Research Report

The neural inhibition network is causally involved in the disembodiment effect of linguistic negation

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ARTICLE INFO

ABSTRACT

Negation applied to action contexts reduces the activation of the motor system. According to the Reusing Inhibition for Negation (RIN) hypothesis, such "disembodiment" effect occurs because understanding negations engages the reuse of inhibitory control mechanisms. Here, we investigated whether the right inferior frontal gyrus (rIFG) – a key area of the inhibitory control system – contributes to primary motor cortex (M1) processing of negated action-sentences. Using a perturb-and-measure paradigm, we applied off-line low-frequency repetitive TMS (rTMS) over the rIFG, before performing a reading task involving action and attentional sentences presented in both affirmative or negative form. During the reading task, motor excitability was assessed by recording motor-evoked potentials (MEPs) induced by single-pulse TMS (spTMS) over the left M1, at two loci in the sentence: the verb or the object. Results show that after sham stimulation (baseline), motor excitability measured on the verb, was reduced for negative, compared to affirmative action sentences. Crucially, neuromodulation of rIFG suppressed this inhibitory effect of negation, since motor excitability was equaled for negative and affirmative action sentences. As expected, no effect of negation was observed for attentional sentences or when the pulse was delivered over the object. Our study confirms that understanding negative action sentences inhibits M1. This effect took place at an early stage of semantic processing (i.e., while processing the verb in our task), and faded at a later time-point. Critically, by highlighting a causal role of rIFG in this motor inhibition, we provide direct neurophysiological support to the RIN hypothesis.

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1.   Introduction

Embodied cognition theories of meaning postulate that the comprehension of action-related language involves the same sensory-motor circuit activated during the execution of the action being described (Barsalou et al., 2008; Fischer & Zwaan, 2008; Gallese & Lakoff, 2005; García & Ibáñez, 2016; Glenberg et al., 2008; Jirak et al., 2010; Pulvermüller, 2005). Numerous neuroimaging (Aziz-Zadeh et al., 2006; de Vega et al., 2014; Raposo et al., 2009; Tettamanti et al., 2005), EEG (Moreno et al., 2013, 2015; van Elk et al., 2010) and brain stimulation studies (Buccino et al., 2005; Oliveri et al., 2004; Papeo et al., 2009; Vitale et al., 2021) have shown that action-related words or sentences activate sensory-motor brain regions to simulate the referred action. However, negation seems to block the conceptual representation of the language meaning (De Vega et al., 2016; Dudschig & Kaup, 2018, 2020; Kaup, 2001; Kaup et al., 2007; Kaup & Zwaan, 2003), leading to a "disembodiment" effect, which is reflected by the reduction of the motor system activation.

Neuroimaging studies, supporting the disembodiment effect of negation, first reported that processing negative action-language reduced the activation of motor and premotor circuits compared to affirmative action-language (Tettamanti et al., 2008; Tomasino et al., 2010). The negation effect on motor system was confirmed by subsequent behavioral studies with dual task paradigms like sentence-action interference (Aravena et al., 2012; Bartoli et al., 2013) and word typing paradigms (García-Marco et al., 2019), reporting less involvement of motor cortex activation for negative action sentences than for their affirmative counterpart. Moreover, physiological measures obtained with non-invasive brain stimulations techniques revealed that negation selectively modulated motor cortex excitability for the sentences with manual content, but no for the sentences with an abstract content (Liuzza et al., 2011; Papeo et al., 2016). Additionally, Papeo et al. (2016), by means of chronometric TMS, reported the difference in motor excitability between affirmative and negative sentences occurs as soon as 250 ms after the verb onset, corroborating the disembodied idea whereby the access to the simulation of a negated meaning is detained. Similarly, processing of the negative marker induced an early inhibitory effect on motor excitability for languages, such as German and Italian, that differ in the grammatical word order, reflecting the rapid impact of negative marker on sensory motor representations (Papitto et al., 2021).

Which is the neural mechanism underlying the processing of negation and leading to the reported reduction of motor activity? Recently, the Reusing Inhibition for Negation (RIN) hypothesis has been proposed, which states that the comprehension of negation reuses the neural circuits of the inhibitory control mechanism (Beltrán et al., 2018; De Vega et al., 2016; Liu et al., 2020). Indirect evidence supporting the RIN hypothesis comes from studies with EEG measures recorded in dual task paradigms in which a Go/No Go task is inserted in a sentence comprehension tasks. The results showed reciprocal effects between inhibition (NoGo trials) and negation; that is, negated action sentences

reduced power of fronto-central theta oscillations, a robust index of neural inhibitory activity, in subsequent NoGo trials (De Vega et al., 2016), while pre-setting an inhibitory state in preceding NoGo trials affected the modulation of the subsequent waveform for negated action sentences compared to their affirmative counterparts (Liu et al., 2020). In the same way, Beltrán et al. (2018) reported that, the comprehension of negative manual-action sentences, combined with a Stop-Signal task leads to enhancement of the inhibition-related N1 component and increment of stop reaction time in comparison with their affirmative counterparts. Critically, the common estimated source of such effects was found in the right inferior frontal gyrus (rIFG), a core region of the inhibitory control mechanism (Zhang et al., 2017; see Aron et al., 2014; Chambers et al., 2009 for review). Compatibly, negation imbedded in a manual-action context delayed typing execution of manual action verbs, suggesting the effector-specificity influence of the inhibitory mechanism (García-Marco et al., 2019). Furthermore, in the Experiment 2 of Papeo et al. (2016), the cortical silent period, an index of GABAergic inhibitory neurons activity, increased for negative action-verbs processing relative to affirmative action-verbs.

As mentioned above, rIFG — particularly, the pars opercularis — seems to play a crucial role in response inhibition. It has been demonstrated that patients with damage of rIFG and "virtual lesion" induced in healthy participants through repetitive TMS (rTMS) presented slower stop reaction time compared to the control group (Aron et al., 2003; Chambers et al., 2006, 2007). Based on these results, Aron proposed that IFG is the key component of a brain network, mainly lateralized in the right hemisphere, which orchestrates the balance between excitation and inhibition, sending inhibitory signals to the motor cortices through fronto-striatal-thalamic circuit during tasks demanding response inhibition (Aron, 2011; Chambers et al., 2009). Then, it is appropriate to hypothesize that rIFG might be responsible for the motor cortex inhibition typically observed for negative action-related sentences, compared to their affirmative counterparts. However, although the aforementioned studies strongly support the RIN hypothesis, they only provide correlational evidence, failing to demonstrate the functional connection between the inhibitory system and the reduction of activation in the motor system during the process of negative action sentences.

One way to directly assessing whether the inhibitory control area is causally involved in the comprehension and motor mapping of negated action-language is through a perturb-and-measure stimulation protocol combining offline low-frequency rTMS and recording motor evoked potential (MEP) induced by single pulse TMS (spTMS) on M1 (Avenanti et al., 2007, 2013; Oldrati et al., 2021; Papeo et al., 2015). The rationale of this refined method is to transiently inhibit neural activity in a target area and test the remote effects of such perturbation on task-related modulations of M1 excitability, demonstrating in this way a causal link between the targeted area and the functional (e.g., language-related) modulation of M1. Here, we employed this method for the first time to provide evidence for the causal role of the inhibitory system in negation processing,

thereby providing unprecedented neurophysiological evidence supporting the RIN hypothesis. To this aim, we perturbed the activity of the rIFG, a key region of the response inhibition mechanism, to assess the consequent modulation of the M1 cortico-spinal excitability during comprehension of affirmative and negative action sentences. In a group of participants, we administered low-frequency rTMS over the rIFG to transiently inhibit this region, whereas in another groups of participants we administered off-line sham stimulation on vertex, as a control (baseline) condition. In both groups, following the stimulation session, we recorded electromyographic (EMG) activity of a target hand muscle in response to spTMS over M1 during a reading task in which participants were presented with affirmative and negative action and attentional sentences. Note that the attentional sentences provide a control condition, as they are not expected to modulate cortico-spinal excitability in any case or being affected by stimulation on rIFG. In normal physiological conditions (i.e., following sham rTMS) we expect to find a reduction of MEP amplitudes for negative action sentences compared to affirmative action sentences and to attentional sentences at the verb locus (Papeo et al., 2016). Crucially, we expect that active rTMS on rIFG would prevent the inhibitory effect of negative action sentences to emerge at the verb; that is, we expected no difference between sentence types following rIFG-rTMS, a result that would provide direct evidence of the critical role of rIFG in the M1 modulation associated with the comprehension of negated action sentences. If so, this would support a strong prediction of the RIN hypothesis.

Additionally, as an exploratory goal we were interested in verifying whether the inhibitory effect of negation (in the sham group) and the expected disruption of such effect (in the active rTMS group) were strictly linked to the (action) verb, or if they were prolonged to a later stage of sentence processing, namely, in the integration of final object noun. To this aim, we used relatively more complex sentences than in previous studies (i.e, *Ahora no agarrarás un cascanueces/Now you will not catch a nutcracker*), and delivered the spTMS either over the verb or over the noun. As mentioned above, we expect disembodiment induced by negation at an initial stage of meaning construction, that is, a selective effect of negation on motor excitability for action contents when the spTMS is applied at the verb locus. Moreover, this disembodiment effect of negation on action sentences could be purely local and short-lasting (i.e., constrained to the verb) or could be detected also at a later stage of semantic integration, i.e., at the end of sentence, when the spTMS pulse is delivered over the noun.

To summarize, this study aims to: 1) replicate the disembodiment effects reported by Papeo et al. (2016, Exp.1) during an early phase of semantic processing (when the pulse was delivered over the verb); 2) and more importantly, assess for the first time if the inhibitory system (rIFG) is causally involved in the processing of negative action sentences, acting on M1. Finally, a more secondary and exploratory objective, was to examine for the first time, whether the negation-induced effects observed on the verb were also extended to the object, at the final phase of the sentences. To this purpose, each subject was tested in two different moments, i.e., just after the presentation of the verb and the object.

2. Method

2.1. Participants

Sixty-four healthy participants took part in this study. We determined the sample size through a power analysis conducted using G*Power 3 software (Faul et al., 2007). We conducted an analysis with power $(1-\beta) = .95$, $\alpha = .05$ and a small/medium effect size (f = .19). The analysis yielded a required total sample of 62 participants. We thus decided to test 64 participants who were randomly assigned to two stimulation groups: 32 participants (8 men, mean age ± SD: 20.6 years ± 2.7) were assigned to the sham rTMS group and 32 participants (6 men, mean age ± SD: 23.5 years ± 4.0) were assigned to the active rTMS group. All participants were right-handed, had Spanish as their mother tongue, and did not report any neurological disease, visual problems, or drug intake. All students gave informed consent and received course credit for volunteering. The Research Ethics Committee of the University of La Laguna approved this study and the experiment was conducted according to the principles expressed in the Declaration of Helsinki. One participant belonging to the sham rTMS group was discarded from the analysis due to recording failure.

2.2. Linguistic material

Verbal stimuli were presented on a 23-inch screen located about 80 cm away from the participant. Two sets of 240 Spanish sentences were used. The lexical material was adapted from a previous study (Vitale et al., 2021), and included 30 manual action verbs, 30 attentional verbs, and 120 nouns referring to manipulable objects. Every sentence (displayed with character height of 36 pt. in Courier New font size) started with the temporal adverb "ahora" (now) followed by the polarity word, then the verb appeared followed by the article and finally by the noun. Each sentence was presented in an affirmative and a negative version (Table 1), resulting in a total of 60 affirmative action sentences, 60 negative action sentences, 60 affirmative attentional sentences and 60 negative attentional sentences for each set. Within each set, each verb appeared in two sentences combined with different objects, and the sentences in the two sets differed in the combination of nouns and verbs in such a way that if a given noun appeared with a manual verb in set 1 (e.g., *Ahora sí apretarás un tornillo*/now you will [yes] tighten a screw), it was associated with an attentional verb in set 2 (e.g., *Ahora sí distinguirás un tornillo*/now you will [yes] distinguish a screw) and vice versa. The material was previously validated using lexical values downloaded from the EsPal database and testing a group of 30 participants not taking part to the present study (see Vitale et al., 2021 for details), ensuring no differences in frequency, length and familiarity between the action and attentional verbs (See Table 2).

2.3. TMS and electromyography recordings

To assess language-related modulation of M1 excitability we administered spTMS over the left M1 using a Magstim 200

Table 1 — Example linguistic material.

Action sentences
Affirmative: *Ahora **sí** agarrarás una tenaza*/now you will [yes] grab a pliers
Negative: *Ahora **no** agarrarás una tenaza*/now you will not grab a pliers
Attentional sentences
Affirmative: *Ahora **sí** apreciarás un libro*/now you will [yes] appreciate a book
Negative: *Ahora **no** apreciarás un libro*/now you will not appreciate a book

Table 2 — Values of linguistic variable: frequency and length values were obtained from the EsPal database. To evaluate the familiarity of the verbs, a behavioural study of 30 participants were conducted where they had to evaluate on a 7-point Likert scale the familiarity of each verb. Mean values were calculated, and t-tests were conducted for every variable, ensuring no differences between the two type of verbs.

	Manual action verbs	Attentional verbs	t	p-level
Frequency	23.83 ± 54.91	56.84 ± 93.87	−1.66	.10
Length	6.67 ± 1.37	7.27 ± 1.87	−1.41	.16
Familiarity	6.24 ± .52	5.97 ± .76	1.55	.13

magnetic stimulator (Magstim, Whiteland, Dyfed, UK) connected to a figure-of-eight magnetic coil (70 mm outer diameter; peak magnetic field 2.2 T) and recorded TMS-induced MEPs from the contralateral right first dorsal interosseous (FDI) using a Biopac MP-35 (Biopac, U.S.A.) electromyography (EMG) system. Surface EMG was recorded from the right FDI with Ag—AgCl electrodes placed in a belly-tendon montage with the ground electrode on the right wrist. EMG signals were band-pass filtered (30—500 Hz), sampled at 5 kHz, digitized and stored on a computer for offline analysis. The TMS coil was held tangentially to the skull, with the handle pointing backward and laterally at 45° from the midline, resulting in a posterior—anterior direction of current flow in the brain. The optimal coil position on left M1 was defined as the point where stimulation consistently evoked the largest MEPs in the right FDI. During the experimental session, TMS intensity was set at 120% of the resting motor threshold (rMT), which was defined as the lowest intensity of output that evoked five small responses (~50 μV) in the relaxed FDI muscle in a series of 10 stimuli (Rossini et al., 2015). Mean motor thresholds (±standard deviation) were 37.3% ± 5.8 and 38.8% ± 4.4 of the maximum stimulator output in sham and active rTMS groups, respectively, and did not differ between groups (t_{31} = −1.51, p = .14).

2.4. *rTMS parameters and site localization*

To perturb rIFG we administered image-guided rTMS using a figure-of-eight coil (70 mm diameter) connected to a Magstim Rapid2 stimulator (Magstim, Whiteland, Dyfed, UK). During active stimulation, the coil was placed tangentially over the *pars opercularis* of the rIFG, with the handle in an upward vertical orientation. During sham rTMS, the coil was tilted at 90° over the vertex, in order to provide some scalp sensations and a similar "clicking" sound, without inducing a current in the brain. Before each spTMS session, 15 min of offline repetitive low-frequency (1 Hz) stimulation at an intensity of 90% of the rMT (see above) was administered. Stimulation site were localized using the BrainSight frameless stereotaxic system (Rogue Research, Canada) with a Polaris (NorthernDigital, Canada) infrared tracking system to measure the position of anatomical landmarks on each participant's head. Prior to the neuronavigation session, for each participant, high-resolution T1 weight anatomic images were acquired with a 3 T GE Sigma Excite MRI scanner at the Magnetic Resonance Service for Biomedical Research, at the University of La Laguna (TR = 8.844 ms, TI = 650 ms, TE = 1.752 ms, flipangle: 10°, voxel size: 1 mm × 1 mm × 1 mm, matrix: 256 × 256 mm, FOV: 256 mm², 196 slice, slice order: sequential, gap: 0) and prepared for the neuronavigator. Then, for each magnetic resonance image (MRI) scan, several anatomical landmarks were marked (tip of nose, left and right intratragus notches). Another infrared tracker was placed over the TMS coil to identify the scalp point where the target was selected in the MRI image and to mark the point on the cap. Each participant's MRI was compared to a normalized space so that TMS coordinates used were identified in a standard space. The rIFG target location was based on previous fMRI meta-analysis (Zhang et al., 2017) exploring the activation of inhibitory control on action withholding and action cancellation and rTMS studies (Chambers et al., 2007; Verbruggen et al., 2010) that provide consisting evidence of the crucial role of rIFG in cancelling a motor response. The stimulation site, set on the following MNI coordinates: x = 53, y = 16, z = 17, corresponded to the rIFG *pars opercularis*, and it was targeted in a locus anterior to the precentral sulcus, between the lateral sulcus and inferior frontal sulcus (Chambers et al., 2007; Verbruggen et al., 2010).

2.5. *Procedure*

The experiment consisted of two separated sessions. In session 1, the structural MRI images from each participant were acquired. In session 2, coil position for M1 and stimulation intensity was established by determining participants' M1 hotspot and rMT, and coil position for the target rTMS site (rIFG) was localized by means of individual anatomical images fed in the neuronavigation (see above). Afterwards, participants received 15-min of sham or active rTMS over the target site, immediately followed by the language comprehension task combined with the spTMS stimulation. The task consisted of 4 blocks of 30 trials taking ~15 min, thus falling within time window where rTMS effects can be observed (Avenanti et al., 2007, 2012; Chen et al., 1997; Münchau et al., 2002; Serino et al., 2011). After a 5-min rest period, a sec 15-min application of sham or active rTMS stimulation − identical to the one previously received − was administered (Goldsworthy et al., 2015; Nyffeler et al., 2006; Terranova et al., 2019). Then, the participants executed 4 additional blocks of 30 trials of the language task and spTMS. Two blocks of 20 MEPs-which served as baseline-were collected using spTMS, before and after the stimulation session. The structure of the sessions is shown in Fig. 1A.

The experiment was programmed using E-Prime software to control sentences presentation and to trigger TMS pulses. Each trial consisted of a sentence, with verbal material presented word by word which started with a 200-ms fixation cross, followed by the temporal adverbial appearing for 200 ms. After that, the polarity operator was presented for 200-ms and then the manual or attentional verb was shown for 300 ms. Successively, the article appeared for 200 ms followed by the noun showed for 300 ms. The words presentation was separated by an interval of 200 ms (see Fig. 1B). In half the trials, the spTMS pulse was delivered at 250 ms of verb onset, while the remaining trials the pulse was delivered at 250 ms of noun onset. Finally, a whole sentence was displayed on the screen that could be the same of the one presented previously one word a time, or differed in some segment of the sentence (e.g., the polarity operator, the verb or the object). Participants had to verbally respond "yes" when the sentence matched the previous one, and "no" when the sentences differed from each other. An experimenter collected the answers by pressing a computer key. In order to avoid changes in motor excitability due to verbal response (Meister et al., 2003; Tokimura et al., 1996), participants were instructed to answer 2—3 s after the final sentence was presented. Moreover, to avoid changes in motor excitability due to TMS per se, after the response a white screen appeared for 3—5 s thus ensuring an inter-pulse interval of about 10 s (Chen et al., 1997).

2.6.   Data analysis

Neurophysiological and behavioral data were processed offline. To corroborate that there was no difference in the accuracy between the groups, a four-way mixed factors ANOVAs with Group (sham rTMS and active rTMS) as between subjects' factor and Locus of stimulation (verb and object), Type of sentence (action and attentional) and Sentence polarity (affirmative and negative) was conducted on the percentage of corrected answers. One participant, from the active group, was eliminated from further analysis due to the high percentage of incorrect responses, which deviated from the mean by 2 SD.

MEPs were measured in mV and computed as the median peak-to-peak amplitude for each condition. MEPs associated with an incorrect answer, were excluded from the analysis (less than 5% in both group). Additionally, MEPs preceded by background EMG of 100 ms deviating from the mean by more than 2 SD were removed from the analysis (less than 5% in both groups), since it is known that EMG background can affect motor excitability (Devanne et al., 1997). To normalize the data distribution, a logarithmic transformation was applied to the MEP values [log (median MEP amplitude value $+$ 1)]. Normalized MEPs were analyzed by means of a four-way mixed factors ANOVA with Group (sham rTMS and active rTMS) as between subjects' factor, and Locus of
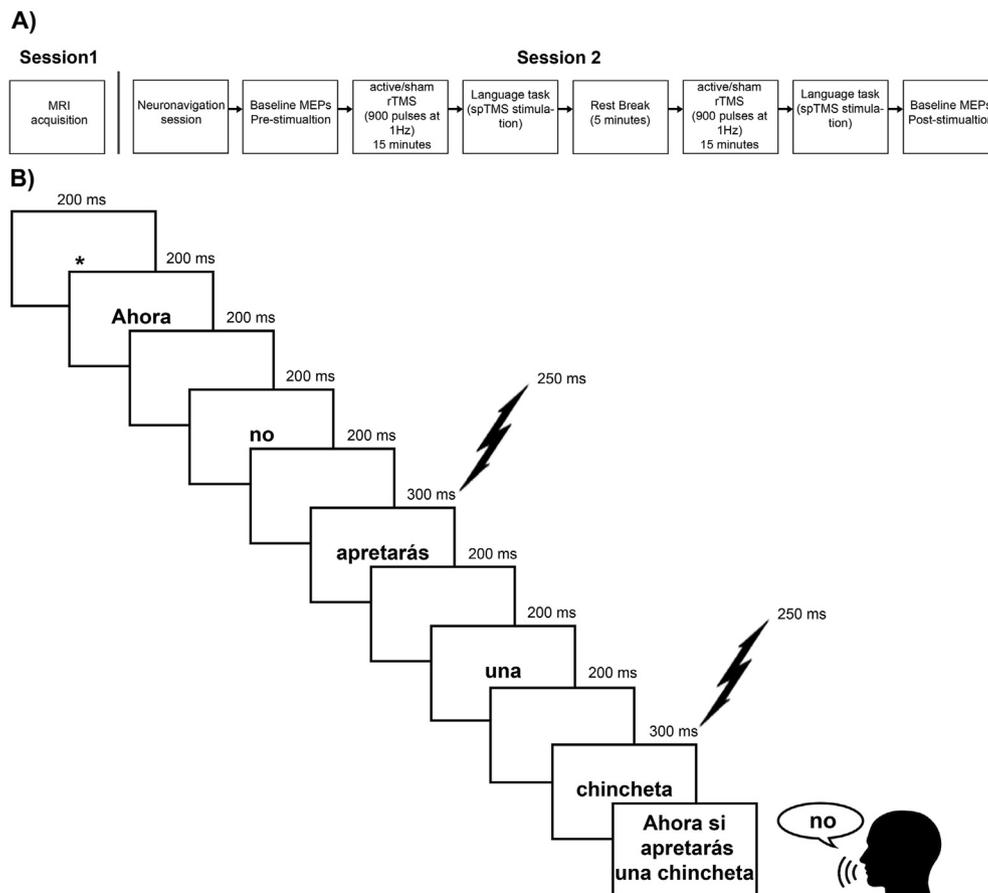

Fig. 1 — Structure of experimental procedure (A) Schematic representation of the experimental sessions. (B) Example of a trial sequence (translation: Now you will not press a thumbtack).

stimulation (verb and object), Type of sentence (action and attentional) and Sentence polarity (affirmative and negative) as within subject factor. Higher order interactions were analyzed by splitting the analysis into separate lower-order ANOVAs as appropriate (Keppel & Wickens, 2004). Post-hoc comparisons were performed using the Duncan's test. Partial eta^2 (η_p^2) was computed as a measure of effect size for the main effects and interactions, whereas repeated measures *Cohen's d* was computed for post-hoc comparisons (Cohen, 1992). To detect the presence of outliers, two Cluster single-linkage analyses, applying the standard Euclidian distance measure, were conducted separately in each Group (Wallmark et al., 2018). The Cluster analysis revealed the presence of four outliers (2 for the sham rTMS group and 2 for the active rTMS), which were removed from all the analysis.

3. Results

3.1. Behavioral performance

Task accuracy was high in both groups (percentage of mean correct answers ± S.D.: sham rTMS: 96% ± 3; active rTMS: 97% ± 2). The Group x Locus of stimulation x Type of sentences x Polarity ANOVA conducted on accuracy showed no main effect or interactions (all $F < 2.04$; $p > .16$), indicating similar accuracy on performance across the two groups and all the experimental conditions.

3.2. Neurophysiological measures

The ANOVA Group x Locus of stimulation x Type of sentences x Polarity conducted on normalized MEPs, showed (see Table S1) a significant Locus of stimulation x Type of sentences interaction ($F_{1,56} = 4.74$, $p = .03$, $\eta_p^2 = .08$), qualified by a non-significant trend for the Type of sentences × Polarity interaction ($F_{1,56} = 2.98$, $p = .09$, $\eta_p^2 = .05$). No main effect of Group ($F_{1,56} = .78$, $p = .38$, $\eta_p^2 = .01$), or 2- or 3-way interaction with this factor (all $F < 2.25$, all $p > .14$) was observed. Interestingly, however, a non-significant trend for the 4-way interaction ($F_{1,56} = 2.80$, $p = .099$, $\eta_p^2 = .05$) was observed (all other effects with $F < 2.35$, $p > .13$; see also Table S1). Because of the theoretical relevance of such non-significant trend, to better investigate the temporal dynamics of negation effect we performed separate Group x Type of sentences x Polarity analyses for the verb and for the object locus.

3.2.1. Changes in MEPs during presentation of verbs
The ANOVA performed on verb locus data (Table S2) showed a strong main effect of Type of sentences ($F_{1,56} = 7.14$, $p < .01$, $\eta_p^2 = .11$), accounted by the higher MEP amplitudes for the attentional sentences (mean MEP amplitudes ± SD: .354 ± .153) compared to action sentences (.345 ± .150). More importantly, the three-way Group x Type of sentences × Polarity interaction was also significant ($F_{1,56} = 4.54$, $p = .04$, $\eta_p^2 = .08$). To further explore such interaction, separate Type of sentences x Polarity ANOVAs were performed for the sham rTMS group and for the active rTMS group. The ANOVA on the sham group confirmed the main effect of Type of sentences ($F_{1,28} = 5.35$, $p = .03$, $\eta_p^2 = .16$), indicating a decrease in motor excitability for

manual action sentences (.360 ± .124) relative to attentional sentences (.372 ± .125). Remarkably, the interaction Type of sentences x Polarity was also significant ($F_{1,28} = 6.05$, $p = .02$, $\eta_p^2 = .18$), driven by a reduction in MEPs when processing negative action sentences. Indeed, post hoc analysis showed lower MEPs amplitude recorded while reading negative action sentences (.354 ± .121) compared to affirmative action sentences (.367 ± .129, $p = .046$, *Cohen's d = .11*), to affirmative attentional sentences (.36 ± .134, $p = .045$, *Cohen's d = .11*) and to negative attentional sentences, (.377 ± .119, $p < .01$, *Cohen's d = .19*), which in turn did not differ from one another (all $p > .16$; see Fig. 2A). On the contrary, the same ANOVA performed on the active group, did not revealed any significant effects of polarity or its interaction (all $F < 2.06$; all $p > .16$).

3.2.2. Changes in MEPs during presentation of nouns
Finally, the Group x Type of sentences x Polarity ANOVA conducted on the MEPs recorded during the object locus (Table S3) did not show any significant result (all $F < 1.93$; all $p > .17$) (Fig. 2B), indicating that the inhibitory negation effect was bounded to the verb, and did not extend to the next stage of the semantic process.

4. Discussion

Processing negative action sentences, compared to their affirmative counterparts, inhibits M1 activation as reflected by the reduction of motor excitability (Liuzza et al., 2011; Papeo et al., 2016). According to the RIN hypothesis, such "disembodiment" effect occurs because negation processing reuses the inhibitory mechanism of motor control (Beltrán et al., 2018; De Vega et al., 2016; Liu et al., 2020).

In the present study, we explored this issue by using a perturb-and-measure paradigm based on the combination of rTMS — to suppress neural activity over a key area of the motor inhibition network, i.e., the rIFG — and spTMS with EMG to assess the M1 excitability during language processing. Under sham rTMS we replicated the disembodiment effects of the negative marker, namely a reduction of motor excitability for action language. Most important, when low frequency rTMS was applied over rIFG to transiently disrupt its activity, we found that, in the verb locus, the disembodiment effect of the negative marker on action sentences was suppressed, since negated action verbs and affirmed action verbs did not differ in M1 excitability. This crucial result strongly suggests a causal role of the inhibitory system, represented by the rIFG, on the processing of negative action sentences in M1. No polarity effect was observed on motor excitability when the spTMS was administered at the noun locus, indicating that the disembodiment effects of negation did not extend to the end of sentence. Finally, as expected, the control attentional sentences did not show any modulation of M1 excitability under any experimental condition.

The decrease of MEPs amplitudes for negative action sentences in the sham group is in line with previous studies (Aravena et al., 2012; Bartoli et al., 2013; Beltrán et al., 2018; De Vega et al., 2016; García-Marco et al., 2019; Liu et al., 2020; Liuzza et al., 2011; Papeo et al., 2016; Tettamanti et al., 2008; Tomasino et al., 2010), reporting a reduction of motor brain
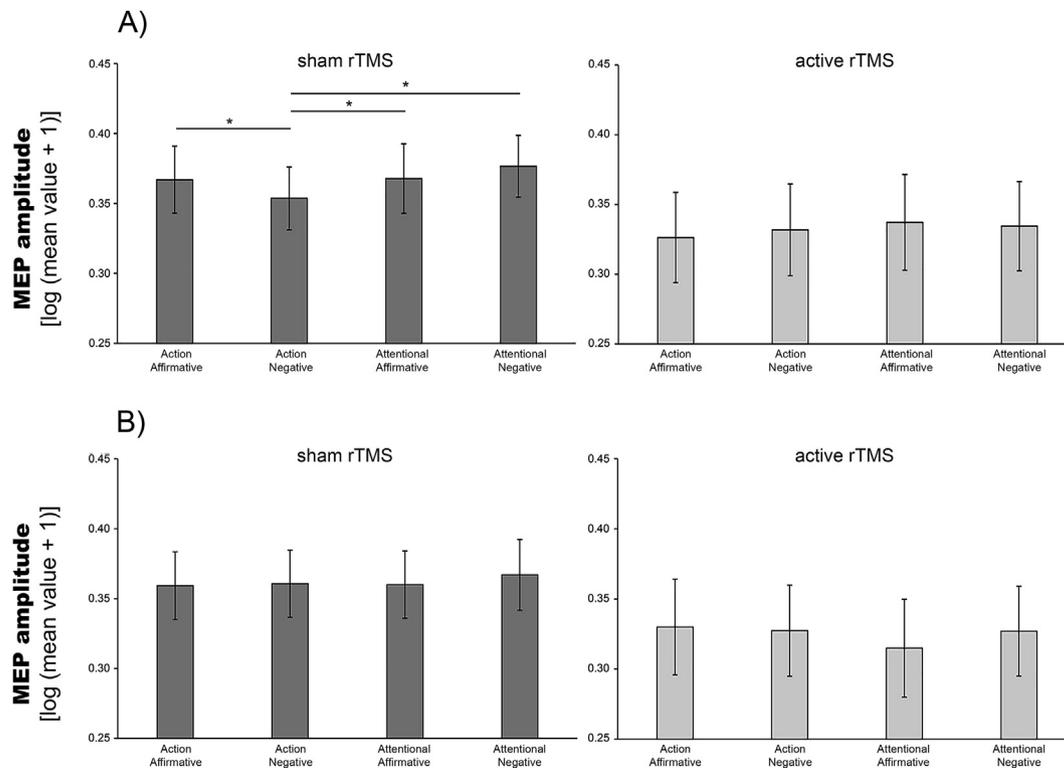
Fig. 2 – MEPs modulation as a function of type of sentence (action vs attentional) and polarity (affirmative vs negative) for the verb locus (A) and for the object locus (B). Error bars indicate standard error of the mean (SEM).

activity associated with negative action-related language. Particularly, we replicated the results of Papeo et al. (2016), showing that the polarity context (affirmative or negative), already modulates the motor cortex excitability at the time of verb presentation. Taken together, these findings confirm that the disembodiment effect of negation occurs at the initial stage of sentence integration processing (see Papeo et al., 2015); that is, once the negation is semantically integrated with the verb, it immediately interferes with the embodied representation, leading to the observed disembodiment.

Nonetheless, the major novelty of our study was to test how the intervention on the inhibition system affects the processing of negative action sentences. We found that the disturbance of the rIFG activity by means of active low-frequency rTMS resulted in the absence of significant effects of polarity or its interaction (all F < 2.06; all p > .16), which confirms that rIFG plays a crucial influence on the deactivation of the motor system during the processing of negative action sentences. In fact, according to our prediction, inhibiting of rIFG disrupts the reduction of motor excitability in negative action sentences as reflected by the null effects on MEPs. By showing that rTMS hindered the functional modulation of M1 excitability when processing negative action sentences, we provided the first neurophysiological evidence that the brain inhibition system is causally involved in the disembodiment effect of negation, thus supporting the RIN hypothesis. These findings go beyond the correlational evidence provided elsewhere by the results of behavioral studies (García-Marco et al., 2019), spTMS (Liuzza et al., 2011; Papeo

et al., 2016) and EEG studies (Beltrán et al., 2018; De Vega et al., 2016; Liu et al., 2020).

The inhibitory circuit is constituted by several brain regions – including the rIFG, dorsolateral prefrontal cortex, pre-supplementary motor area, anterior cingulate cortex and the striatum-subthalami nuclei. According to the model proposed by Aron (2011), the rIFG plays a major role in this network, implementing stopping signals to the motor system through the striatum-subthalamic nucleus pathways (Aron, 2011; Chambers et al., 2009), or, possibly, directly to M1 (Neubert et al., 2010). Our results suggest that this neural inhibition model can be extended to linguistic negation, consistently with the RIN hypothesis. That is, in brain normal states (in sham rTMS) the rIFG would be recruited by negative action statements to inhibit, through direct cortico-cortical or striatum pathways, the motor cortex, resulting in the disembodiment effects of negation obtained here and elsewhere (Aravena et al., 2012; Bartoli et al., 2013; De Vega et al., 2016; García-Marco et al., 2019; Liuzza et al., 2011; Papeo et al., 2016; Tettamanti et al., 2008; Tomasino et al., 2010). However, the disturbance of rIFG activity (in active rTMS) blocks the inhibitory signals at M1, and the motor excitability for negative action sentences becomes similar to that of affirmative sentences.

Another important result in our study is the reduction of MEP amplitudes associated with action verb compared to attentional verb, also consistent with the embodiment prediction, according to which processing action-language consumes motor resources (Barsalou et al., 2008; Buccino et al., 2016; Fischer & Zwaan, 2008; García & Ibáñez, 2016; Glenberg

et al., 2008; Jirak et al., 2010). Notably, such modulation was detected at an early phase of semantic processing, that is, at 250 ms after verb presentation. Consistently with our findings, Buccino et al. (2005) found that listening to hand-sentences decreased hand-M1 activity quite early (end of the second syllable of the verb). In contrast, the stimulation of motor system at a later stage of stimulus processing (500 ms) induced an increment of M1 activity (Oliveri et al., 2004; Papeo et al., 2009). Similar opposing time-dependent patterns of activation were also obtained in studies using dual-task paradigms (e.g., action-compatibility effect paradigm, ACE) that reported a meaning-action interference effect at early temporal window (Boulenger et al., 2006; Chersi et al., 2010; de Vega et al., 2013; Klepp et al., 2015) and a facilitatory effect during a later processing of action verb (de Vega et al., 2013; Kaschak & Borreggine, 2008).

The current study provides strong evidence of the critical role of the inhibition system in the processing of negative statements, although future studies will be needed to fill important knowledge gaps. First, the RIN hypothesis claims that the inhibitory network is a general mechanism underlying negation in different semantic domains, rather than being specific for action language (Beltrán et al., 2019). Yet, in this study we predicted and found a selective effect of polarity during the processing of action sentences under sham stimulation. We propose that the absence of such effects for attentional sentences, was due to the modality-specific activity of M1 – which is mainly involved in processing action language – and to our neurophysiological dependent measure used to detect such activity (MEPs). However, future studies using appropriate materials and designs are needed to investigate the functional role of the inhibitory mechanism of motor control during the processing of sentential negation in non-action domains. Moreover, while our study clarifies that rIFG contributes to the functional M1 modulation during language processing, it leaves open the question of rIFG functional relevance to behavior. Therefore, future causal studies combining rTMS with sensitive behavioral tasks would address whether rIFG is causally essential for language understanding as the RIN hypothesis would predict.

Moreover, although our study clearly indicates a causal influence of rIFG on M1 during the comprehension of negated action sentences, future studies are needed to further test the RIN hypothesis by focusing on the causal involvement of other key nodes of the neural network of inhibitory control such as the pre supplementary motor area (pre-SMA) (Borgomaneri et al., 2020; Zhang et al., 2017). To address neuroanatomical specificity of the findings, further studies will need to include active rTMS on control areas outside the inhibitory control network (e.g., the occipital cortex). In the latter case, a physiological effect similar to that observed for our sham group would be expected, and this would provide supplementary support to the hypothesis that inhibitory control mechanism is responsible for the reduction of motor activity for negated action-languages.

5. Conclusion

In conclusion, our study shed new light on the effect of negation on the motor system. In keeping with the disembodied view, we showed that negation, imbedded in an action context, blocked the simulation of the meaning representation expressed in the sentences (de Vega et al., 2013; Papeo et al., 2016). More relevant, we found that this "disembodiment" effect of negation is caused by the activation of the inhibitory system, supporting the RIN hypothesis.

Data availability statement

All experimental data, as well as the scripts used for their collection and analysis, are fully available online at https://osf.io/nr39j/.

CRediT author statement

Francesca Vitale: Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Funding acquisition. Ilaria Monti: Methodology, Investigation. Iván Padron: Methodology, Data curation. Alessio Avenanti: Methodology, Writing-Review & Editing, Funding acquisition. Manuel de Vega: Conceptualization, Validation, Resources, Methodology, Writing – original draft, Writing-Review & Editing, Supervision, Project administration, Funding acquisition.

Sample size and data exclusion statement

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

Declaration of competing interest

The authors declare no competing financial interests. No part of the study procedures or analyses was pre-registered prior to the research being conducted.

Open practice

The study in this article earned an Open Data and Open Materials badges for transparent practices. Data and Materials for this study can be found at: https://osf.io/nr39j/?view_only=0eb6de4ec2744d808b30c9a04cfae08b.

Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2021.11.015.

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