



## Research report

## A facilitating role for the primary motor cortex in action sentence processing

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## ABSTRACT

The involvement of the motor system in action language comprehension is a hotly debated topic in cognitive neuroscience and psychology. Recent studies suggest that primary motor cortex (M1) response to action language is context-sensitive rather than automatic and necessary. Specifically, semantic polarity (*i.e.* affirmative/negative valence) appears to modulate the intensity of this response, which is stronger for affirmative action sentences. The aim of our study was to examine further the context sensitivity of M1 response. More specifically, we aimed to determine whether M1 response follows semantic polarity or the core meaning of the sentence using two-part action sentences containing interacting polarities. Modulations of M1 activity were recorded using surface electromyography of the first dorsal interosseous muscle of the right hand in 22 healthy participants. Our results show an increase in M1 activity during the first part of the sentence, regardless of semantic polarity. This response was then modulated by the polarity of the second part of the sentence, which carried crucial information regarding the action. These observations suggest that M1 differentially responds to different aspects of action sentences, one response being automatic and the other following the core meaning of the sentence. Our results thus contribute to clarifying the nature of the motor response to action language, which is key to develop more comprehensive and plausible neurobiological models of language processing.

## 1. Introduction

In the last two decades, the existence of a response of the motor system during action language processing has repeatedly been shown by a large number of groups using various cognitive neuroscience methods (*e.g.* [1–7]). However, the precise role of the motor system in action language processing remains a hotly debated topic (*e.g.* [8–10]). The theoretical issue is to determine whether action language processing is embodied, that is, if the motor system takes part in this semantic process or not. For the upholders of a strictly embodied cognition, “specific action representations are activated during action word understanding” [11], a mechanism that is viewed as automatic and necessary to action language comprehension [12,13]. A different view proposes that the motor system does not contain conceptual knowledge of action [14], and that motor activation is due to a spreading from semantic processing areas [5].

Zwaan [10] has proposed that this question will be solved by investigating the conditions under which the motor system is involved in language comprehension. Attentional, lexical, emotional and linguistic contexts have been shown to have an influence on motor response [1,15–17]. Specifically, semantic polarity (*i.e.*, affirmative/negative valence) is a linguistic factor that modulates the amplitude of the motor

response during action language processing. For instance, paired-pulse transcranial magnetic stimulation (TMS) applied over M1 during passive reading of action and control sentences induced a modulation of motor evoked potentials for affirmative action sentences only [18]. Furthermore, by measuring variations in finger pressure, Aravena and colleagues showed that listening to action verbs induces a motor response when they are embedded in affirmative sentences (*e.g.* “Fiona lifts her luggage”), but not in negative sentences (*e.g.* “Fiona *does not* lift her luggage”) [1], thereby confirming that semantic polarity can modulate motor responses during action verb processing. Further characterization of the flexibility of the motor response to action language as a function of polarity will lead to a better understanding of the role of the motor system in action language processing.

The aim of this study was to investigate the time-course of M1 response during the processing of two-part action sentences containing interacting polarities in two different experiments. In study 1, we developed and validated the experimental material that was used in study 2. In study 2, using time-locked electromyography (EMG), we recorded hand motor activity, a proxy for M1 activity, during passive listening of two-part action sentences, composed of a prepositional phrase and a main clause, each containing an action word. Polarity was modulated in the prepositional phrase (Positive, Neutral and Negative) and in the

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main clause (Affirmative, Negative). This experimental design allowed us to investigate whether M1 response strictly mirrors polarity throughout the sentence processing, or whether it follows the main polarity of the sentence, conveyed by the main clause. If the polarity of each sentence part modulates the motor cortex response, it would suggest that M1 responds automatically to the polarity context of action language, regardless of the core meaning of the sentence. If, however, the motor response is solely modulated by the main-clause polarity, it would be evidence that this response follows the core meaning of action sentences.

## 2. Study 1

This preliminary study aimed to validate the sentences used in the main experiment (study 2), by determining whether they were semantically understandable and plausible.

### 2.1. Participants

Healthy native speakers of Canadian French were recruited through emails sent to Université Laval students and employees, employees of CERVO, as well as posters distributed in the community. All participants were right-handed [19], had normal or corrected-to-normal vision and no self-reported history of speech, voice, language or neurological disorder. Participants were screened for cognitive functioning (score  $\geq 26/30$ ) using the Montreal Cognitive Assessment (MoCA) [20]. Normal hearing ( $< 25$  dB of hearing loss) was assessed *via* pure-tone audiometry (PTA) at 0.5, 1 and 2 kHz using an AC40 Interacoustics clinical audiometer in a soundproof room. Informed written consent was obtained for each participant. The study was approved by the Committee on Research Ethics of CERVO (project #2013-349). Two participants were excluded from the semantic judgment task analyses because their performance differed from the group performance by over  $\pm 3$  SD of the group mean. The final group consisted of eighteen (18) participants (mean age 26.82 years  $\pm$  6.93; range 20–40 years; 11 women).

### 2.2. Stimuli

All stimuli were produced by a 24-year-old female Canadian French speaker in a double-walled soundproof room. Stimuli were 240 auditory two-part manual action sentences containing a noun in the prepositional phrase and a manual action verb in the main clause (e.g. “Avec ses ciseaux, Sarah découpe le journal”/“With her scissors, Sarah cuts the newspaper”). Ten different action word pairs were created that consisted of matching tool nouns and manual action verbs (e.g. “scissors” and “cuts”) that were conjointly used in 160 sentences. Ten action-neutral nouns (e.g. “kitchen”) were used in the remaining 80 sentences and were randomly matched to the main clause manual action verb. All nouns were two-syllable long. Half of the manual action verbs were one-syllable words while the other half were two-syllable long. The spoken frequency of occurrence of nouns and verbs was controlled using the French database Lexique [21]. The frequency of occurrence of tool nouns and manual action verbs did not significantly differ ( $t_{(9)} = -3.48, p = 0.74, d = 0.18$ ), neither did the tool and neutral-action nouns ( $t_{(9)} = -2.029, p = 0.07, d = 0.91$ ), or the neutral-action nouns and manual action verbs ( $t_{(9)} = -2.053, p = 0.07, d = 0.93$ ). Semantic polarity was manipulated (Fig. 1a). Specifically, prepositional phrases were either positive (e.g. “Avec ses ciseaux”/“With her scissors”), neutral (e.g. “Dans la cuisine”/“In the kitchen”) or negative (e.g. “Sans ses ciseaux”/“Without her scissors”), while main clauses were either affirmative (e.g. “..., Sarah découpe le journal”/“..., Sarah cuts the newspaper”) or negative (e.g. “..., Sarah ne découpe pas le journal”/“..., Sarah does not cut the newspaper”). In this validation study, each participant was presented with 180 of the 240 sentences. The stimuli were pseudo-randomized across participants.

### 2.3. Procedure

Participants were comfortably seated in a Faraday, double-walled soundproof room, facing a computer screen. They were instructed to answer as rapidly as possible by pressing one of two buttons on a Cedrus response pad RB-830 (Cedrus Corporation, San Pedro, USA) with their index and middle fingers of the right hand. Participants were asked to make two judgments on the sentences in separate runs: a semantic judgment and a plausibility judgment. In the semantic judgment task, participants were asked to determine whether an action was carried out or not in each sentence. In the plausibility task, they were asked to indicate whether they were surprised by the outcome of the sentence. Stimuli were presented auditorily through a high-quality headset (Beyerdynamic, DT 770 Pro, Heilbronn, Germany) at an individually adjusted intensity.

### 2.4. Data analysis

For each task, a 2-way repeated-measure analysis of variance ( $3 \times 2$  ANOVA) with prepositional-phrase polarity (positive, neutral, negative) and main-clause polarity (affirmative, negative) as within-subject factors was performed on the percentage of correct responses using SPSS (IBM) for Macintosh (version 23).

### 2.5. Results

In the semantic judgment task, the percentage of correct responses (mean 98.36%; SD 3.37) showed no significant effect of prepositional-phrase polarity ( $F_{(2,30)} = 0.23, p = 0.80, \eta_p^2 = 0.02$ ), or main-clause polarity ( $F_{(1,15)} = 0.38, p = 0.55, \eta_p^2 = 0.03$ ), nor any significant interaction effect ( $F_{(2,30)} = 1.21, p = 0.31, \eta_p^2 = 0.08$ ). In the plausibility task, percentage of correct responses (mean 58.01%; SD 31.48) showed no significant effect of prepositional-phrase polarity ( $F_{(2,34)} = 0.86, p = 0.43, \eta_p^2 = 0.05$ ), or main-clause polarity ( $F_{(1,17)} = 0.18, p = 0.68, \eta_p^2 = 0.01$ ), nor any significant interaction effect ( $F_{(2,34)} = 1.19, p = 0.32, \eta_p^2 = 0.07$ ).

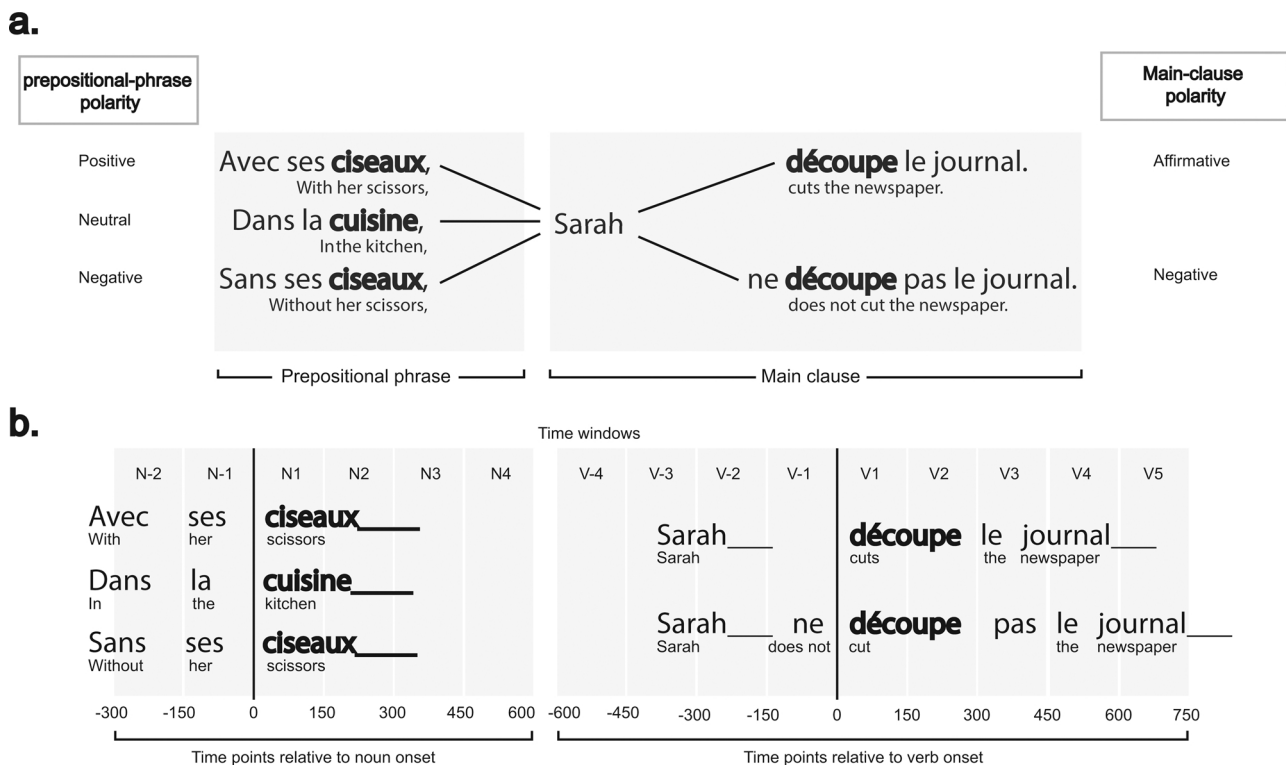
### 2.6. Discussion

Study 1 demonstrated that the sentences are well understood. Although results from the plausibility task showed that sentences were moderately surprising, the semantic judgment task revealed that sentences were very well understood. Importantly, semantic and plausibility judgments did not vary across conditions, revealing that clause polarity does not influence the comprehension of the sentences. Thus, these analyses validate the use of these sentences in the main experiment (study 2).

## 3. Study 2

### 3.1. Participants

Participants were 26 native speakers of Canadian French, recruited through emails sent to Université Laval employees and students, employees of the Institut universitaire en santé mentale de Québec, and flyers distributed in the community. Inclusion and exclusion criteria, as well as the preliminary auditory and cognitive assessments were identical to those of study 1. Two participants were excluded due to technical difficulties, one for a lack of task compliance and one during statistical analyses (see Section 3.5.2). The final group consisted of 22 participants (mean age 35.27, SD = 9.19; range 21–50 years of age; 11 women). Informed written consent was obtained. The study was approved by the Committee on Research Ethics of CERVO (project #2013-349).



**Fig. 1.** Stimuli. A. Sentence structure. Each sentence part contained a target word (in bold) and varied in terms of polarity: from positive, to neutral and negative in the prepositional phrase, and from affirmative to negative in the main clause. B. Time-windows. The EMG signal was analyzed in time-windows of 150 ms, created from the onset of the noun in the prepositional phrase and of the action verb in the main clause. Because two time-points were used to create the time-windows, a small time-window (less than 100 ms) between N4 and V-4 could not be included in the analysis.

### 3.2. Procedure

Participants were seated in a Faraday, double-walled soundproof room, facing a computer screen. The task consisted in passive listening of 240 sentences (Supplementary material S1) described in section 2.2. Stimuli were pseudo-randomized for each participant and presented auditorily through a high-quality headset (Beyerdynamic, DT 770 Pro, Heilbronn, Germany) at an individually adjusted intensity. A visual distractor task was presented to drive participants' focus away from the auditory sentences. It consisted in a blue triangle shown on a black screen that flashed in ~17% of trials. Participants were instructed to move the left foot at each triangle flash in a rapid heel-lifting movement. The task lasted for approximately 20 min.

### 3.3. EMG data acquisition

Throughout the task, physiological data were acquired using a multi-channel surface EMG system (MP150, Biopac Systems Inc, Goleta, CA, USA), measuring the electrical potential reaching muscles in the right hand and left leg. Small bipolar surface electrodes (4 mm Ag-AgCl isolated electrodes) were taped on participants' skin. Pairs of electrodes were placed (1) approximately 1 cm apart on the first dorsal interosseous (FDI) muscle of the right hand to monitor hand motor responses, and (2) on the medial head of the gastrocnemius muscle of the left leg to monitor participants' focus on the distractor task. The ground electrode was placed on the right elbow. Trials containing leg movements were excluded from statistical analyses. EMG signal was amplified online ( $\times 5000$ ) and acquired with a sampling rate of 1000 Hz with a 500 Hz low-pass anti-aliasing filter. Participants held a small 100 mg weight between the first thumb phalanx and second index phalanx in a relaxed arm position (Supplementary materials S2), thus generating a light and constant contraction of the right FDI.

### 3.4. Data analysis

#### 3.4.1. EMG signal pre-processing

EMG signal was exported from Acqknowledge, version 4.3 (Biopac Systems Inc, Goleta, CA, USA) and pre-processed using Matlab, version 2014b (Mathworks Inc, Natick, MA, USA) on an iMac computer running OS 10.9. The signal was filtered using a 10 Hz high-pass filter. A 55–65 Hz notch filter was used to remove electrical noise and a 9-point moving average was applied to smooth the signal. An artifact rejection process led to the discarding of 1.74% of all trials (ranging from 0% to 8.33% per participant). Trials were discarded if (1) EMG signal presented an absence of signal for a duration of 5 ms or more, (2) slow waves were detected (3) a leg movement occurred, and (4) a hand contraction was detected, which was defined as a 50 ms burst of an amplitude at least twice larger than the preceding 50 ms. Next, the signal was rectified using a root mean square function, and baseline corrected by converting EMG signal in the epochs of interest into a percentage of change ( $((a - b)/b) * 100$ ), where  $a$  is the EMG sample value in mV, and  $b$  the mean baseline value in mV. Mean baseline values were extracted from the period of 150 ms preceding the stimuli.

#### 3.4.2. Statistical analyses

The normality of data in each experimental condition was graphically assessed for each participant and at the group level. At the subject-level, trials with signal amplitude of  $\pm 2$  SD from the mean of the condition were discarded; 0.20% of trials was excluded. At the group level, one outlier (*i.e.*, a participant with a mean amplitude of  $\pm 3$  SD from the group mean in at least one condition) was discarded.

The EMG signal recorded during each sentence was split into fifteen (15) 150 ms time-windows (Fig. 1b), with N1 starting at the onset of the noun, and V1 at the onset of the action verb. To test for a habituation effect, the first and third parts of the experiment were separated. A 4-way ( $2 \times 15 \times 2 \times 3$ ) repeated-measure ANOVA with Part (Part1,

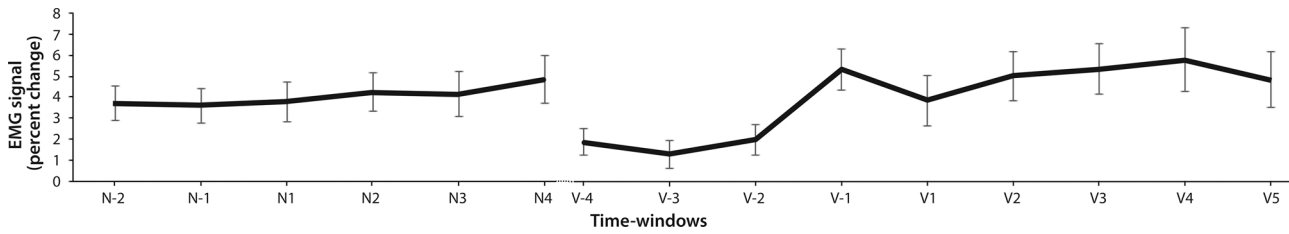


Fig. 2. Main effect of time. Group-level time-course of the EMG signal (in percentage of change from baseline).

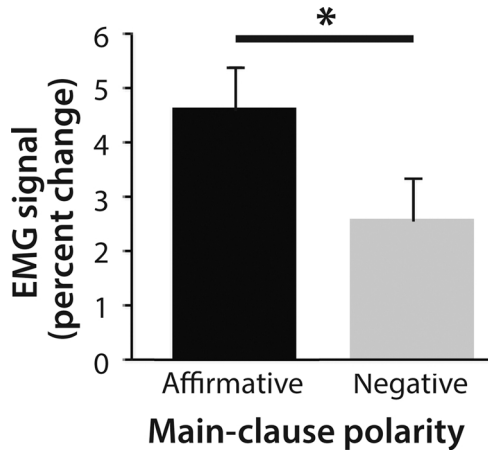


Fig. 3. Main effect of main-clause polarity. Group-level EMG signal as a function of main-clause polarity. Error bars represent the standard error of the mean percent change in EMG signal (SE). Asterisks indicate significance at  $p \leq 0.05$ .

Part3), Time (N-2, N-1, N1, N2, N3, N4, V-4, V-3, V-2, V-1, V1, V2, V3, V4, V5), Prepositional-phrase Polarity (Positive, Neutral, Negative) and Main-clause Polarity (Affirmative, Negative) as within-subject factors, was performed on the percent EMG signal change using SPSS 23 (IBM) for Macintosh. Post-hoc tests were conducted to decompose significant interactions. Measures of effect sizes are provided in the form of partial eta squared ( $\eta_p^2$ ) for F-tests, and Cohen *d* statistics when comparing two means.

3.5. Results

A significant main effect of Time was found ( $F_{(14,308)} = 4.71$ ,  $p = 0.00$ ,  $\eta_p^2 = 0.18$ ), indicating an increase of the EMG response during the V1 time-window (Fig. 2). A significant main effect of Main-clause Polarity was also found ( $F_{(1,22)} = 5.00$ ,  $p = 0.04$ ,  $\eta_p^2 = 0.19$ ), indicating that the EMG response was higher for affirmative than for negative main-clause sentences (Fig. 3). Finally, results revealed a significant interaction between Time and Main-clause Polarity ( $F_{(14,308)} = 1.89$ ,  $p = 0.03$ ,  $\eta_p^2 = 0.08$ ), which showed a difference in the time-course of the EMG response for affirmative and negative main-clause sentences, starting during V3 (Fig. 4). There was no effect of Part ( $F_{(1,22)} = 0.99$ ,  $p = 0.33$ ,  $\eta_p^2 = 0.04$ ), indicating that either there was no habituation effect or that it occurred too rapidly after the beginning of the task to have an impact on the EMG signal. Complete ANOVA

Table 1  
Statistical results for the ANOVA. Inferential statistics for all effects and interactions revealed by the  $3 \times 2$  ANOVA.

Tested effect/interaction	ddl	ddl (error)	F	p	$\eta_p^2$
Part	1	22	0.997	0.329	0.043
Time	14	308	4.714	0.000	0.176
Prepositional phrase polarity	2	44	0.084	0.919	0.004
Main-clause polarity	1	22	5.002	0.036	0.185
Part $\times$ Time	14	308	0.342	0.988	0.015
Part $\times$ prepositional-phrase polarity	2	44	0.415	0.663	0.019
Time $\times$ Prepositional-phrase polarity	28	616	0.973	0.506	0.042
Part $\times$ Time $\times$ Prepositional-phrase polarity	28	616	1.059	0.384	0.046
Part $\times$ Main-clause polarity	1	22	0.152	0.701	0.007
Time $\times$ Main-clause polarity	14	308	1.888	0.027	0.079
Part $\times$ Time $\times$ Main-clause polarity	14	308	0.988	0.465	0.043
Prepositional-phrase polarity $\times$ Main-clause polarity	2	44	0.535	0.589	0.024
Part $\times$ Prepositional-phrase polarity $\times$ Main-clause polarity	2	44	0.301	0.742	0.013
Time $\times$ Prepositional-phrase polarity $\times$ Main-clause polarity	28	616	0.699	0.876	0.031
Part $\times$ Time $\times$ Prepositional-phrase polarity $\times$ Main-clause polarity	28	616	0.488	0.988	0.022

results are reported in Table 1. Post-hoc results are provided in Table 2 for the Time effect and in Supplementary materials S3 for the Time  $\times$  Main-clause Polarity interaction.

4. Discussion

The main objective of our study was to characterize the time-course of M1 response to passive presentation of two-part action sentences with interacting polarities. Specifically, we asked whether M1 response varied online as a function of the polarity of each sentence part (*i.e.* prepositional phrase and main clause), or whether it followed the main polarity of the sentence, conveyed by the main clause. Our main findings are that (1) the EMG recorded an automatic response of M1 during the prepositional phrase regardless of its semantic content and (2) this EMG response was then modulated by the polarity of the main clause regardless of the prepositional phrase polarity. Specifically, the EMG response was weaker for negative than for affirmative main clauses. These findings will be discussed in light of theories of embodied and disembodied cognition.

As above-mentioned, a response occurred during the prepositional phrase, regardless of its semantic polarity. This effect occurred early and was present in all the sentences. Anticipation is a well-known effect

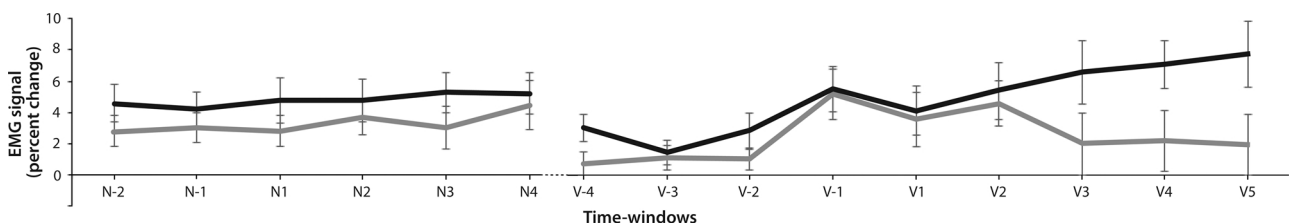


Fig. 4. Interaction between time and main-clause polarity. Modulation of the time-course of the EMG signal for affirmative (black line) and negative (grey line) main-clause sentences.

**Table 2**

Statistical results for the time effect. Rounded-up p-values of Student *t*-tests for the contrast of all pairs of time-window. Bold characters indicate p-values that were significant before false discovery rate (FDR) correction and the asterisk indicates p-values that remained significant after FDR correction.

	N-2	N-1	N1	N2	N3	N4	V-4	V-3	V-2	V-1	V1	V2	V3	V4	V5
N-2		0.89	0.90	0.46	0.58	0.18	0.07	<b>0.02</b>	<b>0.01</b>	0.14	0.90	0.28	0.25	0.19	0.46
N-1			0.74	0.40	0.50	0.16	<b>0.01</b>	<b>0.01</b>	0.06	0.07	0.82	0.15	0.14	0.13	0.43
N1				0.41	0.60	0.18	<b>0.04</b>	<b>0.01</b>	<b>0.03</b>	0.17	0.95	0.25	0.21	0.17	0.51
N2					0.90	0.55	<b>0.02</b>	<b>0.00*</b>	<b>0.00*</b>	0.35	0.75	0.48	0.38	0.27	0.68
N3						0.31	0.05	<b>0.01</b>	<b>0.02</b>	0.33	0.79	0.45	0.36	0.30	0.68
N4							<b>0.01</b>	<b>0.00*</b>	<b>0.00*</b>	0.68	0.39	0.88	0.70	0.55	0.99
V-4								0.43	0.93	<b>0.00*</b>	0.09	<b>0.00*</b>	<b>0.00</b>	<b>0.01</b>	0.08
V-3									0.40	<b>0.00*</b>	0.09	<b>0.00*</b>	<b>0.00</b>	<b>0.01</b>	<b>0.03</b>
V-2										<b>0.00*</b>	0.13	<b>0.01</b>	<b>0.02</b>	<b>0.02</b>	0.07
V-1											0.06	0.67	0.99	0.71	0.72
V1												0.16	0.10	0.13	0.50
V2													0.66	0.53	0.91
V3														0.59	0.76
V4															0.62
V5															

in linguistics (for a review, see Ref. [22]). It consists in the prediction of lexical-semantic and syntactic elements of a sentence based on previously processed linguistic information. Given that all the sentences contained an action verb in the main clause, it is likely that this initial automatic motor response resulted from an anticipation of action, even in neutral prepositional phrases, which could not be used to predict whether an action would be performed or not. Since there was no habituation effect (*i.e.* no difference in performance between the first and third parts of the task), this action anticipation must have occurred very rapidly after the beginning of the task. Anticipation, also called prediction [8,23], has been proposed to constitute a core aspect of embodiment [8] and to participate in action language comprehension [23]. Thus, within this specific language task, M1 automatically responded to auditory stimuli in prediction of upcoming action language, potentially to facilitate its processing.

This automatic M1 response was then modulated by main clause polarity regardless of prepositional phrase polarity. For affirmative sentences, the strong M1 response was maintained, while an EMG signal drop occurred in negative main clause sentences during V3. This is the time-window that contains the French negation marker “pas”, which confirms the absence of the execution of an action in the sentence. This suggests that M1 response decreased in relation to the processing of negation of action. This weaker motor response in relation to negative semantic context is consistent with previous findings [1,18] and adds to the growing evidence that semantic context can modulate the motor response to action language processing (e.g. [1,2,15,24–28]). Specifically, we show that M1 response was modulated by the core meaning of action sentences, which is carried by the semantic polarity surrounding the action verb.

A possible interpretation of this modulatory effect is that the syntactic-semantic processing of action verbs embedded in sentences occurred within M1. This explanation would imply that M1 contains the representations necessary for action language processing [8] and that it takes part in the syntactic processing of action language [29]. However, there is no evidence that M1 plays a role in the complex syntactic-semantic processing of whole sentences. An alternative interpretation is that the syntactic-semantic processing of action sentences occurred in an amodal semantic hub, such as the anterior temporal lobe [5,30]. This interpretation could be viewed as disembodied [31], since M1 response is considered subsequent to amodal semantic processing. But it can also be viewed as moderately embodied, within the framework of Zwaan’s [10] embodied cognition, defined as the result of interactions between amodal and modal systems of representations. In our view, the outcome of the syntactic-semantic processing of action language is communicated by a semantic hub to M1, which provides the listener with online motor feedback by activating or inhibiting adequate motor

representations. The modulation of M1 response can thus be considered a context-sensitive modal step in the semantic processing of action concepts. In other words, here we argue that the context-sensitive nature of M1 response during passive listening of action sentences is not evidence of the disembodiment of language, but, instead, evidence of a flexible embodied (context-sensitive) semantic system.

Overall, our results support the notion that M1 response to action language is both automatic and context-sensitive, and specify that this sensitivity is bound by the processing of the core meaning of the sentence. We interpret both responses of M1 as facilitatory mechanisms within the semantic processing of action language. In line with previous studies (e.g. [1,2,25,27,28]), our results show the relevance of considering context in the study of language embodiment. Context, which according to Zwaan [10], “has been a sleeping giant in the discussion on embodiment”, could be a methodological and theoretical key to understanding the mechanisms underlying motor involvement in language processing, and more generally, to build more comprehensive and plausible neurobiological models of language comprehension. Future research should focus on determining which other linguistic and cognitive factors modulate activity in the motor system and whether different components of this system are distinctly sensitive to these manipulations.

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#### References

- [1] P. Aravena, Y. Delevoeye-Turrell, V. Deprez, A. Cheylus, Y. Paulignan, V. Frak, T. Nazir, Grip force reveals the context sensitivity of language-induced motor activity during action words processing: evidence from sentential negation, *PLoS One* 7 (12) (2012) e50287, <http://dx.doi.org/10.1371/journal.pone.0050287>.
- [2] P. Aravena, M. Courson, V. Frak, A. Cheylus, Y. Paulignan, V. Deprez, T.A. Nazir, Action relevance in linguistic context drives word-induced motor activity, *Front. Hum. Neurosci.* 8 (April) (2014) 163, <http://dx.doi.org/10.3389/fnhum.2014>.

- 00163.
- [3] A.M. Glenberg, M.P. Kaschak, Grounding language in action, *Psychon. Bull. Rev.* 9 (3) (2002) 558–565.
- [4] O. Hauk, I. Johnsrude, F. Pulvermüller, Somatotopic representation of action words in human motor and premotor cortex, *Neuron* 41 (2) (2004) 301–307.
- [5] L. Papeo, A. Lingnau, S. Agosta, A. Pascual-Leone, L. Battelli, A. Caramazza, The origin of word-related motor activity, *Cereb. Cortex* 25 (6) (2014) 1668–1675, <http://dx.doi.org/10.1093/cercor/bht423>.
- [6] P. Tremblay, S.L. Small, From language comprehension to action understanding and back again, *Cereb. Cortex* 21 (5) (2011) 1166–1177, <http://dx.doi.org/10.1093/cercor/bhq189>.
- [7] M. van Elk, H.T. van Schie, R.A. Zwaan, H. Bekkering, The functional role of motor activation in language processing: motor cortical oscillations support lexical-semantic retrieval, *Neuroimage* 50 (2) (2010) 665–677, <http://dx.doi.org/10.1016/j.neuroimage.2009.12.123>.
- [8] A.M. Glenberg, Few believe the world is flat: how embodiment is changing the scientific understanding of cognition, *Can. J. Exp. Psychol./Revue Canadienne de Psychologie Expérimentale* 69 (2) (2015) 165–171, <http://dx.doi.org/10.1037/cep0000056>.
- [9] B.Z. Mahon, The burden of embodied cognition, *Can. J. Exp. Psychol./Revue Canadienne de Psychologie Expérimentale* 69 (2) (2015) 172–178, <http://dx.doi.org/10.1037/cep0000060>.
- [10] R.A. Zwaan, Embodiment and language comprehension: reframing the discussion, *Trends Cognit. Sci.* 18 (5) (2014) 229–234, <http://dx.doi.org/10.1016/j.tics.2014.02.008>.
- [11] F. Pulvermüller, Brain mechanisms linking language and action, *Nature* 6 (2005) 576–582.
- [12] T.H. Bak, J.R. Hodges, The effects of motor neurone disease on language: further evidence, *Brain Lang.* 89 (2) (2004) 354–361, [http://dx.doi.org/10.1016/S0093-934X\(03\)00357-2](http://dx.doi.org/10.1016/S0093-934X(03)00357-2).
- [13] V. Boulenger, L. Mechtouff, S. Thobois, E. Broussolle, M. Jeannerod, T.A. Nazir, Word processing in Parkinson's disease is impaired for action verbs but not for concrete nouns, *Neuropsychologia* 46 (2) (2008) 743–756, <http://dx.doi.org/10.1016/j.neuropsychologia.2007.10.007>.
- [14] B.Z. Mahon, What is embodied about cognition? *Lang. Cognit. Neurosci.* 30 (4) (2015) 420–429, <http://dx.doi.org/10.1080/23273798.2014.987791>.
- [15] C.L. Moody, S.P. Gennari, Effects of implied physical effort in sensory-motor and pre-frontal cortex during language comprehension, *Neuroimage* 49 (1) (2010) 782–793, <http://dx.doi.org/10.1016/j.neuroimage.2009.07.065>.
- [16] D. Samur, V.T. Lai, P. Hagoort, R.M. Willems, Emotional context modulates embodied metaphor comprehension, *Neuropsychologia* 78 (2015) 108–114, <http://dx.doi.org/10.1016/j.neuropsychologia.2015.10.003>.
- [17] W.O. van Dam, I.A. Brazil, H. Bekkering, S.-A. Rueschemeyer, Flexibility in embodied language processing: context effects in lexical access, *Top. Cognit. Sci.* 6 (3) (2014) 407–424, <http://dx.doi.org/10.1111/tops.12100>.
- [18] M.T. Liuzza, M. Candidi, S.M. Aglioti, Do not resonate with actions: sentence polarity modulates cortico-spinal excitability during action-related sentence reading, *PLoS One* 6 (2) (2011) 38–41, <http://dx.doi.org/10.1371/journal.pone.0016855>.
- [19] R.C. Oldfield, The assessment and analysis of handedness: the Edinburgh inventory, *Neuropsychologia* 9 (1) (1971) 97–113, [http://dx.doi.org/10.1016/0028-3932\(71\)90067-4](http://dx.doi.org/10.1016/0028-3932(71)90067-4).
- [20] Z.S. Nasreddine, N.A. Phillips, V. Bédirian, S. Charbonneau, V. Whitehead, I. Collin, H. Chertkow, The montreal cognitive assessment, MoCA: a brief screening tool for mild cognitive impairment, *J. Am. Geriatric Soc.* 53 (2005) 695–699.
- [21] B. New, C. Pallier, L. Ferrand, R. Matos, Une base de données lexicales du français contemporain sur internet: LEXIQUE™/A lexical database for contemporary french: LEXIQUE™, *L'année Psychol.* 101 (3) (2001) 447–462, <http://dx.doi.org/10.3406/psy.2001.1341>.
- [22] K.A. DeLong, M. Troyer, M. Kutas, Pre-processing in sentence comprehension: sensitivity to likely upcoming meaning and structure, *Lang Ling Compass* 12 (2014) 631–645.
- [23] A.M. Glenberg, V. Gallese, Action-based language: a theory of language acquisition, comprehension, and production, *Cortex* 48 (7) (2012) 905–922, <http://dx.doi.org/10.1016/j.cortex.2011.04.010>.
- [24] J. Davey, S.A. Rueschemeyer, A. Costigan, N. Murphy, K. Krieger-Redwood, G. Hallam, E. Jefferies, Shared neural processes support semantic control and action understanding, *Brain Lang.* 142 (2015) 24–35, <http://dx.doi.org/10.1016/j.bandl.2015.01.002>.
- [25] R.H. Desai, L.L. Conant, J.R. Binder, H. Park, M.S. Seidenberg, A piece of the action: modulation of sensory-motor regions by action idioms and metaphors, *Neuroimage* 83 (2013) 862–869, <http://dx.doi.org/10.1016/j.neuroimage.2013.07.044>.
- [26] A. Raposo, H.E. Moss, E.A. Stamatakis, L.K. Tyler, Modulation of motor and pre-motor cortices by actions, action words and action sentences, *Neuropsychologia* 47 (2) (2009) 388–396, <http://dx.doi.org/10.1016/j.neuropsychologia.2008.09.017>.
- [27] L.J. Taylor, R.A. Zwaan, Motor resonance and linguistic focus, *Q. J. Exp. Psychol.* 61 (6) (2008) 896–904, <http://dx.doi.org/10.1080/17470210701625519>.
- [28] W.O. van Dam, M. van Dijk, H. Bekkering, S.-A. Rueschemeyer, Flexibility in embodied lexical-semantic representations, *Hum. Brain Mapp.* 33 (10) (2012) 2322–2333, <http://dx.doi.org/10.1002/hbm.21365>.
- [29] G. de Zubicaray, J. Arciuli, K. McMahan, Putting an end to the motor cortex representations of action words, *J. Cognit. Neurosci.* 25 (11) (2013) 1957–1974, <http://dx.doi.org/10.1162/jocn>.
- [30] K. Patterson, P.J. Nestor, T.T. Rogers, Where do you know what you know? The representation of semantic knowledge in the human brain, *Nat. Rev. Neurosci.* 8 (12) (2007) 976–987, <http://dx.doi.org/10.1038/nrn2277>.
- [31] B.Z. Mahon, A. Caramazza, A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content, *J. Physiol.* 102 (2008) 59–70, <http://dx.doi.org/10.1016/j.jphysparis.2008.03.004>.