

Research Article

Exploring the impact of sentential negation on inhibitory motor networks: Insights from paired-pulse TMS

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ABSTRACT

The embodied approach to language meaning suggests that negation with action verbs decreases activation of the negated concept, reflected in reduced motor-evoked potentials (MEPs) induced by transcranial magnetic stimulation (TMS). This study aims to explore how action negation influences inhibitory and facilitatory mechanisms within the primary motor cortex (M1) using paired-pulse TMS (ppTMS). We evaluated corticospinal excitability (CSE), short intracortical inhibition (SICI), indexing GABAA activity, and intracortical facilitation (ICF), related to glutamatergic activity. Participants read action and attentional sentences, presented in affirmative and negative form, with TMS pulses administered over the left M1 at 250 ms from verb onset. Results show negated action sentences differently modulate CSE and SICI compared to affirmative ones, indicating GABAA activity of negation. No differences emerged for attentional sentences, nor for ICF stimulation. This study confirms the suppressive impact of action negation on CSE and highlights inhibitory networks' role in action negation processing within M1.

1. Introduction

Negation is a universal tool of language, which changes the truth value of a sentence and shifts the focus of discourse away from the negated concept, reducing its accessibility in working memory (Kaup, 2001; MacDonald & Just, 1989). Negation is acquired early in life (Austin et al., 2014; Wode, 1977), often associated with the suppression of ongoing actions as a sort of stop signal. For this reason, during the initial learning of negation the motor inhibitory system of the brain might play some role. In older children and adults, the pragmatics of negation goes beyond inducing motor stop, acquiring a variety of declarative and procedural uses (Givon, 1979; Horn, 1989) and becoming an abstract grammatical operator. However, recent theoretical approaches inspired by the principle of neural reuse (Anderson, 2010) postulate that understanding negative statements, such as "She did not write the letter", compared to their affirmative counterparts "She write the letter", may recruit the motor inhibition brain network (Beltrán et al., 2021; De Vega et al., 2016; García-Marco et al., 2019; Liu et al., 2020; Montalti et al., 2024). In this regard, behavioural and neuroimaging studies reported that negative action sentences (e.g.

"Don't grasp") reduce the involvement of the motor and premotor cortex in comparison with affirmative action sentences (e.g. "Do grasp") (Foroni & Semin, 2013; Tettamanti et al., 2008; Tomasino et al., 2010), and EEG studies revealed that sentential negation modulates fronto-central theta rhythms, which is a signature of motor inhibition (Beltrán et al., 2019; De Vega et al., 2016). Although these studies refer to the effect of negation in sentences with manual action verbs, there are also studies showing that inhibitory neural networks are recruited while processing a variety of negative sentences with non-action verbs (Beltrán et al., 2019) and even sentences with existential negation, which are purely declarative with no mention of agent or action (Liu et al., 2023).

As for non-invasive brain stimulation studies, transcranial magnetic stimulation (TMS)-induced measures of motor evoked potentials (MEPs) showed a reduction of corticospinal excitability (CSE) in negative action sentences compared to affirmative ones (Liuzza et al., 2011; Vitale et al., 2022), and processing sentences with a negative marker reduces MEP amplitudes independently of their different location in Italian and German grammatical constructions (Papitto et al., 2021). In addition, Papeo et al. (2016), demonstrated how negative action sentences,

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compared to their affirmative counterparts, increased the cortical silent period, which is a reliable indicator of gamma-aminobutyric acid type B (GABAB)-mediated inhibitory activity (Hallett, 2007; Paulus et al., 2008; Werhahn et al., 1999). Finally, low-frequency rTMS applied over the rIFG, a key node of the inhibitory circuit, entirely suppress the effects of negation on CSE, suggesting a causal link between the inhibitory control network and the comprehension of action-related negation (Vitale et al., 2022). Both, Papeo et al. (2016) and Vitale et al. (2022) studies clearly support the reusing inhibition for negation hypothesis (Beltrán et al., 2018; De Vega et al., 2016).

The preceding TMS studies focused on corticospinal activity as a dependent measure but did not delve into the underlying intracortical mechanism or neurotransmitter activity, except for one study analyzing the cortical silent period, which is associated with GABAergic activity (Papeo et al., 2016). In the present study, we aim to fill this gap by estimating inhibitory and facilitatory intracortical activity in the left M1 during a language comprehension task, requiring to process sentence with different polarities (affirmative vs. negative) and verb types (action vs. attentional). We specifically assessed short intracortical inhibition (SICI) and intracortical facilitation (ICF), representing inhibitory and excitatory neuron activity at the cortical level, respectively. To achieve this, we measured SICI and ICF through paired-pulse TMS (ppTMS), involving a conditioning stimulus (CS) with low-threshold intensity followed by a suprathreshold test stimulus (TS) delivered over M1 using the same coil. SICI manifested within interstimulus intervals (ISIs) of 1–5 msec (Kujirai et al., 1993), inducing inhibitory effects through the excitation of low-threshold inhibitory interneurons mediated by GABA receptors (Di Lazzaro et al., 1998, 1999; Ilić et al., 2002). On the other hand, ICF occurred at longer ISIs (7–20 ms) (Kujirai et al., 1993), reflecting the activation of facilitatory interneurons mediated by glutamatergic NMDA receptors (Ziemann et al., 1998). Both effects are attributed to cortical-level neural population activation, as evidenced by the lack of impact on the H-reflex, an index of motor neuron excitability at the spinal level (Kujirai et al., 1993; Ziemann, Lönnecker, et al., 1996). Our study utilized paired-pulse protocols to investigate whether inhibitory and facilitatory activity within M1 is modulated during the comprehension of action-negated sentences. First, we aimed to replicate the reduction of corticospinal excitability specific to the processing of negative action sentences observed in previous studies (Papeo et al., 2016; Vitale et al., 2022). Then, we anticipated a specific cortical modulation for the inhibitory mechanism (SICI) based on the inhibitory effect of action negation in M1 activity (Papeo et al., 2016; Vitale et al., 2022), while we had no stronger prior hypothesis regarding ICF.

2. Materials and methods

2.1. Participants

Twenty-two undergraduate students took part in the study (3 men, mean age \pm standard deviation (S.D.): 19.0 years \pm 1.9). Statistical power estimations were performed specifically for single-pulse (SP) and SICI, as these were the primary measures of interest in relation to our hypothesis, using the simulate function from the lmer4 package (Bates et al., 2015) in R (R Core Team, 2018). Different mixed-models were executed to analyze MEPs resulting from SP and SICI stimulation (see data analysis). Then, for each analysis, a simulation of 1000 new data sets, each containing n participants, was iterated by including the same structure used in the main analysis (Type of Verb and Polarity as fixed factors and participants as a random effect). The simulations were generated with the *simulate()* function from the lme4 package in R, which used the parameters estimated from the original mixed-effects structure. Specifically, the simulations relied on the fixed effects (Type of Verb, Polarity, and their interaction), the random intercept variance for participants, and the residual variance as estimated from the fitted model.

During each iteration, trials from these datasets were randomly

designated as missing and excluded. Separate estimations were conducted by steadily increasing differences for the two-way interactions while observing the power for each difference. The percentage of models in which the effect of the two-way interaction from which the data were generated was detected (i.e., for which $p < 0.05$), served as the estimate of statistical power. For both TMS protocols, for $n = 22$ simulated participants, we estimated a statistical power of 1 (i.e., in 1000 out of 1000 simulation runs, the model detected a significant two-way interaction).

All participants had Spanish as their native language, they were right-handed and none of them reported any contraindication to TMS or medical problems. The Research Ethics Committee of the University of La Laguna (CEIBA2023-3250) approved this study, and the experiment was conducted according to the principles expressed in the Declaration of Helsinki.

2.2. Material

The linguistic material was adapted from previous studies (Vitale et al., 2021, 2022), and consisted of two lists of 120 sentences. A total of 60 verbs (30 action and 30 attentional verbs) and 120 nouns of manipulable objects were used to construct the material. In each set, the verb was associated with one object, and the lists were constructed in such a way that if a given noun appeared with a manual verb in set 1 (e.g., Ahora si colgarás un bastón/now you will [yes] hang a cane), it was associated with an attentional verb in set 2 (e.g., Ahora si observarás un bastón/now you will [yes] observe a cane). The sentence structure comprised a temporal adverb (e.g., “Ahora”/“Now”), followed by the polarity adverb, the verb, the article, and ultimately the object. Within each list, the sentences were presented twice, once in an affirmative form and once in a negative form (see Table 1). The material was previously validated (see Vitale et al., 2021) assuring that the action and attentional verb were comparable in frequency (action verbs = 23.83 ± 54.91 , attentional verbs = 56.84 ± 93.87 , $p = 0.10$), number of characters (action verbs = 6.67 ± 1.37 , attentional verbs = 7.27 ± 1.87 , $p = 0.16$) and familiarity (action verbs = 6.24 ± 0.52 , attentional verbs = 5.97 ± 0.76 , $p = 0.13$).

2.3. TMS and MEPs recording

To explore language-related changes in motor excitability, MEPs induced by TMS applied to the left M1 were recorded from the right first dorsal interosseous (FDI) muscle, using a Biopac MP-35 (Biopac, U.S.A.) electromyography (EMG) system, band-pass filtered (30–500 Hz), sampled at 5 kHz, digitized and stored on a computer for offline analysis. Pairs of silver-chloride surface electrodes were placed in a belly-tendon montage with ground electrodes on the right wrist. A figure-of-eight coil connected to a Magstim Bistim² stimulator (Magstim, Whitland, Dyfed, U.K.) was placed over the target M1. 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. Using a slightly suprathreshold stimulus intensity, the coil was moved over the target hemisphere to determine the optimal position from which maximal MEP amplitudes were elicited in the contralateral FDI muscle. The resting motor threshold (rMT) was defined as the lowest

Table 1
Example linguistic material.

	Sentences (Spanish)	Translation
Affirmative action	Ahora si agarrarás un cascanueces	Now you will [yes] grab a nutcracker.
Negative action	Ahora no agarrarás un cascanueces	Now you will not grab a nutcracker.
Affirmative attentional	Ahora si perderás una gorra	Now you will [yes] lose a cap.
Negative attentional	Ahora no perderás una gorra	Now you will not lose a cap.

intensity of output that evoked five small responses (~ 50 mV) in the relaxed FDI muscle in a series of 10 stimuli (Rossini et al., 2015). MEPs were recorded in three different stimulation sessions: a single pulse (SP) session, and two paired-pulse session for assessing Short-interval intracortical inhibition (SICI) and Intracortical facilitation (ICF). In the SP session, the intensity was set to evoked MEP with a peak-to-peak amplitude of ~ 1 mV in the relaxed FDI. Following established protocols (Kujirai et al., 1993; Ziemann, Rothwell, et al., 1996), in paired-pulse session the intensity of the CS was set at 80 % of the rMT, while the intensity of the TS was the same used in the SP stimulation. The ISIs selected were 3 and 12 ms to investigate SICI and ICF, respectively (Borgomaneri et al., 2015, 2017; Kujirai et al., 1993; Ziemann, Rothwell, et al., 1996).

Throughout all the experiment, the absence of voluntary contraction was monitored.

2.4. Procedure and experimental design

The experiment was programmed using E-Prime software (Psychology Software Tools, Pittsburgh, PA), to control sentences presentation and trigger TMS. Participants underwent three experimental sessions (SP, SICI and ICF), with each session presented in blocks due to constraints in the TMS setup. The order of these TMS blocks was counter-balanced across participants to control for potential order effects. Each block consisted of 120 trials, characterized by 60 (30 affirmative and 30 negative) manual-action and 60 (30 affirmative and 30 negative) attentional sentences, with the sentence types fully randomized within each block. Every trial started with a fixation cross lasting 200 ms, and then the verbal material was presented word by word. First, the temporal adverb appeared for 200 ms, followed by the polarity operator showed for 200 ms and, successively, the verb was shown for 300 ms. After that, the article was presented for 200 ms, followed by the noun, lasting 300 ms. The interval between each word consisted of 200 ms (See Fig. 1). We adjusted word presentation times based on grammatical roles, with function words displayed briefly due to their predictability and faster reading times (Hochmann, 2013; Just & Carpenter, 1980; Schmauder et al., 2000). Extending their duration would have felt odd. Although varying word presentation durations (e.g., articles vs. verbs) could theoretically influence MEP modulation due to expectancy effects (Tran et al., 2021), we mitigated this by using a fixed TMS pulse interval. Specifically, in all the trials, the stimulation pulses (SP or TS in the paired-pulse sessions) were delivered at 250 ms of verb onset. This timing was selected as CSE changes for negative and affirmative sentences, occur as soon as 250 ms after the verb onset (Papeo et al., 2016; Vitale et al., 2022). Finally, a complete sentence was presented on the screen, which could either match the previously displayed sentence presented one word at a time or differ in certain segments (such as the polarity operator, verb, or object). Participants were required to verbally indicate “yes” when the sentence matched the previous one and “no”

when there were disparities. An experimenter recorded participants’ responses by pressing a computer key. To prevent potential alterations in motor excitability due to verbal responses, participants were instructed to delay their responses by 2 to 3 s after the final sentence presentation (Meister et al., 2003; Tokimura et al., 1996). Furthermore, to avoid changes in CSE due to TMS itself, a blank screen appeared for 3 to 5 s following the response, ensuring an inter-pulse interval of approximately 10 s (Chen et al., 1997).

To assess that TMS *per se* did not affect the CSE, before and after the experimental sessions, two additional blocks of 12 MEPs, which served as a baseline, were recorded using SP stimulation (Borgomaneri et al., 2015; Vitale et al., 2023). In these blocks, participants held their eyes closed with the instruction to imagine watching a sunset at the beach (Fourkas et al., 2008; Tidoni et al., 2013), while they received the stimulation with an inter-pulse interval of ~ 7 s. As expected, the comparisons between the pre- (mean MEP amplitude \pm S.D.: 1.00 ± 0.18) and post-baselines (1.01 ± 0.28) did not show any changes ($t_{21} = -0.12$, $p = 0.90$).

2.5. Data analysis

Neurophysiological data were recorded and subsequently analyzed offline. The mean of peak-to-peak amplitude, measured in mV, was calculated for each condition. We removed MEPs associated with incorrect responses ($\sim 5\%$). The accuracy was consistently high in all three stimulation sessions (SP mean accuracy \pm S.D.: $94\% \pm 5$; SICI: $92\% \pm 6$ and ICF: $95\% \pm 5$). Indeed, the ANOVA carried out on accuracy data, with “Type of Stimulation” (3 levels: SP, SICI and ICF) as a within-subjects factor, showed no significant result ($F_{2,63} = 1.79$; $p = 0.17$). Furthermore, MEPs with the EMG background deviations exceeding 2 S.D. from the mean were excluded from further analysis ($\sim 7\%$), as such deviations could potentially influence MEP size (Devanne et al., 1997).

In the first analysis, MEPs recorded during SP, SICI, and ICF sessions were expressed relative to the baseline (% of the average of the two baseline blocks) and analyzed through a linear mixed model (using *lmer* function, (Bates et al., 2015)), with Type of stimulation (SP, SICI, ICF), Type of Verb (action and attentional) and Polarity (affirmative and negative) as fixed factor, and participants were accounted for as a random factor in the model. Then, once finding a strong effect of the Type of stimulation, we specifically examined the negation-induced changes within each stimulation condition, separately. To quantify SICI and ICF effects and to rule out a potential contribution of CSE, we calculated the ratio of the mean of the conditioned MEP amplitude to the mean of the unconditioned MEP amplitude for each experimental condition (Borgomaneri et al., 2015, 2017; Matsumoto et al., 2021). The resulting MEPs, relative to the baseline for single-pulse TMS and ratio-expressed for paired-pulse measures, underwent separate analyses using three different mixed models. All models included the Type of Verb (action and attentional) and Polarity (affirmative and negative) as fixed

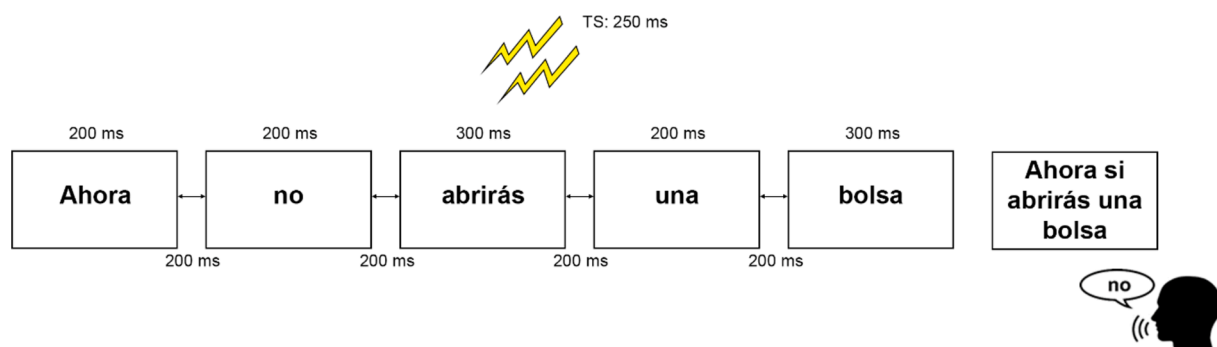


Fig. 1. Structure of experimental procedure. Example of a trial sequence (trial translation: “Now you will not open a bag”; verification sentence translation: “Now you will [yes] open a bag”).

factors, with participants treated as a random factor. We utilized sum coding to contrast-code all fixed effects, ensuring that the intercept of each model reflected the mean value of the respective predictor (Schad et al., 2020). To assess the specific modulation of negation action sentences compared to the affirmative ones in each stimulation session, planned comparisons were employed. Additionally, we implemented the false discovery rate (FDR) correction (Benjamini & Hochberg, 1995) to account for multiple comparisons.

In addition, to complement the frequentist findings and provide a more robust estimation of the effects, the linear mixed models were complemented by their Bayesian implementation using *stan_lmer* function (Goodrich et al., 2020; Muth et al., 2018). For all Bayesian models, we used 4 chains with 4000 iterations per chain. The prior distribution for intercept was set to normal (mean = 0, sd = 1), while the prior for the effect of interest (Type of Verb * Polarity) was set to normal (mean = 0, sd = 0.25) to reflect the medium-to-large effect size observed in our previous study (Vitale et al., 2022, $\eta_p^2 = 0.18$). Finally, the regularization on the covariance matrix of random effects was set to 1. Model convergence was assessed using diagnostics such as Rhat values (all Rhat ≤ 1.01 , (Vehtari et al., 2019)) and effective sample sizes, which indicated satisfactory convergence and good mixing of the chains. To compare model fit, Bayes factors were computed using bridge sampling (Gronau et al., 2020; Meng & Wong, 1996) to quantify evidence for the full models against corresponding null models. The full models included the interaction terms of interest, while the null models contained only the intercept when assessing the main effects, or they contained the main effects when assessing the interaction terms (Rouder et al., 2012). Bayes factors allowed us to evaluate the strength of evidence for the presence of the specified effects.

To quantify the uncertainty around parameter estimates, 95 % Highest Posterior Density (HPD) intervals were computed (Kruschke, 2014). These intervals represent the most credible range for the parameters, containing 95 % of the posterior distribution's probability mass, and provide a direct measure of uncertainty for each effect. If the HPD intervals exclude zero, this indicates strong evidence for the effect in question.

All the analyses were conducted using R Studio (version 2023.06.0) software using *lme4* (Bates et al., 2015) and *rstanarm* (Goodrich et al., 2020) packages for classical and Bayesian models, respectively.

3. Results

The preliminary analysis on MEP amplitude (% of baseline) confirmed the robustness of the SICI and ICF protocols, as reflected by a strong main effect of Type of stimulation ($F_{2,231} = 280.60$; $p < 0.0001$; $\eta_p^2 = 0.71$). Amplitudes of MEPs collected during SICI stimulation (mean amplitude \pm SD: 0.5 ± 0.34) was significantly smaller compared to those recorded during SP session (1.64 ± 0.58 ; $p < 0.0001$) and ICF session (1.89 ± 0.8 ; $p < 0.0001$), that also significantly differed from each other ($p < 0.0001$) (See Fig. 2). Complementary Bayes factor analysis provided overwhelming evidence in favor of the full model compared to the null model ($BF_{01} < 1e^{-5}$), confirming the strong influence of stimulation type on MEP amplitude. Pairwise comparisons between conditions confirmed that MEP amplitudes during SICI stimulation were significantly reduced compared to SP stimulation (median difference = 1.12, HPD [0.999, 1.243]) and ICF stimulation (median difference = -1.382, HPD [-1.504, -1.257]). Additionally, ICF stimulation produced slightly lower MEP amplitudes compared to SP stimulation (median difference = -0.262, HPD [-0.385, -0.144]) (see Table S1 for raw MEP amplitude across experimental conditions and sessions).

The mixed model run on MEPs for SP stimulation showed a significant two-way interaction ($F_{1,63} = 4.02$; $p = 0.049$; $\eta_p^2 = 0.06$). We confirmed the inhibitory effect of negation on CSE in an action context (affirmative sentences: 1.68 ± 0.59 ; negative sentences: 1.55 ± 0.49 ; $p = 0.03$), but not in an attentional context (affirmative sentences: $1.65 \pm$

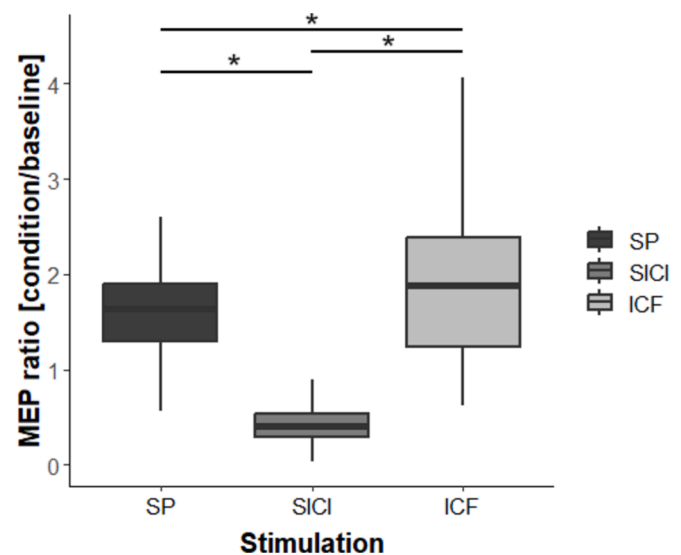


Fig. 2. Modulations of MEP in the three stimulation conditions.

0.63 ; negative sentences: 1.66 ± 0.66 ; $p = 0.75$) (Fig. 3A). Similarly, the Bayesian analysis provided weak support ($BF_{01} = 0.88$) for the interaction model over the null model. Still, the pairwise comparisons showed that MEPs were reduced for action-related negative sentences compared to affirmative sentences (median difference = -0.12, HPD [-0.23, -0.02]). No other significant effects were observed.

The mixed model conducted on SICI measures (expressed as the ratio between unconditioned/conditioned MEP) also showed a significant Type of verb x Polarity interaction ($F_{1,63} = 4.99$; $p = 0.028$; $\eta_p^2 = 0.07$). Surprisingly, as shown in Fig. 3B, action negation sentences increased MEPs amplitude (0.35 ± 0.26) compared to affirmative action sentences (0.30 ± 0.21 ; $p = 0.03$), suggesting a decrease in SICI activity for action negation processing. In contrast, affirmative (0.33 ± 0.26) and negative (0.32 ± 0.21) attentional sentences, did not differently modulate SICI ($p = 0.50$). The Bayesian analysis offered modest support for the interaction model compared to the null model, as indicated by $BF_{01} = 0.59$. The pairwise comparisons further revealed that MEPs were higher for action-negation sentences than for action-affirmative sentences (median difference = 0.048, HPD [0.006, 0.086]). In contrast, no notable differences were found between attentional sentences, as all HPD intervals included zero, implying that sentence polarity did not significantly affect SICI in the attentional context.

Finally, for the ICF session, the analysis did not show any significant results (all $F < 1.48$; all $p > 0.23$), and the Bayesian analysis provided inconclusive evidence, with a slight preference for the simpler model with main effects only ($BF_{01} = 2.21$). This suggests that the interaction may not contribute substantially to explaining the variability in MEP, but stronger evidence would be needed to draw a definitive conclusion (Fig. 3C).

4. Discussion

In the current investigation, we explored how linguistic negation modulates inhibitory and excitatory cortical mechanisms during comprehension of action sentences, building on embodied cognition theories that posit a functional role of sensorimotor systems in meaning construction. According to these theories, understanding action-related language involves partially reactivating the neural circuits that control the described actions – a process known as motor simulation (Barsalou et al., 2008; Fischer & Zwaan, 2008; García & Ibáñez, 2016; Glenberg et al., 2008). When these actions are negated (e.g., “I do not kick”), embodied accounts predict suppression of such simulation processes (De Vega et al., 2016; Dudschig & Kaup, 2018, 2020; Kaup et al., 2007).

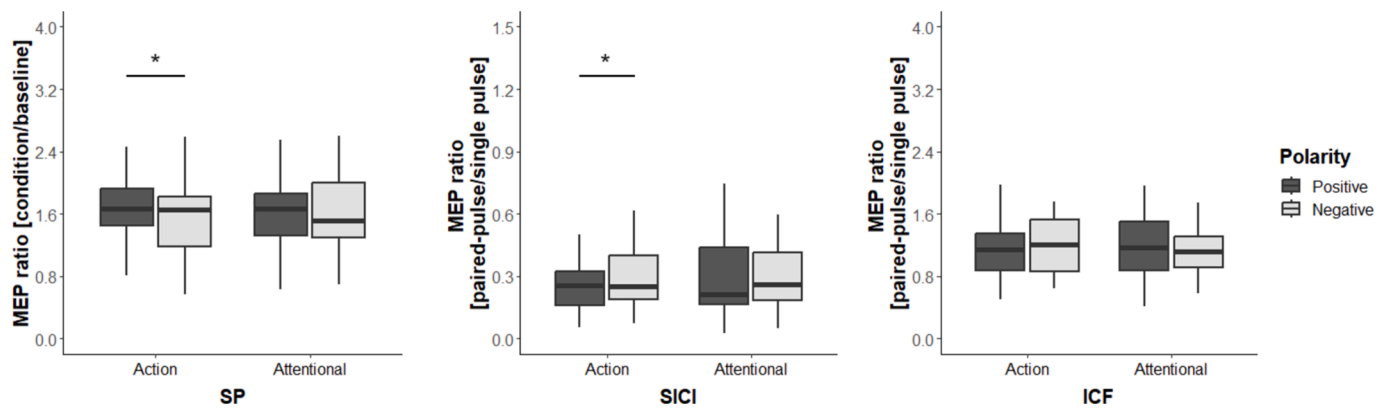


Fig. 3. Changes in MEPs during the language task. Effect of type of verb and polarity on CSE (expressed as MEPs ratio condition/baseline) (A). Box plotting showing cortical motor modulations, expressed as MEPs amplitude ratio (paired pulse/single pulse), of SICI (B) and ICF (C), as a function of type of verb and polarity.

Using single-pulse TMS, we observed that negation selectively reduced CSE exclusively in the context of action sentences, but not during non-action (attentional) sentences. This finding replicates previous evidence of negation's inhibitory effect on motor processes associated with action language comprehension (Papeo et al., 2016; Vitale et al., 2022) and supports theoretical proposals that negation operates by suppressing the simulation of the meaning conveyed by the action verb (de Vega et al., 2016; Papeo et al., 2016; Vitale et al., 2022). A major novel contribution of this study lies in our use of pp-TMS to investigate the specific neurophysiological mechanisms associated with this simulation-blocking effect induced by linguistic negation. We found that negated action sentences led to a reduction in SICI activity, indexed by increased MEP ratios, compared to their affirmative counterparts. This intracortical modulation was selective to GABA-mediated inhibition, with no changes observed in the ICF index. This pattern suggests that linguistic negation recruits GABAergic inhibitory circuits differentially depending on the polarity of the sentence. The fact that purely linguistic processing modulated SICI suggests that the motor system's role extends beyond actual motor execution, with inhibitory motor mechanisms being recruited and modulated also during cognitive processes like language comprehension, proving compelling new evidence for embodied approaches to language. While previous single-pulse TMS studies have shown that processing action-related language – particularly verbs related to manual actions – can modulate the motor cortex, as shown by changes in CSE (Buccino et al., 2005; Candidi et al., 2010; Gianelli & Volta, 2014; Tomasino et al., 2008), our study is the first to demonstrate that language comprehension also engages specific GABAergic intracortical mechanisms within M1, suggesting a more precise neurophysiological architecture for the interface between language and motor systems.

Studies have consistently shown an association between increased SICI and motor response inhibition (Chowdhury et al., 2018; Coxon et al., 2006; Sohn et al., 2002). Accordingly, one might have expected negation-induced inhibition of motor representations during action sentence processing to enhance SICI activity. However, our findings of reduced SICI present a counterintuitive outcome, revealing a reduction in GABA activation. This pattern can be explained by considering previous research demonstrating that processing of action negation increases the duration of the CSP, a measure of GABA-mediated inhibition (Papeo et al., 2016). Another index of inhibitory mechanism mediated by GABA receptors is the long-interval intracortical inhibition (LICI). Notably, research has documented an inverse relationship between different inhibitory mechanisms during volitional inhibition, where reduced LICI corresponds with enhanced SICI (Sohn et al., 2002). This suggests that inhibitory mechanisms operate differently depending on the cognitive function being performed. Recent research has proposed antagonistic interactions between GABA and GABA-mediated

inhibition across premotor-motor networks, whereby increased GABA would reduce GABA activity (Turrini et al., 2023). Supporting this hypothesis, pharmacological studies have shown that administering baclofen, a selective GABA receptor agonist, simultaneously decreases SICI while increasing LICI (McDonnell et al., 2006). This demonstrates that enhancing GABA receptor activation produces different effects on these two measures, leading to a reduction in SICI, which is mediated by GABA transmission.

We propose that linguistic negation operates through similar mechanisms. When processing negated action verbs, the increased GABA-mediated inhibition (as previously demonstrated through CSP measurements; Papeo et al. 2016) is associated with the observed reduction of GABA-mediated inhibition, namely SICI, which may contribute to balancing the overall level of inhibition within M1. These changes ultimately result in a global suppression of CSE, as shown here and in prior work (Papeo et al., 2016; Vitale et al., 2022). It is important to note that, although both CSP and LICI are markers of GABA activity, the former reflects the duration, while the latter reflects the magnitude of the inhibition. Consequently, further studies assessing how the comprehension of negative action language affects LICI, will be crucial for developing a comprehensive understanding of inhibitory mechanisms in linguistic negation.

Consistent with findings from volitional inhibition studies (Sohn et al., 2002), we observed that ICF remained unaffected by negation-induced suppression of meaning representation. This parallel between linguistic and motor inhibition mechanisms further supports the embodied nature of language processing.

A relevant question emerging from our findings is whether GABAergic activity is specifically modulated during the negation of action verbs or extends to other linguistic domains. In the present study, the attentional sentences showed no effect of polarity on SICI. However, this lack of changes does not necessarily exclude GABAergic involvement in other types of negated content. As demonstrated by Beltran et al., (2019), the inhibitory system is engaged during the processing of negated language, suggesting its role extends beyond action contexts. Therefore, it is likely that modulation of GABA activity may be observed in other regions, depending on the domain-specific demands of the processed language. In our study, we observed a specific modulation for action verbs, likely because we measured the cortical activation of M1, which is primarily sensitive to motor-related processes, including action language.

5. Conclusion

In conclusion, our study provides novel insights into how negated action language modulates M1 cortical activity. The findings support an embodied perspective on negation meaning, suggesting that negation in

action sentences blocks the mental representation of the intended meaning through specific neurophysiological mechanisms. Crucially, we provide the first evidence of GABAergic activity modulation within M1 specifically associated with the negation of action-related meanings.

CRedit authorship contribution statement

Francesca Vitale: Writing – original draft, Software, Methodology, Investigation, Funding acquisition, Formal analysis. **Ana Hernández-Sauret:** Methodology, Investigation. **Alessio Avenanti:** Writing – review & editing, Methodology, Funding acquisition. **Manuel de Vega:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.bandl.2025.105536>.

Data availability

Data and code are available at <https://osf.io/m46u3/>

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