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

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

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4

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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](http://lsa.colorado.edu); Landauer et al., 1998) was  
176 used to assure that manual action verbs ( $0.294 \pm 0.257$ ) and non-manual verbs  
177 ( $0.295 \pm 0.269$ ) 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:  $11.34 \pm 16.69$   
183 and  $30.80 \pm 53.70$  for manual action verbs and non-manual verbs, respectively), but  
184 not for number of characters ( $p=0.604$ ; Mean ratios:  $6.37 \pm 1.63$  and  $6.51 \pm 1.57$  for  
185 manual action verbs and non-manual verbs, respectively) nor spelling neighbors  
186 ( $p=0.136$ ; Mean ratios:  $5.95 \pm 5.03$  and  $4.73 \pm 4.74$  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 ( $4.36 \pm 0.34$ ) and non-manual  
 195 ( $1.43 \pm 0.54$ ) 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

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## **Procedure**

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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.

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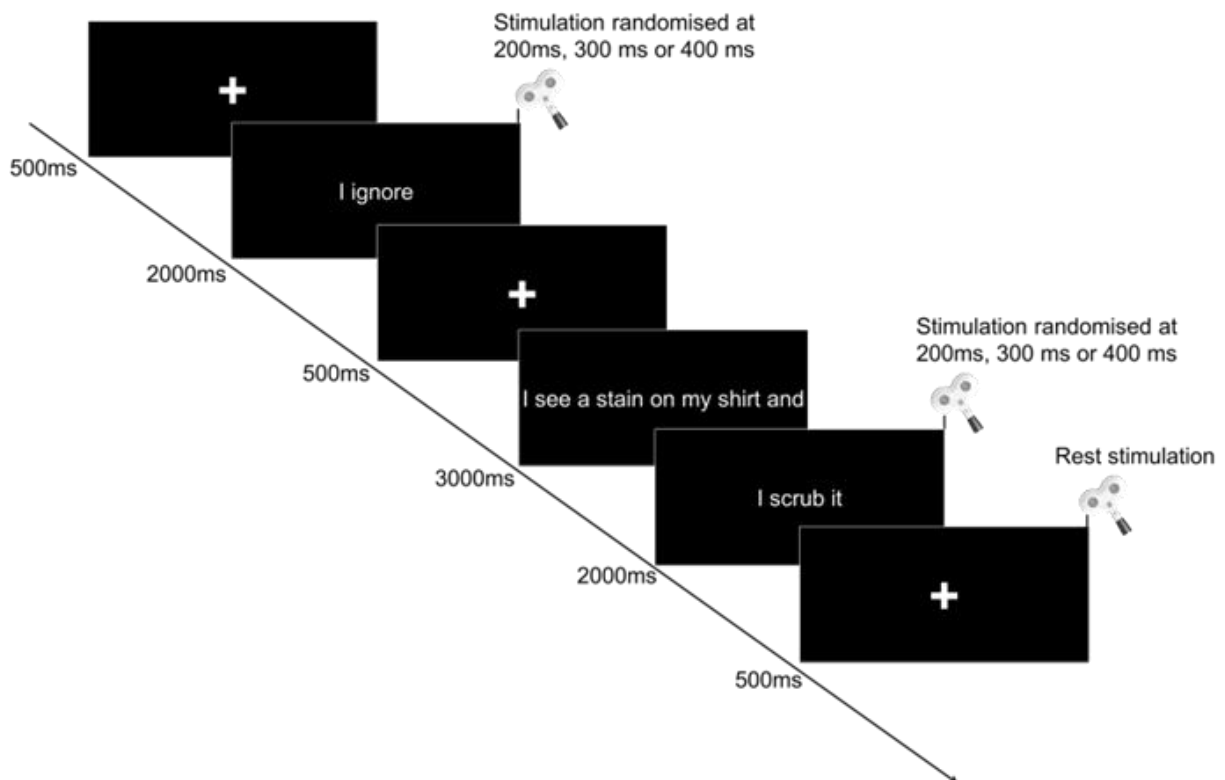
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Before the experimental trials, the participants performed four familiarization trials, each with a fixation cross, followed by a minimal sentence or a rich sentential context, then a black screen before the next trial. Once the participant understood 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 $\mu$ 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

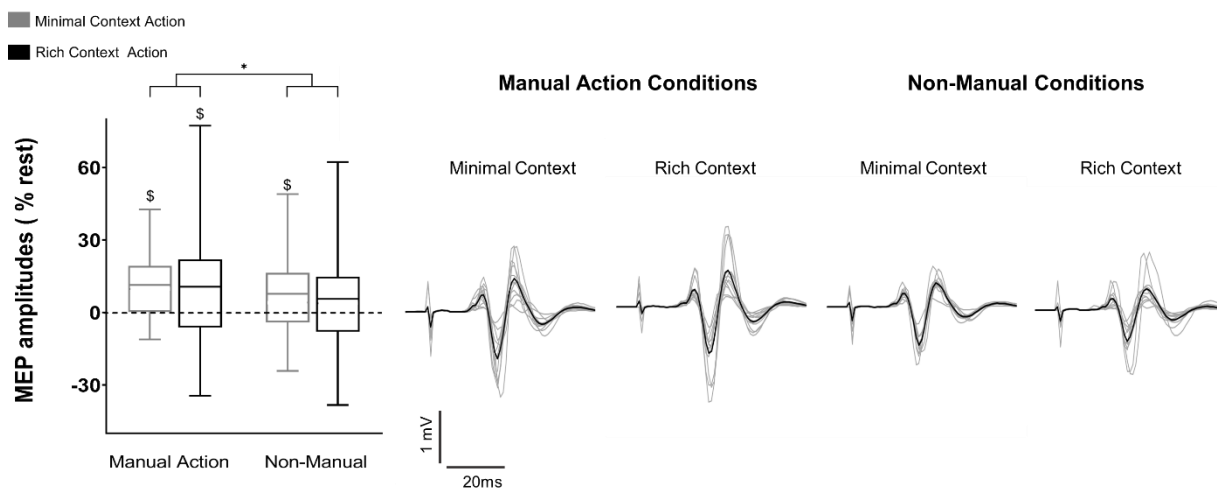


306 normalized MEPs at zero for each condition to assess whether corticospinal  
307 excitability during reading changed from baseline. Finally, in order to ensure that our  
308 results were not contaminated by muscular pre-activity, we tested with Wilcoxon tests  
309 if the EMGrms before the TMS artifact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



322

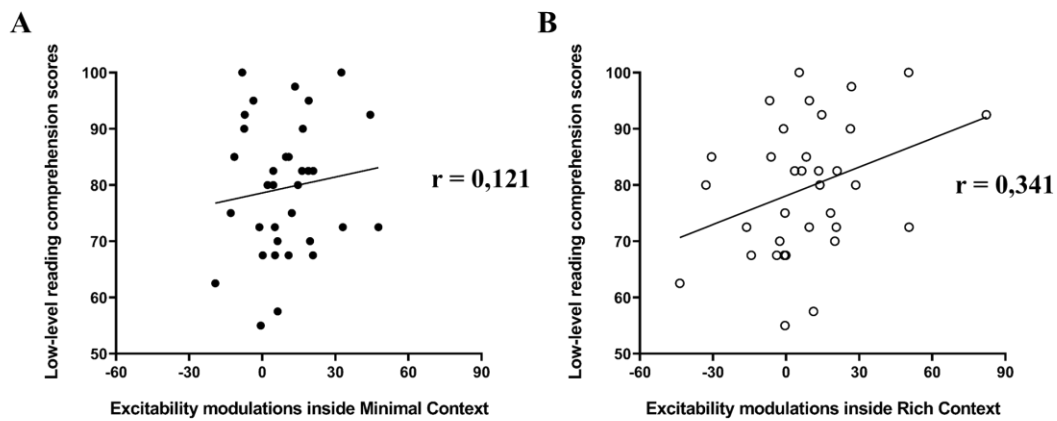
323 *Figure 2. Corticospinal excitability in Rich and Minimal Context. Box plots on the left side represent normalized*  
324 *MEPs. The line represents the mean. The box and the whiskers represent the 25th/75th quartile and the 5th and 95th*

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).*

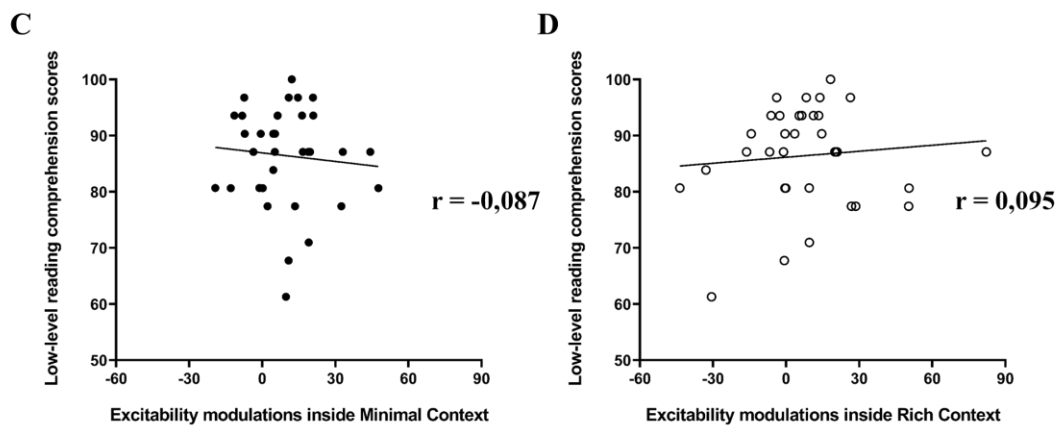
328       Using one-sample t-tests, we found that normalized MEPs of all conditions were  
329 different from baseline (all  $p$ 's $<0.05$ ), except for non-manual verbs in the rich context  
330 ( $p=0.167$ ). This finding reveals the possible importance of context for reducing  
331 residual activation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



## Higher context-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](https://osf.io/5zmq/?view_only=82c93af470fd42be8ca33969b14f1c37)

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