead to greater motor cortex activation in general. Indeed,
99 Wurm and Caramazza (2019) report a stronger decoding of action scenes relative to
100 short sentences in frontoparietal representations, which they attribute to a difference
101 in richness of detail. Although motor representations can be triggered by the reading
102 or perception of an action, these researchers suggest that action reading leads to a
103 less specific and robust motor representation. Following this logic, increasing
104 sentence context (specifying the action) could increase motor cortex activation in
105 general, thereby “strengthening” motor representations.

106 Another possibility is that greater sentence context leads to a “sharpening” of
107 motor representations, making them more precise yet not always stronger. This idea
108 is consistent with studies in which the context surrounding action verbs selectively
109 engages motor representations. For instance, Taylor and Zwaan (2008) observed
110 facilitation for rotating a knob when the direction of rotation (clockwise) matched
111 rather than mismatched the direction described in concurrent sentences (*The*
112 *gardener noticed that the water was still running. He approached the faucet which he*
113 *turned off quickly*). Interestingly, the motor facilitation was observed at the moment

114 of processing the verb, and reappeared at the post-verbal adverb, only if that adverb
115 qualified the action (“slowly” or “quickly”), and not if the adverb instead shifted focus
116 to the agent (e.g., “obediently” or “eagerly”). This suggests that context can
117 selectively activate motor representations, and furthermore, that these motor
118 representations are temporally pinned to the verb, or any word that draws the
119 contextual focus to the action itself.

120 In the current study, we investigated whether context leads to a general
121 strengthening or a condition-specific sharpening of the motor representations. We
122 used the TMS methodology to probe how context modulated activation in the motor
123 cortex during the reading of verbs. Participants were instructed to read manual-
124 action or non-manual verbs that appeared either in a rich sentential context (full
125 sentence) or in a minimal context (pronoun-verb pair). TMS pulses were delivered
126 over the pointer finger area of the left primary motor cortex at three latencies after
127 verb presentation (200, 300, or 400 ms) to better capture individual corticospinal
128 modulation during reading. We expect to replicate the effect of action often seen in
129 the literature, characterized by a greater corticospinal excitability increase for action
130 compared to non-action sentences. However, this effect may be modulated by
131 sentence context. The strengthening idea would predict greater corticospinal
132 excitability in the rich sentential context than in the minimal context for both manual
133 and non-manual verbs. The sharpening idea, on the other hand, would predict an
134 intensified action effect in the rich context, with an increase of corticospinal
135 excitability for manual verbs but not for non-manual verbs.

136 **Material and method**

137 **Participants**

138 Thirty-five healthy right-handed adults (12 women; mean age = 23.79 years-old;
139 range 18-29 years) participated in the experiment at the laboratory. As context may
140 have only a subtle effect on the motor system, this sample size was chosen based on
141 a power analysis using a small effect size of 0.25 (G*Power, version 3.1.9.2., Faul et
142 al., 2007). Handedness was assessed by the Edinburgh inventory (Oldfield, 1971).
143 All participants had normal or corrected-to-normal vision, without neurological,
144 physical and cognitive pathologies. The experiment was conducted in two sessions:
145 1) an experimental TMS recording and 2) a reading comprehension assessment.
146 Volunteers were first approved for participation by a medical doctor, and confirmed
147 their participation with written consent. The Ethics Committee approved experimental
148 protocol (CPP SOOM III, ClinicalTrials.gov Identifier: NCT03334526) and procedures
149 in accordance with the Declaration of Helsinki.

150 **Stimuli**

151 One hundred and forty-four French verbs were generated; half referred to
152 *Manual Action* (e.g., “I scrub”) and half were *Non-Manual* (including non-action as “I
153 ignore” as well as actions that did not implicate the hand as “I kick”). These verbs
154 were presented either in a *Rich context* that helped to specify the verb (e.g., “I see a
155 stain on my shirt and I scrub it” or “I see a stain on my shirt and I ignore it”), or in
156 *Minimal context* (e.g., “I scrub” or “I ignore”; see Table 1 for details). Sentences
157 always appeared in the first-person present tense. All rich-context sentences were
158 created such that the target verb occurred at the end of the sentence (see Figure 1).
159 This final pronoun-verb segment was presented alone on a subsequent screen after
160 the beginning of the sentence was presented, thus yielding an identical or very
161 similar presentation screen to the minimal sentence version.

162 A list was generated, in which 36 of the manual action verbs, and 36 of the non-
163 manual verbs occurred within rich sentence contexts, while the other 36 manual
164 action verbs, and 36 non-manual verbs occurred in minimal sentence context. A
165 second list presented these same verbs in the opposite rich and minimal context
166 versions. Each manual action verb (to scrub) was paired with a non-manual verb (to
167 ignore), sharing the same rich-context sentence (I see a stain on my shirt and I
168 scrub/ignore it), and each verbal stimulus only appeared once in the list. Thereby,
169 across participants, each verb appeared in both conditions, but a given participant
170 saw each verb and each sentence only once. For example, for the scrub/ignore pair,
171 if a given participant read the minimal sentence “I scrub”, she/he would also read the
172 rich context sentence “I see a stain on my shirt and I ignore it”. And another
173 participant would read “I ignore” as well as “I see a stain on my shirt and I scrub it”. In
174 addition, TMS latencies were counterbalanced within each list.

175 Latent Semantic Analysis (LSA: lsa.colorado.edu; Landauer et al., 1998) was
176 used to assure that manual action verbs (0.294 ± 0.257) and non-manual verbs
177 (0.295 ± 0.269) did not significantly differ in their association scores to the preceding
178 sentence fragments ($P=0.868$). We also compared various psycholinguistic factors
179 (written frequency, number of characters, and spelling neighbors) between manual
180 action verbs and non-manual verbs using the Lexique.org database (New et al.,
181 2004). Corrected t-tests (modified Hochberg’s procedure; Rom, 1990) yielded a
182 significant difference only for written frequency ($p=0.004$; Mean ratios: 11.34 ± 16.69
183 and 30.80 ± 53.70 for manual action verbs and non-manual verbs, respectively), but
184 not for number of characters ($p=0.604$; Mean ratios: 6.37 ± 1.63 and 6.51 ± 1.57 for
185 manual action verbs and non-manual verbs, respectively) nor spelling neighbors
186 ($p=0.136$; Mean ratios: 5.95 ± 5.03 and 4.73 ± 4.74 for manual action verbs and non-

187 manual verbs, respectively). The frequency difference is largely due to a few high-
 188 frequency non-manual verbs such as “to read.” Furthermore, as higher frequency
 189 would typically increase facilitation and excitability, this difference could only hurt the
 190 chances of observing the predicted effect of action. To confirmed the accuracy of the
 191 manual and non-manual distinctions of the stimuli, 8 participants were asked to rate
 192 on a scale from 1-5 whether a sentence described a manual action or not (1=
 193 absolutely not a hand action, and 5= entirely a hand action). A t-test revealed a
 194 significant difference ($p < 0.001$) between the manual (4.36 ± 0.34) and non-manual
 195 (1.43 ± 0.54) verbs.

196 Table 1. Example of lexical stimuli used in the experiment. In grey lines are the
 197 English translation of the French verbs/sentences presented.

Manual action		Non-manual	
Minimal Context	Rich Context	Minimal context	Rich context
Je mélange	Les cartes sont sur la table et je les mélange	Je memorise	Les cartes sont sur la table et je les mémorise
<i>I shuffle</i>	<i>The cards are on the table and I shuffle them</i>	<i>I memorize</i>	<i>The cards are on the table and I memorize them</i>
Je frotte	Je vois une tache sur mon t-shirt et je la frotte	J'ignore	Je vois une tache sur mon t-shirt et je l'ignore
<i>I scrub</i>	<i>I see a stain on my shirt and I scrub it</i>	<i>I ignore</i>	<i>I see a stain on my shirt and I ignore it</i>
Je ferme	L'enveloppe est prête et je la ferme	Je relis	L'enveloppe est prête et je la relis
<i>I close</i>	<i>The envelope is ready and I am closing it</i>	<i>I reread</i>	<i>The envelope is ready and I reread it</i>
J'accorde	La nouvelle guitare est très belle et je l'accorde	J'écoute	La nouvelle guitare est très belle et je l'écoute
<i>I tune</i>	<i>The new guitar is very beautiful and I tune it</i>	<i>I listen</i>	<i>The new guitar is very beautiful and I listen to it</i>

Je paraphe	Après avoir lu le contrat, je le paraphe	Je contemple	Après avoir lu le contrat, je le contemple
I initial	After reading the contract, I initial it	I contemplate	After reading the contract, I contemplate it

198

199

200

Procedure

201

202

203

204

205

206

207

208

209

210

211

212

213

214

Participants sat in an armchair. Stimuli were presented on a 19-inch LCD monitor by a home-made software, which controlled TMS triggering and synchronized physiological recordings. Throughout the recording, participants were instructed not to move, while they silently read sentences (passive reading). Corticospinal excitability was recorded at rest, as well as during the reading task at various stimulation latencies (200, 300 or 400ms after the verb onset). These latencies were chosen based on electroencephalogram studies showing 200ms as a minimal latency for semantic processing in anterior regions (Pulvermüller et al., 2001; Hauk et al., 2006). In addition, later latencies are related to changes of P300 in parietal and frontal regions (Pulvermüller et al., 2001), but also N400 in posterior regions (Kellenbach et al., 2002; Beres, 2017) when participants read action words compared to abstract words. In the present study, these different latencies were used to account for individual differences in the speed of semantic integration, which would yield variable peaks of motor cortex involvement.

215

216

217

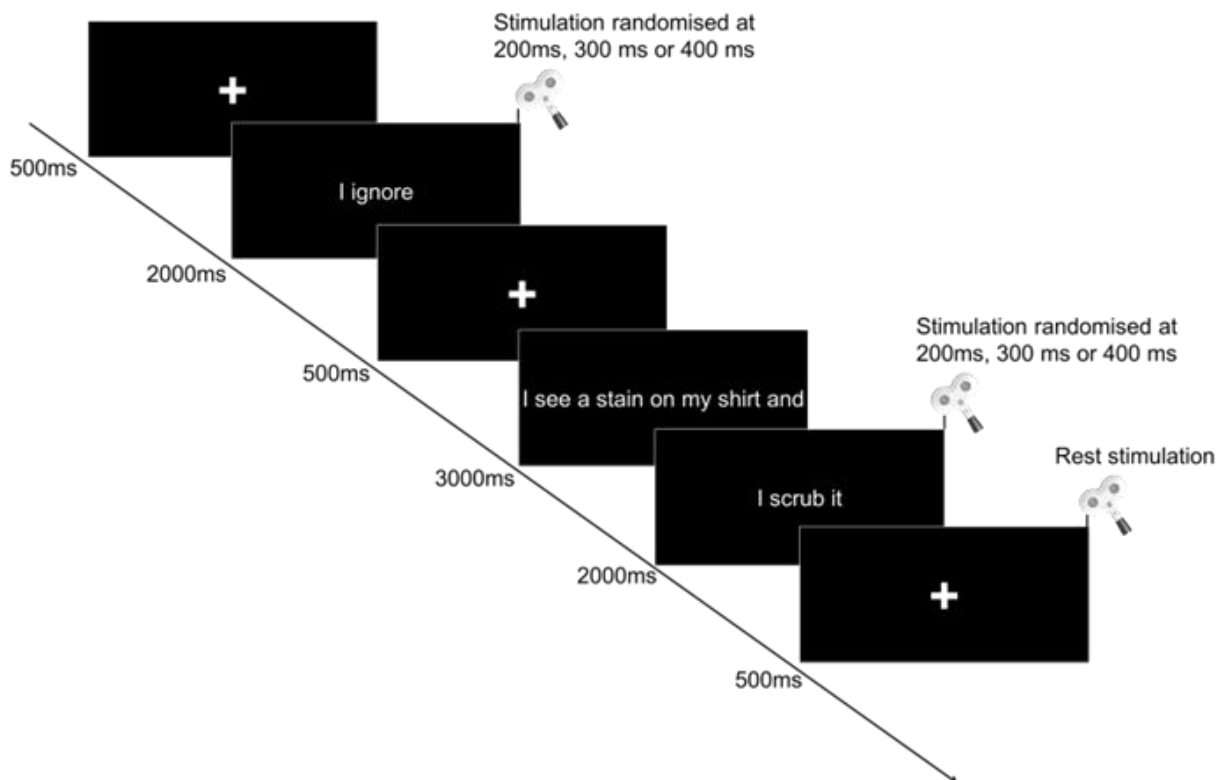
218

219

Before the experimental trials, the participants performed four familiarization trials, each with a fixation cross, followed by a minimal sentence or a rich sentential context, then a black screen before the next trial. Once the participant understood this procedure, four new practice trials were presented, now including TMS pulses after the appearance of the target verb. Then, the experimental session was divided

220 into 3 blocks, each comprised of 56 trials, yielding 168 trials total in the experiment.
221 Among the 56 trials in each block, 8 trials were interspersed with TMS pulses only at
222 rest (fixation cross), which served as reference stimulations and allowed
223 comparisons across experimental conditions in that block. Therefore, participants
224 saw 48 experimental trials in each of the three blocks, and 144 trials in total.
225 Moreover, to avoid mental fatigue and lack of concentration, there was a two-minute
226 break between each block, allowing participants to be as attentive as possible during
227 experimental blocks. In each block, the number of stimulations was equally
228 distributed between all conditions, but also between the three different stimulation
229 latencies.

230



231

232 *Figure 1. Experimental procedure. Sentences in a Minimal or Rich context were presented on a screen in*
233 *front of the participant. Single-pulse TMS was triggered over the left hemisphere and motor-evoked potentials*
234 *recorded in the right index finger.*

235 Several weeks later, individuals participated in a second experimental session, in
236 which two levels of contextual reading comprehension ability were assessed. This
237 session was included in order to account for the possible effect of individual
238 differences in the use of context during reading comprehension. To investigate
239 sensitivity to lower-level memory-based context, we administered a "Remember
240 versus Know" paradigm (Tulving, 1985), in which they had to identify whether words
241 were encountered in a previously read text (yes or no response), and in what context
242 they were encountered. To assess higher-level use of context during comprehension,
243 we used a Curriculum-Based Measurement-Maze (Parker et al., 1992), in which
244 readers rely on inferences to select a contextually-appropriate word from three
245 alternatives. After the first sentence, every seventh word in the passage is replaced
246 with that correct word and two distractors. Participants must use the context to select
247 the word that fits best with the rest of the passage.

248 **TMS**

249 Single-pulse TMS was generated from an electromagnetic stimulator Magstim
250 200 (Magstim Company Ltd, Whitland) and using a figure-of-eight coil (70 mm in
251 diameter). The coil was placed over the contralateral left hemisphere to target the
252 motor area of the First Dorsal Interosseous (FDI) muscle of the right hand. The coil
253 rested tangential to the scalp with the handle pointing backwards and laterally at a
254 45° angle away from the midline. First, the mapping of the motor cortex of each
255 participant determined the precise stimulation site (hotspot) corresponding to the
256 location, where the MEPs amplitude of the FDI muscle was the highest and the most
257 consistent for the same stimulation intensity. The resting motor threshold of each
258 participant was determined as the minimal intensity of TMS necessary to induce a
259 MEP of 50 μ V peak-to-peak amplitude in the right FDI muscle for 4 trials out of 8.

260 During the experimental session, TMS intensity was set at 130% of the resting motor
261 threshold. This intensity was chosen not only to stimulate the participant above the
262 motor threshold, but also to achieve a stimulus intensity near the middle of the
263 stimulus-response curve (Groppa et al., 2012), from which point it would be possible
264 to observe both increases and decreases in MEP amplitude

265

266 **EMG recording**

267 The EMG signal was recorded through 10mm-diameter surface electrodes
268 (Contrôle Graphique Médical, Brice Comte-Robert, France) placed over the FDI
269 muscle of the right hand. Before placing the electrodes, the skin was shaved and
270 cleaned in order to reduce noise in the EMG signal (< 20µV). The EMG signals were
271 amplified and bandpass filtered on-line (10-1000 Hz, Biopac Systems Inc.) and
272 digitized at 2000 Hz for off-line analysis. We also measured the root mean square of
273 EMG signal (EMGrms), to ensure that participants were at rest in all conditions.
274 Throughout the experiment, EMGrms was monitored for the 100 ms preceding every
275 TMS pulse to ensure complete muscle relaxation, using the following formula (MD =
276 movement duration):

$$RMS = \sqrt{\frac{1}{MD} \int_0^{MD} (EMG)^2 dt}$$

277

278 **Data and statistical analysis**

279 EMG data were extracted with Matlab (The MathWorks, Natick, Massachusetts,
280 USA) and we measured peak-to-peak MEP amplitude. We first eliminated outliers for
281 each participant within each stimulation latency and condition; data falling 2 SDs

282 above or below individual means for each experimental condition were removed
283 before analysis (4.13% of total). Then, the average MEP amplitude for each condition
284 was normalized with reference to baseline MEP amplitude (rest condition):

$$\left(\frac{\text{Mean condition} - \text{Mean rest}}{\text{Mean rest}} \right) \times 100$$

285 Importantly, no analysis on the timing factor was performed as we rather isolated the
286 highest average amplitude (over 12 trials) among the three stimulation times (200,
287 300, or 400ms) for each participant in each condition. Thus, for each participant, we
288 use the data from only one of these three latencies for each condition, presumably
289 corresponding to the moment when the motor representation was most active.
290 Individuals can vary greatly in speed of decoding, as well as lexical access (Sereno
291 et al., 1998; Dambacher et al., 2006) and semantic integration (Kutas and Hillyard,
292 1980; Brown and Hagoort, 1993; Van Berkum et al., 1999). In addition, the motor
293 activation that we aimed to measure is likely punctual and fleeting in nature.
294 Therefore, this method of stimulation at multiple latencies after the target verb
295 (informed by previous investigations) was designed to maximize the chances of
296 tapping into the fleeting motor representation, which may might not even be present
297 at all latencies. Selecting only the latency with the highest average MEP helps to
298 account for inter-individual variability in the latency of the motor representation, and
299 its consequential increase in corticospinal excitability. Finally, Grubbs test identified
300 extreme mean values for one participant, who was excluded from the final analysis.
301 All data analyses were performed using the software Statistica (Stat Soft, France).

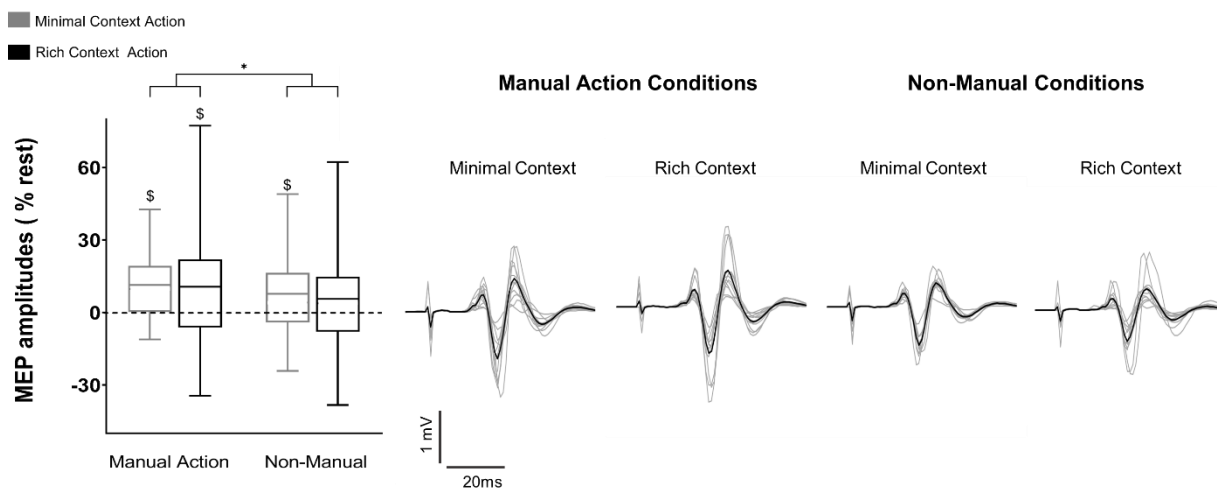
302 Data normality was confirmed by the Shapiro-Wilk test. To assess the influence
303 of *Action* and *Context* on corticospinal excitability, we performed a 2 by 2 repeated
304 measures ANOVA with *Action* (Manual action vs. Non-manual) and *Context* (Minimal
305 vs. Rich) as within-subject factors. Then, one-sample t-tests were used to compare

306 normalized MEPs at zero for each condition to assess whether corticospinal
307 excitability during reading changed from baseline. Finally, in order to ensure that our
308 results were not contaminated by muscular pre-activity, we tested with Wilcoxon tests
309 if the EMGrms before the TMS artifact was not different from zero in our experimental
310 conditions.

311 To assess the influence of participants' comprehension ability on their
312 corticospinal excitability modulations by context, we performed Pearson correlations
313 between the context effect (Minimal vs. Rich) and the memory-based, as well as the
314 higher context-level comprehension scores. The data are presented as mean values
315 (\pm standard error) and the alpha value was set at 0.05.

316 3. Results

317 The overall ANOVA revealed a main effect of *Action* ($F_{1,33} = 4.811$, $p = 0.035$,
318 $\eta^2 = 0.127$), with larger MEP ratios for manual action verbs ($11.02 \pm 3.25\%$) than non-
319 manual verbs ($6.76 \pm 3.19\%$). We did not observe a main effect of *Context* ($F_{1,33}$
320 $= 0.168$, $p = 0.683$, $\eta^2 = 0.005$) nor an *Action* by *Context* interaction ($F_{1,33} = 0.064$
321 $p = 0.801$, $\eta^2 = 0.001$) (Figure 2).



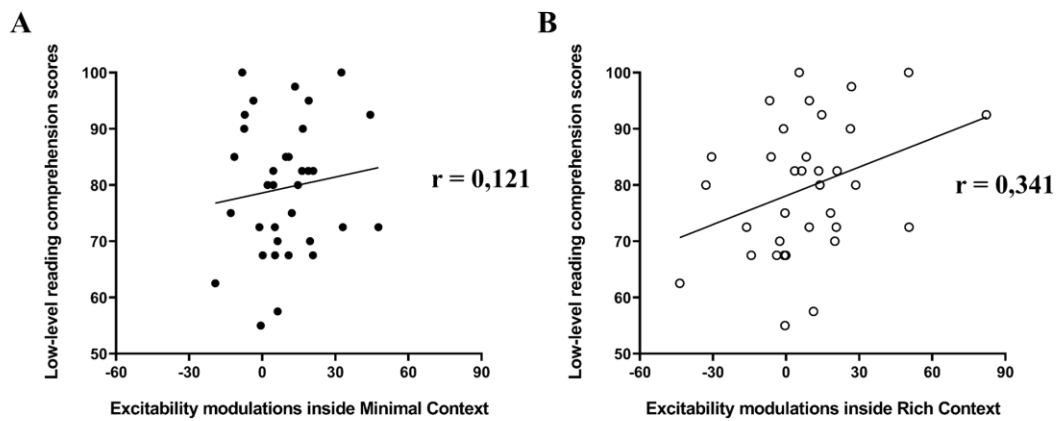
323 *Figure 2. Corticospinal excitability in Rich and Minimal Context. Box plots on the left side represent normalized*
324 *MEPs. The line represents the mean. The box and the whiskers represent the 25th/75th quartile and the 5th and 95th*

325 *percentile. Anova revealed an action effect for rich context but no effect for minimal context. The right side of the panel*
326 *illustrates raw MEPs of a typical subject (grey lines). The black line is the average MEP of the condition for this participant.*
327 ** = $p < 0.05$. \$= $p < 0.05$ indicates a significant difference from zero (Trick trials).*

328 Using one-sample t-tests, we found that normalized MEPs of all conditions were
329 different from baseline (all p 's <0.05), except for non-manual verbs in the rich context
330 ($p=0.167$). This finding reveals the possible importance of context for reducing
331 residual activation for non-manual verbs that may be unclear in the absence of
332 sentence context.

333 Low and high-level reading comprehension abilities influenced these outcomes,
334 and in particular the context effect. We observed a positive correlation between the
335 modulations of corticospinal excitability in rich context conditions and the low-level
336 reading comprehension scores ($p=0.048$; $r=0.341$). Specifically, higher scores in
337 memory-based comprehension yielded greater corticospinal excitability in rich
338 context conditions but not minimal ($p=0.495$; $r=0.121$). This finding reveals that the
339 modulation of corticospinal excitability varies across individuals, and that
340 comprehension ability may partially explain such variability. No significant
341 correlations were observed for the high-level context-based comprehension scores
342 (minimal context: $p=0.623$; $r=-0.087$; rich context: $p=0.590$; $r=0.095$) (Figure 3). The
343 four correlations were evaluated using the modified Hochberg's correction procedure
344 (Rom, 1990).

Memory-based comprehension scores



345

346 *Figure 3. Correlations between the corticospinal excitability modulations depend on the context (Minimal*
347 *vs. Rich) and the comprehension scores (memory vs. context-level). (A and B) represent correlations between the*
348 *excitability modulations in Minimal context (A) and Rich context (B) with the memory-based comprehension*
349 *scores. (C and D) represent correlations between the excitability modulations in Minimal context (C) and Rich*
350 *context (D) with the higher context-level comprehension scores.*

351 Finally, we analyzed the EMGrms prior to TMS artifacts to test for confounds in
352 MEP modulation. We did not observe any difference between baseline (mean \pm SD =
353 $1.76 \pm 1.06 \mu\text{V}$) and the other conditions (all p 's > 0.05 ; in minimal context, for manual
354 verbs: $1.83 \pm 1.10 \mu\text{V}$, for non-manual verbs: $1.84 \pm 1.13 \mu\text{V}$; in rich context, for manual
355 verbs: $1.90 \pm 1.48 \mu\text{V}$, for non-manual verbs: $1.83 \pm 1.11 \mu\text{V}$). This indicates that MEP
356 modulations were not influenced by background EMGrms.

357 **Discussion**

358 The results of this study support the importance of the type of stimuli in
359 modulating the involvement of the motor cortex during action language processing.
360 We observed action-specific modulation of corticospinal excitability, with increased
361 MEP amplitude for manual action verbs compared to non-manual verbs.
362 Nonetheless, we did not observe a main effect of context nor an interaction between
363 action and context. These findings do not support the “strengthening” idea, whereby
364 sentence context would generate greater motor activation in general. However, there
365 does seem to be some evidence for the idea of “sharpening,” as motor activation did
366 not differ from rest when the verb phrase was presented in combination with a
367 sentence context that makes it clear that there is no manual action.

368 The activation of the motor cortex is presumed to arise from reading events
369 describing actions, typically verbs. However, even a non-action verb may be able to
370 evoke some degree of motor activation if it is underspecified, because the event
371 representation is vague. Indeed, it seems odd that non-manual verbs presented in a
372 minimal context might increase the corticospinal excitability in hand muscles.
373 However, in the absence of context, it is possible that lexical access to the less
374 constrained meaning evokes a broad distributed activation, including the motor
375 system for some words. Additionally, our non-manual-action verbs included actions
376 that were not manual, and when presented out of context, perhaps these could
377 broadly activate the motor system, including the hand area. Contextual constraints
378 may reduce the possibilities for such broad activation and eliminate unintended
379 meanings. If the verb is well contextualized, the motor representation is more
380 precise, yielding activation of only the appropriate effectors in the motor system that
381 are relevant to the event. This is reflected in our results where all conditions resulted
382 in a higher state of corticospinal excitability from the baseline, except for non-manual

383 verbs in the rich context. This suggests that the motor cortex can be automatically
384 activated at some level even by non-action verbs in the absence of context [see also
385 motor activation in abstract verbs (Sakreida et al., 2013) and metaphoric sentences
386 (Desai et al., 2013; Reilly et al., 2019)].

387 While we did not observe any boost in motor activation when a rich context
388 specifies the nature of the described situation, we did observe a lack of residual
389 motor activation from non-manual verbs for which the representation may have been
390 unclear in the absence of context. The rich context may lead to a disambiguation of
391 the meaning of the verb, especially when the verb is vague or has multiple meanings.
392 This would not apply to all of our stimuli, as for some verb phrases, it was already
393 clear whether a manual action was implicated or not, even without the context.
394 However, at least some of our non-manual stimuli were interpreted as implicating
395 less manual action when presented in combination with a receding sentence context.
396 Consistent with Mahon and colleagues (Mahon and Caramazza, 2008; Mahon,
397 2015), motor cortex activation may therefore play an important role in embellishing
398 certain aspects of word meaning that are relevant in a given context.

399 Moreover, an action effect in minimal context is consistent with previous studies
400 (Papeo et al., 2009; Innocenti et al., 2014), reporting that many manual action verbs
401 would activate the motor cortex to a greater extent than non-manual verbs without
402 context. However, we expected a greater difference for these same stimuli if
403 accompanied by more contextual information to better specify the action, supporting
404 the sharpening idea. Indeed, the manual nature of the meaning of some verbs is
405 quite precise regardless of context (e.g., “I write”) whereas others can be rather
406 vague (e.g., “I take”). As mentioned above, this vagueness can even introduce motor
407 cortex activation in verbs that are intended to be non-action stimuli. Although we did

408 not observe a greater effect of action in the rich compared minimal context, further
409 research is currently underway to further test this idea of sharpening motor activation.

410 The present study suggests that the context effect is sensitive to individual
411 factors, such as memory-based comprehension ability. We found that participants
412 with higher comprehension ability exhibited a greater increase in excitability when
413 reading rich-context sentences, regardless of verb type. This does not necessarily
414 mean that context automatically strengthens motor activity (since no main effect of
415 context was observed), but rather that the engagement of the motor cortex can vary
416 across situations and across individuals, and may depend on parameters such as
417 comprehension ability.

418 Based on the current findings and previous studies (Zwaan et al., 2010; Van
419 Dam et al., 2012; van Dam et al., 2012; Gilead et al., 2013; Van Dam et al., 2014;
420 Beauprez et al., 2018, 2020; Wurm and Caramazza, 2019), language-induced motor
421 representations are flexible and at least to some extent sensitive to linguistic context.
422 It appears that context may play a role in strengthening motor activation for good
423 comprehenders, as well as eliminating residual motor activation for non-action verbs.
424 These findings are consistent with cognitive theories that accommodate semantic
425 flexibility and top-down processes, whereby relevant features and alternative
426 meanings are determined by the semantic context very early as each new word is
427 encountered (e.g., Gentner, 1981; Marslen-Wilson, 1987; Tomasino and Rumiati,
428 2013).

429 The question remains as to whether activation of the primary motor cortex is
430 necessary to process action language (see also: Wurm and Caramazza, 2019).
431 Researchers observed that disturbances of motor areas caused by repeated TMS

432 during language processing can yield a decrease in performance, implying the
433 engagement of the motor cortex in this process (Willems et al., 2011; Repetto et al.,
434 2013; Vukovic et al., 2017; Courson et al., 2018). While understanding might be
435 disturbed, diminished, or less effective, it is not completely blocked. Although
436 language comprehension may be able to proceed without the involvement of the
437 primary motor cortex, our findings suggest that it may play a role in the optimization
438 of this process, refining linguistic understanding and making it more effective when
439 necessary.

440 One potential limitation of the current study is the number of experimental trials
441 per participant. Since we cannot know exactly when the motor representation will
442 engage and reach its maximum for each subject, we have to probe at several
443 latencies on separate trials, and select the peak afterwards. This can be considered
444 a strength of our study in that we consider individual differences in processing time,
445 but it can also be a limitation in that we reduce the number of experimental trials. In
446 future investigations, we plan to overcome this limitation by calibrating each subject's
447 individual processing time prior to the test session, as well as employing continuous
448 measures, such as EEG. Finally, while we strove to maximize the control between
449 the rich and minimal context conditions, we could not avoid the additional pronoun
450 which sometimes preceded the verb in the rich context condition. When this
451 occurred, the target verb was rendered grammatically transitive in the rich context (*Je*
452 *le frotte*; I scrub it) while it remained intransitive in the minimal context (*Je frotte*; I
453 scrub). Otherwise, the probe screens were identical for the two conditions.

454 In conclusion, this study provides relevant information about the role of
455 sentential context on primary motor cortex activation. We found that linguistic context
456 serves to focus the motor representation of the described action, eliminating residual

457 motor activation for non-action verbs. Moreover, the context effect appears to be
458 sensitive to individual differences in reading comprehension. Consistent with the idea
459 of semantic flexibility and top-down processes, when target verb phrases are
460 presented with a sentence context that makes it clear that no manual action is
461 evoked, the motor cortex does not contribute to the meaning representation.

462 **Declaration of competing interest**

463 None declared.

464 **Author Contributions**

465 Experiment design: WD, CML, FL, CP

466 Data collection: WD

467 Statistical analysis: WD, CML, FL

468 Manuscript preparation: WD, CP, CML, FL

469 **Data availability statement.**

470 All data from this study are available at

471 https://osf.io/5zmq/?view_only=82c93af470fd42be8ca33969b14f1c37

472 **Acknowledgement**

473 The authors are very grateful to Cyril Sirandré for help with the custom
474 Neurostim software and the experimental setup.

475 **References**

476 Andres M, Finocchiaro C, Buiatti M, Piazza M (2015) Contribution of motor
477 representations to action verb processing. *Cognition* 134:174–184.

478 Aziz-Zadeh L, Wilson SM, Rizzolatti G, Iacoboni M (2006) Congruent Embodied
479 Representations for Visually Presented Actions and Linguistic Phrases Describing
480 Actions. *Current Biology* 16:1818–1823.

481 Barsalou LW (1999) Perceptual symbol systems. *Behavioral and Brain*
482 *Sciences* 22:577–609.

483 Barsalou LW (2008) Grounded Cognition. *Annual Review of Psychology*
484 59:617–645.

485 Barsalou LW, Simmons WK, Barbey AK, Wilson CD (2003) Grounding
486 conceptual knowledge in modality-specific systems. *Trends in Cognitive Sciences*
487 7:84–91.

488 Beauprez SA, Blandin Y, Almecija Y, Bidet-Ildei C (2020) Physical and
489 observational practices of unusual actions prime action verb processing. *Brain and*
490 *Cognition* 138.

491 Beauprez SA, Toussaint L, Bidet-Ildei C (2018) When context modulates the
492 influence of action observation on language processing. *PLoS ONE* 13.

493 Beres AM (2017) Time is of the Essence: A Review of Electroencephalography
494 (EEG) and Event-Related Brain Potentials (ERPs) in Language Research. *Applied*
495 *Psychophysiology Biofeedback* 42:247–255.

496 Brown C, Hagoort P (1993) The processing nature of the N400: Evidence from
497 masked priming. *Journal of Cognitive Neuroscience* 5:34–44.

498 Buccino G, Riggio L, Melli G, Binkofski F, Gallese V, Rizzolatti G (2005)
499 Listening to action-related sentences modulates the activity of the motor system: A
500 combined TMS and behavioral study. *Cognitive Brain Research* 24:355–363.

501 Courson M, Macoir J, Tremblay P (2018) A facilitating role for the primary motor
502 cortex in action sentence processing. *Behavioural Brain Research* 336:244–249.

503 Dalla Volta R, Gianelli C, Campione GC, Gentilucci M (2009) Action word
504 understanding and overt motor behavior. *Experimental Brain Research* 196:403–412.

505 Dambacher M, Kliegl R, Hofmann M, Jacobs AM (2006) Frequency and
506 predictability effects on event-related potentials during reading. *Brain Research*
507 1084:89–103.

508 de Zubicaray G, Arciuli J, McMahon K (2013) Putting an “end” to the motor
509 cortex representations of action words. *Journal of cognitive neuroscience* 25:1957–
510 1974.

511 Decety J, Grèzes J (2006) The power of simulation: Imagining one’s own and
512 other’s behavior. *Brain Research* 1079:4–14.

513 Desai RH, Conant LL, Binder JR, Park H, Seidenberg MS (2013) A piece of the
514 action: Modulation of sensory-motor regions by action idioms and metaphors.
515 *NeuroImage* 83:862–869.

516 Faul F, Erdfelder E, Lang A-G, Buchner A (2007) G*Power 3: a flexible
517 statistical power analysis program for the social, behavioral, and biomedical
518 sciences. *Behav Res Methods* 39:175–191.

519 Fischer MH, Zwaan RA (2008) Embodied language: A review of the role of the
520 motor system in language comprehension. *Quarterly Journal of Experimental*
521 *Psychology* 61:825–850.

522 Franklin ZC, Wright DJ, Holmes PS (2020) Using action-congruent language
523 facilitates the motor response during action observation: A combined transcranial
524 magnetic stimulation and eye-tracking study. *Journal of Cognitive Neuroscience*
525 32:634–645.

526 Gallese V, Lakoff G (2005) The brain’s concepts: The role of the sensory-motor
527 system in conceptual knowledge. *Cognitive Neuropsychology* 22:455–479.

528 Gentilucci M, Benuzzi F, Bertolani L, Daprati E, Gangitano M (2000) Language
529 and motor control. *Experimental Brain Research* 133:468–490.

530 Gentner D (1981) Verb semantic structures in memory for sentences: Evidence
531 for componential representation. *Cognitive Psychology* 13:56–83.

532 Gianelli C, Kühne K, Lo Presti S, Mencaraglia S, Dalla Volta R (2020) Action
533 processing in the motor system: Transcranial Magnetic Stimulation (TMS) evidence

534 of shared mechanisms in the visual and linguistic modalities. *Brain and Cognition*
535 139.

536 Gilead M, Liberman N, Maril A (2013) The language of future-thought: An fMRI
537 study of embodiment and tense processing. *NeuroImage* 65:267–279.

538 Glenberg AM, Gallese V (2012) Action-based language: A theory of language
539 acquisition, comprehension, and production. *Cortex* 48:905–922.

540 Groppa S, Oliviero A, Eisen A, Quartarone A, Cohen LG, Mall V, Kaelin-Lang A,
541 Mima T, Rossi S, Thickbroom GW, Rossini PM, Ziemann U, Valls-Solé J, Siebner HR
542 (2012) A practical guide to diagnostic transcranial magnetic stimulation: Report of an
543 IFCN committee. *Clinical Neurophysiology* 123:858–882.

544 Grossman M, Koenig P, DeVita C, Glosser G, Alsop D, Detre J, Gee J (2002)
545 Neural representation of verb meaning: An fMRI study. *Human Brain Mapping*
546 15:124–134.

547 Hauk O, Davis MH, Ford M, Pulvermüller F, Marslen-Wilson WD (2006) The
548 time course of visual word recognition as revealed by linear regression analysis of
549 ERP data. *NeuroImage* 30:1383–1400.

550 Hauk O, Johnsrude I, Pulvermüller F (2004) Somatotopic Representation of
551 Action Words in Human Motor and Premotor Cortex. *Neuron* 41:301–307.

552 Innocenti A, De Stefani E, Sestito M, Gentilucci M (2014) Understanding of
553 action-related and abstract verbs in comparison: a behavioral and TMS study.
554 *Cognitive processing* 15:85–92.

555 Jeannerod M (2008) *Motor Cognition: What Actions Tell the Self.*

556 Kellenbach ML, Wijers AA, Hovius M, Mulder J, Mulder G (2002) Neural
557 differentiation of lexico-syntactic categories or semantic features? Event-related
558 potential evidence for both. *Journal of Cognitive Neuroscience* 14:561–577.

559 Kemmerer D (2015) Are the motor features of verb meanings represented in the
560 precentral motor cortices? Yes, but within the context of a flexible, multilevel
561 architecture for conceptual knowledge. *Psychonomic Bulletin and Review* 22:1068–
562 1075.

563 Klepp A, van Dijk H, Niccolai V, Schnitzler A, Biermann-Ruben K (2019) Action
564 verb processing specifically modulates motor behaviour and sensorimotor neuronal
565 oscillations. *Scientific reports* 9:15985.

566 Kutas M, Hillyard SA (1980) Reading senseless sentences: Brain potentials
567 reflect semantic incongruity. *Science* 207:203–205.

568 Labruna L, Fernández-Del-Olmo M, Landau A, Duqué J, Ivry RB (2011)
569 Modulation of the motor system during visual and auditory language processing.
570 *Experimental Brain Research* 211:243–250.

571 Lambon Ralph MA, Pobric G, Jefferies E (2009) Conceptual knowledge is
572 underpinned by the temporal pole bilaterally: Convergent evidence from rTMS.
573 *Cerebral Cortex* 19:832–838.

574 Lambon Ralph MA, Sage K, Jones RW, Mayberry EJ (2010) Coherent concepts
575 are computed in the anterior temporal lobes. *Proceedings of the National Academy of
576 Sciences of the United States of America* 107:2717–2722.

577 Landauer TK, Foltz PW, Laham D (1998) An introduction to latent semantic
578 analysis. *Discourse processes* 25:259–284.

579 Longe O, Randall B, Stamatakis EA, Tyler LK (2007) Grammatical categories in
580 the brain: The role of morphological structure. *Cerebral Cortex* 17:1812–1820.

581 Mahon BZ (2015) What is embodied about cognition? *Language, Cognition and
582 Neuroscience* 30:420–429.

583 Mahon BZ, Caramazza A (2008) A critical look at the embodied cognition
584 hypothesis and a new proposal for grounding conceptual content. *Journal of
585 Physiology Paris* 102:59–70.

586 Marslen-Wilson WD (1987) Functional parallelism in spoken word-recognition.
587 *Cognition* 25:71–102.

588 New B, Pallier C, Brysbaert M, Ferrand L (2004) Lexique 2: A new French
589 lexical database. *Behavior Research Methods, Instruments, and Computers* 36:516–
590 524.

591 Oldfield RC (1971) The assessment and analysis of handedness: The
592 Edinburgh inventory. *Neuropsychologia* 9:97–113.

593 Papeo L, Lingnau A, Agosta S, Pascual-Leone A, Battelli L, Caramazza A
594 (2015) The origin of word-related motor activity. *Cerebral Cortex* 25:1668–1675.

595 Papeo L, Pascual-Leone A, Caramazza A (2013) Disrupting the brain to
596 validate hypotheses on the neurobiology of language. *Frontiers in Human*
597 *Neuroscience* 7.

598 Papeo L, Rumiati RI, Cecchetto C, Tomasino B (2012) On-line changing of
599 thinking about words: The effect of cognitive context on neural responses to verb
600 reading. *Journal of Cognitive Neuroscience* 24:2348–2362.

601 Papeo L, Vallesi A, Isaja A, Rumiati RI (2009) Effects of TMS on different
602 stages of motor and non-motor verb processing in the primary motor cortex. *PLoS*
603 *one* 4:e4508.

604 Parker R, Hasbrouck JE, Tindal G (1992) The Maze as a Classroom-Based
605 Reading Measure: Construction Methods, Reliability, and Validity. *The Journal of*
606 *Special Education* 26:195–218.

607 Patterson K, Nestor PJ, Rogers TT (2007) Where do you know what you know?
608 The representation of semantic knowledge in the human brain. *Nature Reviews*
609 *Neuroscience* 8:976–987.

610 Perani D, Cappa SF, Schnur T, Tettamanti M, Collina S, Rosa MM, Fazio F
611 (1999) The neural correlates of verb and noun processing a PET study. *Brain*
612 122:2337–2344.

613 Pobric G, Jefferies E, Lambon Ralph MA (2010) Amodal semantic
614 representations depend on both anterior temporal lobes: Evidence from repetitive
615 transcranial magnetic stimulation. *Neuropsychologia* 48:1336–1342.

616 Pulvermüller F, Härle M, Hummel F (2001) Walking or talking?: Behavioral and
617 neurophysiological correlates of action verb processing. *Brain and Language*
618 78:143–168.

619 Pulvermüller F, Hauk O, Nikulin V V., Ilmoniemi RJ (2005) Functional links
620 between motor and language systems. *European Journal of Neuroscience* 21:793–
621 797.

622 Rabahi T, Fargier P, Rifai Sarraj A, Clouzeau C, Massarelli R (2013) Effect of
623 Action Verbs on the Performance of a Complex Movement. *PLoS ONE* 8:e68687.

624 Rabahi T, Sarraj AR, Fargier P, Clouzeau C, Massarelli R (2012) Action verb
625 and motor performance. *Kinesitherapie* 12:42–46.

626 Raposo A, Moss HE, Stamatakis EA, Tyler LK (2009) Modulation of motor and
627 premotor cortices by actions, action words and action sentences. *Neuropsychologia*
628 47:388–396.

629 Reilly M, Howerton O, Desai RH (2019) Time-course of motor involvement in
630 literal and metaphoric action sentence processing: A TMS study. *Frontiers in*
631 *Psychology* 10.

632 Repetto C, Colombo B, Cipresso P, Riva G (2013) The effects of rTMS over the
633 primary motor cortex: The link between action and language. *Neuropsychologia*
634 51:8–13.

635 Rogers TT, Hocking J, Noppeney U, Mechelli A, Gorno-Tempini ML, Patterson
636 K, Price CJ (2006) Anterior temporal cortex and semantic memory: Reconciling
637 findings from neuropsychology and functional imaging. *Cognitive, Affective and*
638 *Behavioral Neuroscience* 6:201–213.

639 Rom DM (1990) A sequentially rejective test procedure based on a modified
640 bonferroni inequality. *Biometrika* 77:663–665.

641 Rüschemeyer SA, Brass M, Friederici AD (2007) Comprehending prehending:
642 Neural correlates of processing verbs with motor stems. *Journal of Cognitive*
643 *Neuroscience* 19:855–865.

644 Sakreida K, Scorolli C, Menz MM, Heim S, Borghi AM, Binkofski F (2013) Are
645 abstract action words embodied? An fMRI investigation at the interface between
646 language and motor cognition. *Frontiers in human neuroscience* 7:125.

647 Scorolli C, Jacquet PO, Binkofski F, Nicoletti R, Tessari A, Borghi AM (2012)
648 Abstract and concrete phrases processing differentially modulates cortico-spinal
649 excitability. *Brain Research* 1488:60–71.

650 Sereno SC, Rayner K, Posner MI (1998) Establishing a time-line of word
651 recognition: Evidence from eye movements and event-related potentials.
652 *NeuroReport* 9:2195–2200.

653 Taylor LJ, Zwaan RA (2008) Motor resonance and linguistic focus. *Quarterly*
654 *Journal of Experimental Psychology* 61:896–904.

655 Tomasino B, Rumiati RI (2013) At the Mercy of Strategies: The Role of Motor
656 Representations in Language Understanding. *Frontiers in Psychology* 4.

657 Tulving E (1985) Memory and consciousness. *Canadian*
658 *Psychology/Psychologie canadienne* 26:1–12.

659 Van Berkum JJA, Hagoort P, Brown CM (1999) Semantic integration in
660 sentences and discourse: Evidence from the N400. *Journal of Cognitive*
661 *Neuroscience* 11:657–671.

662 Van Dam WO, Brazil IA, Bekkering H, Rueschemeyer SA (2014) Flexibility in
663 embodied language processing: Context effects in lexical access. *Topics in Cognitive*
664 *Science* 6:407–424.

665 Van Dam WO, Desai RH (2017) Embodied Simulations Are Modulated by
666 Sentential Perspective. *Cognitive science* 41:1613–1628.

667 Van Dam WO, Rueschemeyer SA, Bekkering H (2010) How specifically are
668 action verbs represented in the neural motor system: An fMRI study. *NeuroImage*
669 53:1318–1325.

670 van Dam WO, Rueschemeyer SA, Lindemann O, Bekkering H (2010) Context
671 effects in embodied lexical-semantic processing. *Frontiers in Psychology* 1.

672 Van Dam WO, Van Dijk M, Bekkering H, Rueschemeyer SA (2012) Flexibility in
673 embodied lexical-semantic representations. *Human Brain Mapping* 33:2322–2333.

674 van Dam WO, van Dongen E V., Bekkering H, Rueschemeyer SA (2012)
675 Context-dependent changes in functional connectivity of auditory cortices during the
676 perception of object words. *Journal of Cognitive Neuroscience* 24:2108–2119.

677 Vukovic N, Feurra M, Shpektor A, Myachykov A, Shtyrov Y (2017) Primary
678 motor cortex functionally contributes to language comprehension: An online rTMS
679 study. *Neuropsychologia* 96:222–229.

680 Willems RM, Labruna L, D’Esposito M, Ivry R, Casasanto D (2011) A Functional
681 Role for The Motor System in Language Understanding: Evidence from Theta-Burst
682 Transcranial Magnetic Stimulation. *Psychological Science* 22:849–854.

683 Wurm MF, Caramazza A (2019) Distinct roles of temporal and frontoparietal
684 cortex in representing actions across vision and language. *Nature Communications*
685 10.

686 Xu X, Kang C, Guo T (2016) Imageability and semantic association in the
687 representation and processing of event verbs. *Cognitive Processing* 17:175–184.

688 Zwaan RA, Taylor LJ (2006) Seeing, acting, understanding: Motor resonance in
689 language comprehension. *Journal of Experimental Psychology: General* 135:1–11.

690 Zwaan RA, Taylor LJ, de Boer M (2010) Motor resonance as a function of
691 narrative time: Further tests of the linguistic focus hypothesis. *Brain and Language*
692 112:143–149.

693 Zwaan RA, van der Stoep N, Guadalupe T, Bouwmeester S (2012) Language
694 comprehension in the balance: the robustness of the action-compatibility effect
695 (ACE). *PLoS one* 7:e31204.

696