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TITOLO TESI:
EXPLORING THE MOTOR ROOTS OF JOINT ACTION:
INSIGHT FROM A NEUROPHYSIOLOGICAL INVESTIGATION

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Le azioni congiunte (Joint Actions, JA) richiedono una precisa coordinazione temporale e spaziale tra agenti. Si basano sia su meccanismi riflessi di basso livello, sia su processi cognitivi di ordine superiore, come la co-rappresentazione dell'azione e la rappresentazione di obiettivi condivisi. Gli esperimenti qui presentati si focalizzano proprio su questi ultimi, esaminando in particolare come gli obiettivi collettivi vengano rappresentati nell'azione congiunta e come l'inibizione della risposta sia modulata dalla co-rappresentazione.

Obiettivi:

Studio I: Determinare se gli obiettivi collettivi siano rappresentati a livello motorio, utilizzando stimolazione magnetica transcranica con co-registrazione elettroencefalografica (TMS-EEG). L'ipotesi prevedeva una modulazione significativa dell'eccitabilità corticospinale durante la JA, segnale di una rappresentazione motoria dell'obiettivo collettivo, e l'assenza di tale modulazione nella condizione individuale.

Studio II: Indagare il ruolo della co-rappresentazione dell'azione nelle JA, in particolare nei processi di cancellazione e riattivazione motoria dell'azione. A tale scopo è stata somministrata, durante la registrazione EEG, una variante dello Stop-Signal Task, lo Stop-Change Task (SCT), per valutare il controllo motorio durante la coordinazione congiunta. Ipotizzavamo latenze di stop più lunghe, una riattivazione motoria più lenta e pattern EEG modulati durante l'arresto dell'azione congiunta.

Metodi:

Studio I: Abbiamo somministrato un compito di reazione a turni con co-registrazione TMS-EEG. Sono stati registrati potenziali evocati motori (MEP) e potenziali evocati da TMS (TEP) in condizioni individuali e congiunte, per valutare l'eccitabilità corticospinale e corticale.

Studio II – Esperimento di controllo positivo: Al fine di garantire che le caratteristiche fondamentali del compito rappresentassero con precisione i processi inibitori, è stato impiegato uno SCT selettivo bimanuale, utilizzato come proxy della co-rappresentazione nelle JA, e confrontato con una corrispondente versione unimanuale. È stata inoltre validata una versione grafica “gamificata” dello SCT in confronto alla versione standard.

Studio II – Esperimento JA: Lo SCT unimanuale gamificato e validato è stato somministrato a partecipanti naïve in condizioni congiunte e individuali, previa induzione sperimentale di specifiche credenze funzionali al compito congiunto. Per differenziare i contributi dell'inibizione “globale” e “selettiva”, l'analisi si è basata sul quadro teorico dei modelli a due processi, in particolare sul modello “pause-then-cancel” (PTC). Marcatori comportamentali (EMG di risposta parziale, prEMG, e tempo di reazione al segnale di stop, SSRT) e neurofisiologici (potenziale evento-correlato P3 frontocentrale da segnale di stop, o stop-P3) sono stati impiegati per quantificare il processo di Pausa (Pp) e quello di Cancellazione (Cp).

Risultati:

Studio I: A livello motorio non è emersa alcuna modulazione significativa della rappresentazione motoria degli obiettivi congiunti. In particolare, la misura principale, la differenza di MEP tra l'extensor carpi ulnaris e il flexor digitorum superficialis, non ha mostrato effetti di rilievo. Le analisi dei TEP sono risultate inconclusive.

Studio II – Esperimento di controllo positivo: I maggiori costi cognitivi associati allo SCT selettivo bimanuale hanno influenzato trasversalmente preparazione, arresto e riattivazione motoria. La versione gamificata dello SCT è stata validata, senza evidenziare differenze significative rispetto a quella standard.

Studio II – Esperimento JA: È stato rilevato uno SSRT più lungo e un'insorgenza più tardiva della stop-P3 durante la condizione congiunta, confermando l'ipotesi iniziale e sottolineando l'importanza del Cp nelle JA. Contrariamente alle aspettative, né i prEMG (marcatori del Pp), né i tempi di reazione al segnale di cambio (Change-RTs, misura della riattivazione motoria) differivano tra le condizioni.

Conclusioni:

Studio I: Non sono emerse evidenze a supporto della nostra ipotesi iniziale: almeno nel nostro contesto sperimentale i risultati non suggeriscono una rappresentazione a livello motorio degli obiettivi condivisi. Nonostante i risultati nulli, lo studio fornisce indicazioni preziose per future indagini sugli obiettivi collettivi.

Studio II: I nostri esperimenti ampliano la comprensione dei meccanismi inibitori nelle JA. I dati comportamentali mostrano che la co-rappresentazione durante la JA influenza in modo significativo l'inibizione reattiva. Tuttavia, tale effetto non si traduce in tempi di Change-RT più lunghi, a indicare che la riprogrammazione dell'azione resta relativamente efficiente anche in contesti di azione congiunta. È emersa inoltre una discrepanza tra i marcatori precoci di inibizione (prEMG) e gli indici comportamentali (SSRT) e neurofisiologici più tardivi (stop-P3), suggerendo che la co-rappresentazione incida in particolare sulle fasi più avanzate dei processi inibitori. I recenti modelli a due processi, in particolare il modello PTC, offrono una prospettiva convincente su come le diverse fasi dell'inibizione possano essere modulate in modo distinto nelle JA.

EXPLORING THE MOTOR ROOTS OF JOINT ACTION: INSIGHT FROM A NEUROPHYSIOLOGICAL INVESTIGATION

TABLE OF CONTENTS

Summary.....	5
1. Introduction	7
1.1. Joint Actions: acting in a social world	7
1.2. Theoretical Frameworks of Joint Actions.....	7
1.2.1. Emergent versus goal-directed coordination	7
1.2.2. Co-representation in joint action research.....	8
1.2.3 A joint interference task: the joint Simon.....	9
1.2.4 The modulation of the joint Simon effect and the importance of the collective goal	9
1.3. Neurophysiological mechanisms in joint actions.....	10
1.3.1. Mirror, simulation, and ideomotor theories: Foundational frameworks for understanding the neurophysiology of social interaction.....	10
1.3.2. Key neurophysiological findings	11
1.3.3. Neurocognitive mechanisms of agency and co-representation: The role of believed intentionality in joint action.....	12
1.3.4. The relevance of inhibitory control and response inhibition in joint actions.....	13
1.3.5. Balancing Co-Representation: Final remarks.....	13
1.4. Joint Action in psychiatric and neurological disorders	14
1.4.1. Joint actions in autism spectrum disorder.....	15
1.5. The present work and applied techniques	16
1.5.1. Techniques of Study I: MEPs and TMS-EEG	16
1.5.2. Techniques of Study II: Stop-Change Task, partial response EMG, and stop-signal P3 ERP	17
2. Study I	20
2.1 Background	20
2.1.1 Limitations of Barchiesi et al. (2022)	21
2.1.2 Design of the new study and aims.....	22
2.2. Methods	22
2.2.1. Power analysis, participants, and general procedures	22
2.2.2. Task setup	23
2.2.3. Trial time-sequence and experiment structure	24
2.2.4. MEPs acquisition and TMS-EEG setup	27
2.2.5. Computation of the muscular engagement index and EMG-accuracy.....	28

2.2.6. Statistical analysis of behavior	28
2.2.7. MEPs preprocessing and statistical analysis	29
2.2.8. TEP preprocessing and statistical analysis	29
2.3. Results.....	30
2.3.1. Behavioral results	30
2.3.2. MEPs	32
2.3.3. TEPs.....	33
2.4. Discussion	35
2.5. Conclusion	37
3. Study II	38
3.1. Background	38
3.1.1. Slower Inhibition in Joint Actions: Co-Representation, Referential Coding, or Attentional Bias? ..	38
3.1.2. Selective Inhibition: Measurement, Mechanisms, and Implications for Joint Actions.....	39
3.2. Aims of Study II	40
4. Study II: Positive Control Experiment	42
4.1. Background	42
4.1.1. The bimanual selective Stop-Change Task as a positive control.....	42
4.1.2. Gamification of the Stop-Change Task for the Joint and Bimanual Positive Control Task	43
4.1.3. Aims and Hypotheses of the Positive Control Experiment.....	44
4.2 Methods	44
4.2.1. Participants, sample size estimation, and exclusion criteria	44
4.2.2. Procedure	45
4.2.3. Bimanual and unimanual Stop-Change Task	46
4.2.4. Task instructions and formats.....	47
4.2.5. Stimuli and trial time-sequence in gamified and standard-format versions	48
4.2.6. Statistical analysis of behavioral data	51
4.2.7. Partial response EMG preprocessing and analysis	51
4.3. Results.....	52
4.3.1. Horse race model assumptions	52
4.3.2. Response modes significantly impact all types of reaction time modalities.....	54
4.3.3. Measures of reactive inhibition: SSRT and prEMG.....	56
4.4. Discussion	59
5. Study II: Joint Experiment.....	61
5.1 Background and Hypotheses.....	61
5.2 Methods	61
5.2.1. Participants, sample size estimation, and exclusion criteria	61

5.2.2. Procedure	62
5.2.3. Joint Stop-Change Task setup	63
5.2.4. Belief induction.....	64
5.2.4. Storytelling and instructions.....	65
5.2.7. ERP preprocessing	66
5.2.6. Statistical analysis of behavioral data, prEMGs, and ERPs.....	66
5.3. Results.....	67
5.3.1. Horse race model assumptions	67
5.3.2. Conditions do not modulate proactive control (HP1).....	68
5.3.3. Measures of reactive inhibition: SSRT and prEMG (HP2)	69
5.3.4. Event-related potentials	71
5.4. Discussion	74
5.4.1 Establishing collective vs. individual goals: A belief-induction approach	75
5.4.2 Why referential coding fails to account for our results	76
5.4.3 Balancing difficulty and joint coordination: Insights from SSD and Change RT effects	77
5.4.4. Significant differences in the frontocentral stop-P3	77
5.4.5 Integrating our results with previous joint SST literature.....	78
5.4.7. Conclusions.....	80
6. Final conclusions.....	81
References	83

SUMMARY

Background

Joint actions (JAs) require precise temporal and spatial coordination between co-agents and draw on both low-level reflexive mechanisms and higher-level cognitive processes, such as action co-representation and shared goal representation. The experiments in this PhD thesis focus on these processes, particularly examining how collective goals are represented in joint action and how response inhibition is modulated by co-representation.

Aims:

- Study I: To determine whether collective goals are represented at the motor level, using transcranial magnetic stimulation with electroencephalography co-registration (TMS-EEG). We anticipate a significant modulation of corticospinal excitability during JA, indicative of motorical representation of collective goal, and no modulation in the solo condition.
- Study II: To investigate the role of action co-representation in JAs, specifically, in action cancellation and re-engagement, and to distinguish between lower-level emergent coordination and higher-level goal-directed or planned coordination. For this purpose, a variant of the Stop-Signal Task, the Stop-Change Task (SCT), is employed during EEG, capturing reactive motor control essential for joint coordination. We anticipate longer stopping latencies, a slower action re-engagement, and altered EEG patterns during joint action stopping.

Methods:

- Study I: A turn-based joint action reaction-time task was administered, co-registered with TMS-EEG. Motor-evoked potentials (MEPs) and TMS-evoked potentials (TEPs) were recorded from solo and joint conditions to assess corticospinal and cortical excitability.
- Study II: Positive Control Experiment: A bimanual selective SCT was used as a proxy for action co-representation in JA and compared to an unimanual SCT, to ensure that its key features accurately capture inhibitory control processes. Furthermore, a gamified graphic version of the SCT was validated against a standard version.
- Study II: Joint Experiment: The validated unimanual gamified SCT was administered to naïve participants in joint and solo conditions with belief manipulation. Two-process accounts, including “pause-then-cancel” (PTC) models, are used to differentiate the roles of global and selective stopping. Behavioral (partial response EMG, prEMG, and the stop-signal reaction time, SSRT) and neurophysiological (stop-signal frontocentral P3 event related potential) markers quantify the Pause process (Pp) and the Cancel process (Cp).

Results:

- Study I: No significant modulation of motor-level representation for the co-actor’s action emerged in the Joint condition. Specifically, the primary measure, MEP difference in extensor carpi ulnaris (ECU) versus flexor digitorum superficialis (FDS), showed no notable effect. Cluster-based analyses of TEPs were inconclusive.
- Study II: Positive Control Experiment: The greater motor-planning demands inherent in a bimanual selective SCT affected motor preparation, stopping, and re-engagement in a transversal manner. The gamified SCT was validated, revealing no significant differences compared to the standard graphical version.
- Study II: Joint Experiment: The gamified SCT revealed longer SSRT and an later onset of the stop-P3 during the joint condition, confirming our initial hypothesis and highlighting the importance of the Cp in JA. Contrary to our expectations, prEMGs (markers of the Pp) did not differ between conditions.

Furthermore, reaction times to respond to the change signal (Change RTs; our measure of action re-engagement), also did not differ.

Conclusion:

- Study I: Even after accounting for the methodological constraints outlined by previous research, we found no evidence to support our initial conjecture, as all results point away from a motoric representation of shared goals, at least with our experimental setting. Despite these null findings, our study provides valuable insights and methodological guidance for future investigations of collective goals.
- Study II: With our joint SCT, we advanced the understanding of action cancellation in shared-action contexts. By highlighting the contrast between collective and individual goals using belief induction and gamification, and by incorporating prEMG and EEG measures, consistent with prior research, our behavioral findings suggest that co-representation during JA significantly influences reactive inhibition. However, this influence did not manifest as slower Change RTs, indicating that action reprogramming remains relatively efficient even under joint conditions. Importantly, we observed an apparent mismatch between early inhibition markers (prEMGs) and later behavioral (SSRT) and neurophysiological indices (stop P3), implying that co-representation may specifically affect later inhibitory processes. Recent two-process frameworks, particularly the PTC model, offer a compelling perspective on how different phases of inhibition may be distinctly affected in JAs.

1. INTRODUCTION

1.1. Joint Actions: acting in a social world

Joint actions are broadly defined as two (or more) individuals coordinating in space and time to accomplish a common outcome (Clark, 2020; Knoblich et al., 2011; Sebanz et al., 2006a). The relatively recent and widespread interest in joint action reflects a growing body of evidence suggesting it is crucial to the development of executive functions and the social mind in two key ways: phylogenetically, by shaping cooperative capacities over the course of human evolution, and ontogenetically, by fostering interpersonal skills and social cognition within an individual's lifetime (Miss et al., 2022). Accordingly, joint actions are a central focus in neuroscience, evolutionary biology, psychology, and philosophy (Gallotti et al., 2017; Hasson et al., 2012; Milward and Carpenter, 2018; Tomasello, 2020). Each discipline investigates a range of phenomena under this umbrella, including conceptually related constructs such as joint attention (Siposova and Carpenter, 2019), joint agency (Zapparoli et al., 2022), shared intentionality (Tomasello et al., 2005), shared (or collective) goals (Butterfill, 2012; Butterfill and Sinigaglia, 2023; Sinigaglia and Butterfill, 2020), and joint commitment (Genty et al., 2020). However, a significant challenge lies in the conceptual and operational complexity of joint action and its related constructs. Ambiguous definitions and inconsistent terminology across disciplines hinder the establishment of effective interdisciplinary connections. As a result, findings have not been thoroughly integrated, and many phenomena investigated through neuroscientific methods remain only loosely linked to the "jointness" described in psychological (or philosophical) frameworks. Growing consensus suggests that joint action and its related concepts are pivotal for understanding human cognitive functioning and evolution (see Miss *et al.*, 2022 for a comprehensive review), as well as for elucidating certain psychiatric and neurological disorders (Cerullo et al., 2021; Liepelt et al., 2012b). Consequently, clarifying the precise relationships between these phenomena must be a high priority in neuroscientific research.

A productive strategy to address this issue is to directly examine the behavioral and neurophysiological mechanisms humans employ when coordinating in joint actions. This empirical, bottom-up approach contrasts with more abstract, top-down theoretical methods, and can illuminate both commonalities and differences in how humans achieve coordinated behavior. In this PhD research, I adopt both perspectives: a theoretical top-down framework in the first experiment and a bottom-up empirical approach in the third. The central focus are co-representation and shared goals, empirical phenomena regarded as critical to joint action. In this introduction, I will begin by discussing a range of theoretical definitions, encompassing both low- and high-level constructs that describe joint action and show where co-representation (and shared goals) may fit into these frameworks. Next, I will summarize the classical behavioral paradigms used to quantify co-representation and the key factors that influence it. Subsequently, I will review the neurophysiological underpinnings of co-representation and examine how inhibitory control plays a role. I will then consider how joint actions are affected in clinical populations and outline the connections between co-representation and joint goals, highlighting how these concepts converge to shed light on the mechanisms underlying joint actions. Finally, I will briefly conceptualize the present PhD work to discuss the applied techniques used throughout the experiments.

1.2. Theoretical Frameworks of Joint Actions

1.2.1. Emergent versus goal-directed coordination

During joint action, inter-individual coordination can occur across diverse contexts and may draw on either low-level, reflexive, and automatic mechanisms or higher-level, cognitively demanding processes that involve reasoning about others' mental states. Low-level conceptualizations of joint action are often referred to as emergent coordination, which arises spontaneously and produces similar behavior among individuals who

have no explicit plan to act together (Knoblich *et al.*, 2011). Notably, emergent coordination does not rely on shared knowledge or an understanding of others' intentions. Instead, it stems from factors such as common affordances, entrainment, perception-action matching, and action simulation within common predictive models. (Knoblich *et al.*, 2011). More specifically, common affordances arise when multiple individuals perceive the same object simultaneously, eliciting shared or complementary action possibilities (Gibson, 1977). For instance, a two-seater swing typically prompts two people to sit down together. On the other hand, entrainment refers to the automatic synchronization of a shared (or even different but compatible) action or action sequence. Take the two-seater swing example, people usually start to synchronize their rocking frequencies spontaneously (Richardson *et al.*, 2007). Other examples are the spontaneous alignment of hand-clapping rhythms (Schmidt *et al.*, 2011), or people falling into the same walking pace (van Ulzen *et al.*, 2008). Another mechanism central to emergent coordination is perception–action matching, in which observing an action activates the observer's corresponding motor representations. For example, if a person has dancing experience, watching someone else dance will engage the relevant representations in their own motor repertoire (Hommel *et al.*, 2001). Finally, action simulation within common predictive models is crucial for emergent coordination. By mapping observed actions onto their own motor system, individuals can accurately predict the timing and outcomes of those actions (Wolpert *et al.*, 2003). Returning to the dance example, a dancer observing her partner initiate a jump can anticipate the partner's landing position and timing. Perception–action matching and predictive models can similarly promote automatic alignment in conversational settings, where speakers adapt to each other's speaking rate or emulate each other's word choices, ultimately aligning their vocabulary and syntax (Ruch *et al.*, 2018).

Whereas emergent coordination primarily relies on reactive and externally driven processes, goal-directed (or planned) coordination is generally initiated internally, guided by the joint action's desired outcome, namely, achieving the collective goal. At the lower end of this goal-directed spectrum, individuals must possess at least a basic understanding of the joint action's intended result, recognize their own contribution to it, and be aware that success depends on another individual's cooperation (Knoblich *et al.*, 2011). At the higher end, however, coordination may include considerations of the co-actor's motives, perspectives, emotions, thoughts, knowledge, and beliefs, potentially involving empathy (Lamm *et al.*, 2016; Lamm *et al.*, 2019). In these cases, joint action plans can be refined and flexible when actors account for each other's knowledge and intentions, thus optimizing their strategies or achieving long-term objectives. Accordingly, the degree to which co-actors represent each other's perspectives and mental states can vary considerably in planned coordination (Knoblich *et al.*, 2011; Vesper *et al.*, 2010).

1.2.2. Co-representation in joint action research

Increasing evidence indicates that action co-representation, i.e., the mental representation of both one's own and a partner's actions (Ruissen and de Bruijn, 2016; Sebanz *et al.*, 2003; Sebanz *et al.*, 2006b; Vesper *et al.*, 2010), plays a pivotal role in goal-directed coordination (Knoblich *et al.*, 2011; Miss *et al.*, 2022). This process may also involve monitoring the task rules that govern how actions are to be performed (Vesper *et al.*, 2013). Co-representation presumably facilitates joint actions by enabling individuals to better coordinate their behavior. This mechanism possibly relies on processes that achieve self–other (SO) motor integration and distinction, whereby individuals accurately differentiate their own actions from those of a partner (Miss *et al.*, 2022). As a result, precision and predictability of one's own and the co-actor's actions increase (Meyer *et al.*, 2015) as mutual anticipation and monitoring of both sets of actions (and their shared outcome) becomes possible (Sebanz and Knoblich, 2009). Furthermore, when pursuing collective goals, co-representation can foster a shared responsibility for the overall task by incorporating a co-actor's actions and task requirements into one's own action planning (Beyer *et al.*, 2017; Butterfill, 2012). From a theoretical standpoint, an optimal equilibrium between SO distinction and integration, adapted to the specific situation, may be required for

smooth motor coordination (Vesper et al., 2017). As we will see in the next section, achieving this balance likely involves top-down control processes that permit individuals to mentally represent their partner's actions while maintaining a clear distinction between self- and other-generated behaviors (Knoblich et al., 2011). Most co-representation studies have focused on dyadic tasks requiring partners to coordinate complementary or identical movements, such as joint grasping, lifting, pulling, or synchronization tasks (for a comprehensive review, see Miss et al., 2022). Other dyadic paradigms that feature coordinated yet distinct movements, such as problem-solving/social games (Gräfenhain et al., 2013), joint music performance (Novembre et al., 2016), social play (Heesen et al., 2017), are likewise presumed to involve co-representation.

1.2.3 A joint interference task: the joint Simon

The joint Simon task (Sebanz et al., 2003), is the most extensively studied joint paradigm that illuminates both the cognitive demands of co-representation and the mechanisms by which SO motor integration and distinction are regulated during dyadic coordination. Notably, this paradigm showcases a situation in which co-representation impairs joint performance rather than facilitating it. In a typical setup, two participants each handle one of two possible response options when presented with an external stimulus (in the regular Simon task participants operate individually both response options with each hand; Simon and Wolf, 1963). This arrangement elicits a pronounced tendency toward SO integration, reflected in the so-called joint Simon effect, which in turn undermines performance and cooperation success (i.e., correct response selection). By co-representing the partner's actions, individuals find it difficult to disambiguate their own task affordances from those of the partner, leading to interference in executing their assigned responses. Two main accounts, i.e., referential response coding and co-representation, have been proposed to explain the joint Simon effect. According to the referential coding approach (Dolk et al., 2014), the effect arises from purely perceptual processes, where the co-actor (or any attention-grabbing object) is used as a spatial reference point to classify one's own actions as left or right. This discrimination between internally and externally generated events then induces a spatial compatibility effect, even in the absence of a social partner actively performing the task (Dolk et al., 2011; Dolk et al., 2013). However, the mere presence of a conspecific not engaged in joint action does not elicit this effect in non-human primates (Miss and Burkart, 2018) or humans (Sebanz et al., 2003; Sebanz et al., 2007). By contrast, the co-representation account posits that the joint Simon effect emerges from mental representations of both one's own and the partner's actions (and possibly the associated task rules) in a functionally equivalent manner. Each individual effectively incorporates the partner's action alternative into their own action planning, behaving as though they were responsible for both her own and the co-actor's actions (Knoblich et al., 2011; Sebanz et al., 2006a; Vesper et al., 2010).

1.2.4 The modulation of the joint Simon effect and the importance of the collective goal

Various social factors significantly influence the strength of co-representation, as reflected by joint Simon task outcomes. For instance, the joint Simon effect diminishes, or even disappears, under competitive, rather than cooperative, conditions (Iani et al., 2014; Ruissen and de Bruijn, 2016). Similarly, when group categorizations are salient, the effect is weaker if participants are paired with an outgroup instead of an ingroup member (McClung et al., 2013; Müller et al., 2011). Inducing negative affect or introducing an antagonistic co-actor has the same weakening effect (Hommel et al., 2009; Kuhbandner et al., 2010). By contrast, cognitive empathy correlates positively with co-representation among friends or closely bonded co-actors (Ford and Aberdein, 2015; Shafaei et al., 2020). The effect can also be enhanced by nasal oxytocin administration (Ruissen and de Bruijn, 2015) and by the belief that one is interacting with an intentional rather than an algorithmically generated partner (Ruys and Aarts, 2010; Sahai et al., 2019; Tsai et al., 2008). Overall, these findings underscore the importance of social factors in modulating co-representation, thus supporting a social co-

representation perspective over purely referential response coding. At the same time, familiarity biases, which act as attentional biases, may underlie these social effects, implying that referential response coding could be more pronounced when partners share a stronger bond or higher familiarity.

A likely resolution for reconciling referential response coding with co-representation is that collective goals activate co-representation in social task settings, whereas purely perceptual factors drive referential coding when no joint outcome is highlighted. Several studies illustrate how a task's design and instructions can make the joint goal salient by stipulating cooperative intentions, sharing rewards, or providing immediate feedback to both participants and thereby fostering co-representation (Miss *et al.*, 2022). For instance, in common marmosets, the mere physical presence of a conspecific did not induce co-representation unless both partners were jointly engaged with shared rewards (Miss and Burkart, 2018). Similarly, in humans, instructing partners to collaborate on the same task amplifies co-representation (Sebanz *et al.*, 2003; Sebanz *et al.*, 2007), whereas exclusively individual goals attenuate it (Dolk *et al.*, 2011).

In sum, referential coding can explain the joint Simon effect in non-social contexts but fails to account for robust social modulations, such as the impact of relationship quality, empathy, or the intentionality of the co-actor, observed when a task is demonstrably shared. Thus, co-representation emerges most clearly in set-ups where a common outcome is emphasized, underscoring that shared goals are pivotal for a genuinely social effect (Sebanz *et al.*, 2006a). For adults, a simple verbal instruction to “cooperate” can establish this joint goal, whereas for children or non-human subjects, a joint reward structure may suffice to foster interdependence and co-representation.

1.3. Neurophysiological mechanisms in joint actions

The most common neurophysiological technique used to study joint actions is electroencephalography (EEG), with its related analysis of event-related potentials (ERPs), particularly the lateralized readiness potentials (LRPs). Functional magnetic resonance imaging (fMRI) and functional near-infrared spectroscopy (fNIRS) are other techniques frequently used.

1.3.1. Mirror, simulation, and ideomotor theories: Foundational frameworks for understanding the neurophysiology of social interaction

The mirror mechanism (Rizzolatti and Sinigaglia, 2007; 2010), simulation theory (Gallese and Goldman, 1998), along with ideomotor or common coding approaches (Hommel *et al.*, 2001; Prinz, 1997), have all been employed to explain social interactions. For example, mirror neurons, initially identified in macaques, discharge both when an action is executed and when the same action is observed in another individual (Di Pellegrino *et al.*, 1992; Gallese *et al.*, 1996; Rizzolatti *et al.*, 1996). Based on evidence suggesting a similar mirror neuron system in humans (Rizzolatti and Craighero, 2004), generating a cortical representation of an observed action within the observer's motor system provides a plausible neural mechanism for merging self- and other-generated actions into a shared representation (Gallese *et al.*, 1996; Rizzolatti *et al.*, 2001). On the other hand, numerous studies indicate that individuals internally simulate their partner's actions (Gallese and Goldman, 1998) and, during joint action, integrate these simulations with their own action goals within a common predictive model (Bekkering *et al.*, 2009b; Sebanz *et al.*, 2007). Notably, the familiarity or sensorimotor experience with a given task appears to facilitate the simulation of a co-actor's actions (Hadley *et al.*, 2015; Novembre *et al.*, 2016). A key part of this process hinges on the brain's ability to encode the perception of the co-actor's action and one's own self-generated action production in a similar manner, commonly referred to as perception–action matching (Hommel *et al.*, 2001), thus allowing actions and their outcomes to be maintained in a common representational format (Rizzolatti and Sinigaglia, 2010). One

interpretative framework is provided by ideomotor theories (James, 1890; Lotze, 1852) and their modern adaptations (Hommel *et al.*, 2001; Prinz, 1997; Shin *et al.*, 2010). These theories propose that once associations between actions and their outcomes, irrespective of whether these outcomes correspond to individual or shared goals, are established, the mere perception or cognition of the outcome automatically activates the corresponding action representations, as both are encoded within a common representational medium. In joint actions, therefore, observing another person's actions engages the same representational structures involved in one's own action planning and control (Jordan and Knoblich, 2004). The co-actor's perceived motor behavior is likely integrated into one's own motor repertoire, enabling it to be incorporated into subsequent action planning (Tsai & Brass, 2007). However, ideomotor theory may not fully account for the flexibility required in social interactions where co-actors must coordinate and pursue joint goals, as this theory was originally formulated for within-individual motor programming (Sebanz *et al.*, 2006a; Sebanz *et al.*, 2003). Likewise, during joint action, a purely bottom-up mirroring of action goals appears insufficient, as there is no one-to-one mapping between observed movements and their associated goals (Lamm and Majdandžić, 2015). In summary, while perception-action matching and SO motor integration, as proposed by mirror mechanisms, simulation, and ideomotor theories, may be sufficient to explain emergent coordination, goal-directed coordination likely requires some interaction with additional cognitive mechanisms (Miss *et al.*, 2022).

1.3.2. Key neurophysiological findings

Electrophysiological studies, as well as fMRI studies of joint actions, primarily derived from the joint Simon and joint Simon-like tasks, demonstrate that top-down executive control processes are engaged to predominantly suppress responses during the partner's turn (Knoblich *et al.*, 2011). A key interpretation of these findings is that SO integration must be inhibited to maintain SO distinction, thereby optimizing goal-directed coordination. This dynamic underscores the role of inhibitory control, a fundamental component of executive functions (Diamond, 2013; Wessel and Anderson, 2023). The no-go/stop P3 event-related potential (ERP) is widely recognized as a neural marker of action control and response inhibition (Hervault *et al.*, 2024; Huster *et al.*, 2020; Nguyen *et al.*, 2020). In the joint Simon task, no-go trials (where the co-actor's response is required) elicit a larger P3 amplitude compared to no-go trials in the half-task control condition (i.e., when participants act alone, effectively converting the task into a go/no-go paradigm). This enhanced P3 is interpreted as reflecting increased response inhibition to prevent an individual from acting during the partner's turn, likely mediated by a common representational system that encompasses both partners' actions (Ruissen and de Bruijn, 2015; Sebanz *et al.*, 2006b; Tsai *et al.*, 2006). These findings highlight the principle of co-representation and emphasize the importance of maintaining a dynamic balance between SO integration and distinction in joint action contexts. In their study, Tsai *et al.* (2006) also investigated another ERP as an index of motor preparation to the stimulus, i.e., the lateralized readiness potential (LRP, time-locked to the stimulus onset; Coles, 1989). Interestingly, both compatible no-go and incompatible go trials exhibit LRP in the Joint condition compared to the solo half-task condition. This enhancement in LRP amplitude may reflect increased action anticipation and monitoring, which in turn facilitates improved motor control during joint action (Tsai *et al.*, 2006). Comparable outcomes were observed in a joint turn-taking task employing centrally presented stimuli alongside a half-task control condition (Holländer *et al.*, 2011). Consistent with previous ERP findings (Sebanz *et al.*, 2006b; Tsai *et al.*, 2006), a seminal fMRI study by Sebanz *et al.* (2007) compared a joint Simon task condition with a half-task condition. Notably, during go-trials in the Joint condition, there was increased activation in the medial frontopolar cortex (Brodmann area 10). The authors suggested that the representation of a partner as a potential co-actor enhances the salience of self-relevant stimuli, a function attributed to this region, which has been linked to joint attention and SO distinction (Mitchell *et al.*, 2006; Williams *et al.*, 2005) as well as processing others' intentions and engaging in visual perspective-taking (Amodio and Frith, 2016). Furthermore, joint performance during go-trials elicited

heightened activation in the orbitofrontal cortex, indicative of enhanced monitoring processes to ensure that responses are executed at the appropriate time. In contrast, during trials requiring the co-actor's response (i.e., no-go trials), increased activation was observed in the parietal lobule, precuneus, and supplementary motor area (SMA), which the authors interpreted as reflecting enhanced action co-representation triggered by the observation/perception of the partner's actions (Sebanz *et al.*, 2007).

1.3.3. Neurocognitive mechanisms of agency and co-representation: The role of believed intentionality in joint action

Supported by behavioral and neurophysiological indices (P3 and LRP) from a joint Simon task with explicit cooperative instructions, Tsai *et al.* (2008) observed enhanced action control and response inhibition in the co-actor's trials exclusively when participants believed they were interacting with an unseen intentional human agent, as opposed to a computer located in another room. This finding suggests that the mere belief in another's intentionality is sufficient to trigger an agency-dependent social Simon effect, thereby modulating action planning and anticipation, consistent with the notion that co-representation of human action is an evolutionarily tuned default of the human motor system (Tsai *et al.*, 2008). In a study extending the findings of Tsai *et al.* (2008), Wen and Hsieh (2015) employed a similar belief paradigm in an fMRI experiment in which participants performed the joint Simon task under two conditions (with a human co-actor or computer). The authors reported that, during compatible trials, activation in the medial prefrontal cortex was significantly higher in the human co-actor condition than in the computer condition. In line with the arguments presented by Sebanz *et al.* (2007), they hypothesized that this elevated neural activity reflects enhanced SO distinction when individuals believe they are engaging with a biological co-actor. Ramnani & Miall (2004), during an fMRI experiment, administered an associative joint stimulus-response task, where visual cues specified future actions for co-actors located in adjacent rooms, thus enabling participants to generate predictions of the other's actions based on their task representation and action anticipation processes. In this task, the instruction cue color designated the acting agent: scanned participant, co-actor, or computer (non-agent control), while the cue shape specified the finger movement. Some cues required agents to withhold a response until a trigger, preventing motor planning in advance. Critically, the neural activation patterns differed between preparing one's own responses and anticipating another's. Preparation of specific, cued, first-person responses was associated with activation of the dorsal premotor cortex (PMd), while anticipation of a co-actor's responses instead engaged the paracingulate cortex, superior temporal cortex, and interconnected regions of the premotor cortex (Ramnani and Miall, 2004). These findings support the notion that the human brain employs distinct neural subsystems within the motor control network, one for self-generated actions and another for predicting others' actions, possibly via simulation of their mental processes (Ramnani and Miall, 2004). Interestingly, these regions, which lie outside the classical mirror system, have also been implicated in mental state attribution processes (Frith and Frith, 1999; Gallagher and Frith, 2003). Engagement in others' actions has been linked to increased uncertainty regarding agency, that is, ambiguity about which individual is responsible for a given action (Beyer *et al.*, 2017; Colzato *et al.*, 2012; Stenzel *et al.*, 2012). In a study of dyadic musical performance, Novembre *et al.* (2016) reported that neural activity in the right centroparietal region overlapped with regions traditionally associated with the sense of agency, particularly the anterior medial prefrontal cortex and the right temporoparietal junction (rTPJ). The latter, specifically, is thought to play a critical role in agency attribution (Blakemore and Frith, 2003; Decety and Lamm, 2007), assist in synchronizing one's own movements with those of others (Brass *et al.*, 2005), and is also an area closely linked to Theory of Mind (ToM, Apperly *et al.*, 2004). These findings, again, illustrate the complex interplay and balance between SO integration and distinction during social interactions.

1.3.4. The relevance of inhibitory control and response inhibition in joint actions

Although converging evidence underscores the role of response inhibition in joint actions, it is noteworthy that only two studies have implemented a joint version of the Stop-Signal Task (SST, Cardellicchio et al., 2021a; Cavallo et al., 2014). This paradigm (Logan and Cowan, 1984) is widely considered a cornerstone paradigm in neuroscience for isolating “pure” response inhibition, i.e., action cancellation, rather than simple action restraint (Raud et al., 2020b). By requiring participants to halt already-initiated actions when a stop signal is presented, it offers a valuable measure of response inhibition, making it an essential tool for investigating the neural and cognitive mechanisms underpinning inhibitory control (Verbruggen et al., 2019). Behaviorally, both studies demonstrated diminished reactive inhibition in the joint condition, evidenced by an increased stop-signal reaction time (SSRT) compared to the solo condition. On the neurophysiological front, Cavallo et al. (2014) evaluated cortico-spinal excitability (CSE) in non-effector muscles, and their findings suggest the engagement of a more selective, and consequently slower, stopping mechanism (Aron and Verbruggen, 2008; Majid et al., 2012), during joint actions. Conversely, utilizing a reaching version of the SST, Cardellicchio et al. (2021a) examined the role of the left dorsal premotor cortex (IPMd) through a continuous theta burst stimulation (cTBS) protocol, revealing that this region modulates stopping performance in joint action contexts. Both studies interpret these results in terms of co-representation (Knoblich et al., 2011; Sebanz et al., 2006a). The concurrent processing of action co-representation appears to delay the detection and processing of infrequent stop-signals. In this regard, Cardellicchio et al. (2021a), in line with Cavallo et al. (2014), propose that the IPMd recruits a more selective inhibitory mechanism to control joint responses by suppressing interfering parallel motor plans, with action co-representation serving as the primary driver of this effect. Supporting this interpretation, Cardellicchio et al. (2020) previously reported that, in a similar reaching task without stop-trials, the joint condition was associated with reduced short-interval intracortical inhibition (SICI) and prolonged cortical silent period (CSP) during the reaching phase. More recently, Vescovo et al. (2024) replicated these findings, further demonstrating that CSP modulation does not occur prior to movement onset but emerges later in the reaching phase, independent of advance information. Moreover, SSRT, considered a measure of the overall duration required to implement stopping (Diesburg and Wessel, 2021), has been found to correlate positively with CSP length (Paci et al., 2021) and negatively with SICI strength (Cardellicchio et al., 2021b; Chowdhury et al., 2018). This pattern of associations further emphasizes the critical role of inhibitory control mechanisms in modulating joint actions.

1.3.5. Balancing Co-Representation: Final remarks

In conclusion, converging evidence from behavioral, electrophysiological, and neuroimaging studies demonstrates that joint actions rely on a delicate interplay between high- and low-level co-representational processes, which can emerge relatively automatically. While foundational models, such as the mirror mechanism, simulation theory, and ideomotor frameworks, effectively describe how SO motor integration, perception–action matching, and action simulation facilitate emergent coordination, these processes must be supported by top-down executive functions, particularly inhibitory control, to address the demands of goal-directed social interaction. Indeed, results from joint Simon and Stop-Signal Task paradigms indicate that co-representation of actions imposes a processing cost, evidenced by slower response inhibition and amplified neural markers (e.g., heightened P3 and LRP amplitudes). Additionally, fMRI investigations reveal that brain regions linked to social cognition, such as the medial prefrontal cortex and orbitofrontal cortex, are differentially engaged when individuals interact with human co-actors compared to non-human agents or act alone, underscoring the role of perceived intentionality in shaping action planning and monitoring. Consistent with this, correlations between response inhibition measures (SSRT, CSP, and SICI) and joint action performance further emphasize inhibitory mechanisms as essential for balancing the integration and distinction of self- and other-generated actions. Ultimately, these findings highlight the complex neural

circuitry underlying joint actions and illustrate that, in specific contexts, optimal behavior and accurate discrimination of self-versus-other actions may necessitate suppressing co-representation to resolve conflicts between SO integration and distinction.

1.4. Joint Action in psychiatric and neurological disorders

Clinical investigations of joint action have encompassed populations with socio-cognitive impairments due to various etiologies, such as Parkinson's disease (PD), focal brain lesions, or schizophrenia. However, most of the clinical joint action research has focused on autism spectrum disorder (ASD). To the best of my knowledge, no joint action studies have been conducted involving individuals with Alzheimer's disease, obsessive-compulsive disorder, or bipolar disorder. Notably, adult neurological patients with damage to frontal regions, the posterior parietal cortex (PPC), or the temporoparietal junction (TPJ), all areas closely linked to ToM (Apperly *et al.*, 2004), did not manifest the joint Simon effect under typical testing conditions (Humphreys and Bedford, 2011). ToM denotes the ability to conceptualize both one's own and others' mental states, encompassing intentions, beliefs, desires, and knowledge (Baron-Cohen *et al.*, 1985; Frith and Frith, 1999; Premack and Woodruff, 1978). These neurological patients showed impairments on both first-order ToM tasks (requiring an understanding of another individual's beliefs) and second-order ToM tasks (requiring the attribution of beliefs regarding a third party's mental state). Intriguingly, when specifically prompted to attend to their co-actor, the same patients with PPC/TPJ lesions exhibited the joint Simon effect (Humphreys and Bedford, 2011), suggesting that targeted attentional cues can partially compensate for underlying ToM deficits. By contrast, individuals with schizophrenia, who frequently experience a disturbed sense of agency and atypical activity in the medial prefrontal cortex (MPC) and TPJ, did not exhibit the joint Simon effect (Liepelt *et al.*, 2012a). However, De la Asuncion *et al.* (2015) reported a joint Simon effect in schizophrenia patients, even though they exhibited generally slower response times compared to the controls. Interestingly, electrophysiological data revealed a marked difference in the no-go P3 amplitude: healthy participants showed increased no-go P3 amplitude in the joint condition, as previously reported (Ruissen and de Bruijn, 2015; Sebanz *et al.*, 2006b; Tsai *et al.*, 2006), with respect to half-task control. Schizophrenia patients did not show this pattern, suggesting altered processing necessary for successful joint action in schizophrenia. Only one study assessed joint actions in PD. Fabbri *et al.* (Fabbri *et al.*, 2018) administered to PD patients and healthy controls a go/no-go Flanker task under both joint and individual conditions, alongside measures of cognitive and affective ToM. Results showed that only PD patients with higher cognitive ToM scores exhibited a joint Flanker effect, whereas controls displayed this effect regardless of the score. Moreover, PD patients with lower affective ToM scores experienced greater interference effects, whereas the opposite pattern emerged for HCs. In regression analyses, cognitive and affective ToM predicted performance only in the joint condition, underscoring the role of frontostriatal circuitry in PD. The heterogeneity of these results emphasizes the importance of accounting for both the severity and the anatomical locus of brain dysfunction when examining the presence or absence of the joint Simon effect in populations with impaired social cognition (Miss *et al.*, 2022). Surprisingly, although personality disorders are characterized by interpersonal and affective disturbances that often involve deficits in social cognition, thus rendering the study of joint actions especially valuable for uncovering how these deficits manifest during real-time interpersonal exchanges, despite a comprehensive literature review, no studies appear to have investigated joint actions specifically in the context of the DSM-5 personality disorder clusters (A, B, and C; American Psychiatric Association, 2013). Insights derived from such research may facilitate the development of targeted interventions and refine theoretical models of a given disorder and social dysfunction in general.

1.4.1. Joint actions in autism spectrum disorder

A growing body of research underscores the importance of joint action coordination for understanding the core social difficulties observed in ASD and also for developing early interventions. As already mentioned, successful joint action relies on bottom-up sensory-motor processes, along with top-down executive functioning, to integrate both motor and social cues. Considering the data of joint actions in psychiatric and neurological patients, it appears evident that besides the mirror neuron system (and related low-level emergent coordination processing), another key neural network appears to be pivotal, i.e., the mentalizing, or theory of mind, system (Bekkering et al., 2009a; Newman-Norlund et al., 2008). In fact, individuals with ASD frequently exhibit abnormal activity in these networks (Dickstein et al., 2013). Gonzalez et al. (2013) investigated how ASD patients plan and execute tool-passing actions in joint-action scenarios requiring consideration of a partner's comfort and end-goals. While some participants with ASD did adopt personally uncomfortable postures to facilitate the partner's comfort, akin to controls, their overall behavior showed more variability and less consistent accommodation of the partner's needs. These findings highlight that although some aspects of movement planning in joint-action contexts may align with normal patterns, individuals with ASD can exhibit greater heterogeneity in their ability to integrate the partner's end-state comfort into their own motor actions. In another study of adults with autism or Asperger Syndrome, who also demonstrated ToM impairments, as indicated by comparatively poorer ToM task performance than neurotypical individuals, all but one of these participants met the criteria for passing at least one level of ToM task (first- or second-order), and they did show a robust joint Simon effect (Sebanz et al., 2005b). This finding implies that, despite observable deficits in social cognition, certain aspects of action co-representation may remain sufficiently intact to support joint action processing in ASD. Fulceri et al. (Fulceri et al., 2018) examined whether children with ASD can adapt their movements in joint tasks when they must rely solely on kinematic information to achieve a shared goal. While children with ASD and typically developing (TD) children performed comparably when the movement's end-point was visually specified (Clear End-Point), those with ASD exhibited greater reaction time variability. In contrast, during the Unclear End-Point task, where participants needed to infer the target solely from kinematic cues, children with ASD were less accurate and performed more slowly than their TD counterparts. Notably, their movement patterns did not differ between the two tasks, whereas TD children became more consistent and committed fewer errors when forced to rely on kinematic information alone. These findings show an impaired ability in ASD to use kinematic cues to anticipate and coordinate actions with a partner, thereby underscoring the importance of perceptual-motor coupling in social interactions. In a cross-sectional study examining joint action skills, ASD children and adolescents performed mirroring and complementing tasks with either a co-actor or a nonsocial partner (computer). ASD patients showed more pronounced difficulties with peer dyads and lagged behind age-matched TD peers in overall JA abilities (Bar Yehuda and Bauminger-Zviely, 2024). Leveraging real-world social interactions, Trevisan et al. (2021) conducted an experiment in which children with ASD and TD controls were tasked with moving tables either independently or collaboratively through a maze, an activity requiring strategic action coordination, a key element of the joint action process. Children with ASD were less likely to benefit from peer collaboration and displayed reduced step synchronization compared to TD children. However, these differences were largely attenuated when an adult provided scaffolding. These findings could not be attributed to generalized motor delays in the ASD group. The authors contend that in children with ASD, joint action coordination manifests as atypical synchronization of both cognitive and motor domains.

In conclusion, although many individuals on the spectrum can understand others' goals and intentions, it is evident that they often struggle to share these goals in cooperative joint motor tasks (for a comprehensive review, see Cerullo *et al.*, 2021). This may stem from difficulties in low-level motor processes (e.g., coordinating movements in time and space), possibly due to reduced attention to others' actions or impaired perception of temporal and social cues (Von Der Lühe et al., 2016; Wild et al., 2010). Moreover, sensorimotor impairments, manifesting as altered movement perception, planning, and timing, can inhibit both the

communication of intentions and the coordination of motor interactions in ASD (Casartelli et al., 2016; Cook, 2016). The bidirectional nature of these impaired social exchanges is evident, as typical individuals also report difficulties interpreting autistic individuals' cues (Brewer et al., 2016), whereas people with (high-functioning) ASD find interactions with similar partners more fluid (Schilbach et al., 2013). Thus, multiple layers of joint action processes, i.e., cooperative ability, temporal coordination, and anticipatory motor planning, may be compromised in ASD, with deficits in sensorimotor integration playing a key role (Cerullo et al., 2021). Since the mirror mechanism and ToM processing are central to action representation and prediction (Friston, 2010; Sinha et al., 2014), supporting their function through interventions that foster motor and predictive skills could bolster social interaction outcomes (see Cerullo et al., 2021). Ultimately, incorporating joint action coordination as a specific target in early treatment may enable children with ASD to better develop shared attention, action goals, and intentions, potentially improving their social experiences (Brewer et al., 2016; Casartelli et al., 2016; Cook, 2016).

1.5. The present work and applied techniques

During my PhD, I employed a range of neurophysiological and electrophysiological techniques to investigate the neural mechanisms underlying joint action. In the first study, I used a TMS-EEG paradigm to explore the extent to which collective goals are encoded at the motor level by targeting the primary motor cortex hand area (M1-hand) and the supplementary motor area (SMA). In the second study, I validated a gamified stop-change task with a bimanual design, which I subsequently adapted into a unimanual joint version for a third study. Across these latter two experiments, I combined EMG and EEG measures to determine how inhibitory control is modulated in Joint versus Solo conditions.

1.5.1. Techniques of Study I: MEPs and TMS-EEG

Transcranial magnetic stimulation (TMS) has revolutionized human brain research (Barker et al., 1985) and is currently the method of choice to modulate neural activity in the human brain (Siebner et al., 2022). The TMS pulse induces a transient time-varying electric field in the brain that enables the transient, controlled, and non-invasive perturbation of the activity of neurons located in the cerebral cortex under the coil.

The induced electric field is modulated by the tissue compartments' conductive properties (Aberra et al., 2020) and is most intense in the superficial regions of targeted cortical gyri and the underlying white matter (Siebner et al., 2022). TMS likely activates axons of both excitatory and inhibitory neurons, with each axon's firing threshold dependent on its geometry, myelination, spatial alignment relative to the electric field, and the neuron's physiological state (Di Lazzaro and Rothwell, 2014; Li et al., 2017). Indeed, TMS is inherently state-dependent because the neuron's state is shaped by transsynaptic dendritic and somatic inputs, intrinsic membrane potential, and firing rate (Kasai et al., 1997; Silvanto et al., 2007; Sohn et al., 2003).

Motor-evoked potentials (MEPs) are a central measure of corticospinal excitability in TMS studies. When TMS is applied over the primary motor cortex, it induces descending volleys that activate spinal motor neurons. The resulting electrical response, recorded via surface electromyography (EMG) from a contralateral target muscle, is known as the MEP. The amplitude and latency of MEPs reflect corticospinal pathway excitability and integrity, making them a key physiological index (Siebner et al., 2022). The M1-hand motor cortex is the preferential target when studying the mechanisms of TMS, as this area forms a characteristic knob-like structure (hand-knob), is superficially located, easily identifiable on structural MRI scans, and readily accessible for stimulation (Yousry et al., 1997). The short latency of the resulting MEP indicates that excitation is carried by large, fast-conducting corticospinal fibers forming monosynaptic connections with cervical motor neurons, which is ideal for neurophysiological and neurocognitive research (Siebner et al., 2022). Another

pivotal neurophysiological property of the MEP, and perhaps the most striking illustration of TMS “state dependency”, is that even minimal pre-activation of the target muscle can induce substantial MEP facilitation. This facilitation stems from physiological changes at both spinal and cortical levels, thereby rendering the propagation of neuronal signals more efficient (Lazzaro et al., 1998; Mills et al., 1987; Ugawa et al., 1995).

The neurophysiology underlying MEPs is complex, as they result from synchronized corticomotor excitation of fast-conducting motor neurons and propagation to the subsequent motor units (Siebner and Rothwell, 2003). Given an imperfect physiological synchronization at the cortical, spinal, and muscular level, MEPs show a substantial trial-to-trial variability (Groppa et al., 2012). This means that phase cancellation of descending volleys can substantially reduce MEP amplitude (Magistris et al., 1998). Despite the complexity of its underlying physiology, MEP-based studies have provided important insights into how TMS acts on M1, highlighting the method’s capabilities and limitations that must be recognized when disentangling state-related changes in corticomotor excitability (Spampinato et al., 2023).

However, the cortical perturbation induced by transcranial stimulation is not confined to a single site but rather propagates across multiple cortical regions. An effective way to investigate the cascade of events triggered by this perturbation is to combine TMS with electroencephalography (EEG, Berger, 1929), which provides a favorable balance of good spatial and excellent temporal resolution (Thut and Miniussi, 2009).

The effects of a TMS pulse extend beyond the targeted cortical area, engaging distant cortical and subcortical regions connected via long-range projections (Valero-Cabré et al., 2001). The initial neuronal depolarization beneath the coil generates action potentials that travel along specific anatomical pathways, with trans-synaptic effects dependent on both the strength and the inhibitory/excitatory nature of these connections (Momi et al., 2021; Valero-Cabré et al., 2007). It is also important to recognize that TMS signal propagation is not solely dictated by anatomical connections but it is influenced by the initial functional state of the stimulated area (Silvanto *et al.*, 2007) allowing to study different neurocognitive states and clinical conditions (Bortoletto et al., 2015; Farzan and Bortoletto, 2022; Parmigiani et al., 2023). In fact, the combined use of TMS and EEG provides a unique window into effective connectivity (Bortoletto *et al.*, 2015; Miniussi and Thut, 2010), understood as the causal relationship among brain areas (Friston et al., 2013).

TMS-EEG represents a highly promising methodology for investigating human brain dynamics (Ilmoniemi and Kicić, 2010; Kitajo et al., 2015). The EEG response to TMS can be examined using TMS-evoked potentials (TEPs), which serve as the equivalent of event-related potentials in standard EEG (Chung et al., 2015). TEPs serve as a robust measure of cortical excitability, as they vary with the stimulation site, intensity, and orientation—underscoring their sensitivity—while remaining stable over time, confirming their reproducibility (Casarotto et al., 2010). Most research has examined TEPs generated in the motor cortex (for a recent review, see Beck et al., 2024). However, to the best of our knowledge, only a handful of (recent) studies have investigated TEPs in SMA (Busan et al., 2019; Casula et al., 2024; Casula et al., 2022; Leodori et al., 2024; Salo et al., 2018; Song et al., 2025; Thong et al., 2024).

1.5.2. Techniques of Study II:

Stop-Change Task, partial response EMG, and stop-signal P3 ERP

A core construct of inhibitory control, a key executive function, is response inhibition, i.e., the ability to stop actions reactively (Diamond, 2013). Response inhibition is mainly characterized by the stop-signal reaction time (SSRT), a behavioral measure derived from the Stop-Signal Task (SST, Logan et al., 1984), the most common paradigm for studying inhibition (Verbruggen *et al.*, 2019). In the SST, participants repeatedly respond to a go signal but must inhibit this response whenever a stop signal appears, with a variable delay (stop-signal delay, SSD). The SSRT is estimated (typically via the integration method) from the distribution of

go reaction times, mean SSDs, and the probability of commission errors on stop trials. (Verbruggen *et al.*, 2019). This estimation rests on the independent race (or “horse race”) model, which posits that the go and stop processes independently compete against each other, and whichever process completes first (i.e., “wins” the race) determines whether the action is ultimately executed or inhibited (Band *et al.*, 2003; Logan and Cowan, 1984). Notably, the theoretical basis of this model has neurophysiological plausibility and is well-established in the literature (Boucher *et al.*, 2007a; Boucher *et al.*, 2007b).

A popular extension of the SST is the Stop-Change Task (SCT, Logan, 1994). Both paradigms have identical stimuli and mechanics but differ regarding the number of required cognitive processes. In the SCT, an additional response re-engagement process is involved to initiate an alternative action (elicited by the stop-signal, called change-signal in this case). Thus, while engaged in an SCT, a go process, an inhibition process (Verbruggen *et al.*, 2008) and a re-engagement process is activated, with all three of them mainly operating independently (Boecker *et al.*, 2013). This means that the change-signal RT (CSRT) and SSRT are comparable, as the horse-race model is also applicable to stop-change inhibition (Logan, 1994). Discrepancies between these two measures, usually found when assessed in separate blocks or sessions, are likely caused by the different cognitive demands of the task requirements but not by differences in the underlying inhibitory process (Boecker *et al.*, 2013; Verbruggen *et al.*, 2008).

The SCT more closely reflects everyday behavior than the SST, which measures “pure” response inhibition by requiring complete suppression of actions without subsequent behavioral adjustment. In reality, environmental or internal cues often require us to cancel a planned or ongoing action and then quickly switch to a new, more appropriate response—exactly what the SCT captures. An additional advantage of the SCT is that it provides a second behavioral parameter, the change-response reaction time (change-RT), reflecting the interval between the change signal and the initiation of the alternative action. To avoid ambiguous terminology, hereafter, I will refer to the latency between the change-signal and the resulting inhibition simply as “SSRT” (underscoring the importance of the stop-process), and to the latency between the change-signal and the execution of the alternative action as “change-RT”.

The SST/SCT is a valuable method for investigating reactive inhibition across diverse conditions and settings. Clinically, impairments in effective behavioral control—reflected by slower SSRTs—have been observed in a range of populations, including those with attention-deficit/hyperactivity disorder, obsessive-compulsive disorder, drug abuse, schizophrenia, Parkinson’s disease, and Tourette syndrome (Di Caprio *et al.*, 2020; Jahanshahi *et al.*, 2015; Lipszyc and Schachar, 2010; Mancini *et al.*, 2018a; Mancini *et al.*, 2018b; Smith *et al.*, 2014; Snyder *et al.*, 2015; Wylie *et al.*, 2013; Yaniv *et al.*, 2018). Inhibition deficits found in most of these patient populations could be largely replicated by employing the SCT (Bekker *et al.*, 2005; Fishbein *et al.*, 2007; Geurts *et al.*, 2004).

Nonetheless, growing evidence indicates that SSRT estimations may be unreliable in certain practical settings, particularly in cases of trigger failures (failure to initiate the stop process), pronounced slowing of go responses, or violations of independence assumptions at shorter SSDs (Bissett *et al.*, 2021; Bissett and Logan, 2014; Matzke *et al.*, 2017; Skippen *et al.*, 2019; Verbruggen *et al.*, 2013). Recently, partial response EMG (prEMG) has been introduced as a complementary and more direct physiological measure of response inhibition (Raud *et al.*, 2022). EMG recordings from effector muscles frequently reveal small bursts of muscle activity in successful stop-trials. These bursts represent responses initiated after the go signal but terminated before the muscle activity leads to a button press. This partial response provides a means to determine the precise time point when motor activity begins to decline, indicating the implementation of the inhibitory process (Atsma *et al.*, 2018; Raud and Huster, 2017). PrEMGs serve as a reliable measure of action stopping. While similar to the SSRT, these two measures should not be used interchangeably but rather as complementary measures. SSRT is an indirect metric reliant on assumptions that may not always hold in empirical data and appears more strongly influenced by behavioral strategies compared to prEMGs. In

contrast, the latter provide directly observable action-stopping latencies at a single-trial level, with relatively stable peak latencies. Neither measure serves as an unambiguous marker of neural response inhibition, and they appear to be determined mainly by state-like and situational factors (Thunberg et al., 2024). However, when investigating joint actions and comparing them with individual actions—a comparison inherently situational and state-like dependent—these measures, used together, should offer significant potential for advancing our understanding of the brain mechanisms underlying inhibitory control.

Another area of focus within SST/SCT research, particularly in studies utilizing EEG (and also fMRI), has been the identification and application of a precise and reliable neural index of inhibitory control (Wessel, 2023). The primary challenge arises from the dependency of successful stopping on the precise timing of the inhibition processes in relation to action initiation (Bissett *et al.*, 2021; Boucher *et al.*, 2007a; Schall et al., 2017). This suggests that the distinction between successful and failed stopping may depend less on the involvement of specific brain regions and more on the precise timing of their activation. Given its high temporal resolution, EEG represents an ideal technique for investigating the neural mechanisms underlying inhibitory control. An event-related potential (ERP) proposed since the early 1990s as an index of inhibitory control is the frontocentral stop-signal P3 (also referred to as stop-signal P300, hereafter referred to simply as P3; see De Jong et al., 1990; Kok et al., 2004; Wessel and Aron, 2015b), though not without controversy (e.g., Huster, Messel, Thunberg, & Raud, 2020; Skippen et al., 2020; Thunberg, Wiker, Bundt, & Huster, 2024).

A wealth of studies has provided empirical evidence suggesting that the P3 may serve as an index of inhibitory control during action-stopping (for a recent review, see Hervault *et al.*, 2024). This evidence can be summarized as follows, i) stop-signals elicit larger P3 amplitudes compared to go-signals; ii) P3 onset latency is shorter in successful stop trials compared to failed stop trials; iii) the P3 indexes individual differences in SSRT; iv) P3 onset occurs either earlier or around the same time as the SSRT; v) P3 latencies correlate with physiological markers of motor-system inhibition; vi) P3 amplitudes correlate with reduced force during action-stopping; and vii) modulation of cognitive processes and sub-processes that contribute to stopping performance similarly influences the P3 (Hervault *et al.*, 2024). In conclusion, SSRT, prEMGs, and the stop-signal P3 have been widely recognized as reliable markers for investigating inhibitory control—and seem especially promising for studying response inhibition in joint actions. We are convinced that combining these measures is a promising and comprehensive approach to effectively characterize the cognitive states that shape inhibition when individuals act alone or collaboratively toward a collective goal.

2. STUDY I

2.1 Background

As highlighted in the introduction, coordinating with others is an essential part of everyday life. People frequently engage in joint activities: walking or dancing together, working and playing (video) games, or lifting and moving heavy objects collaboratively. Yet, as theoretical and empirical research on joint action demonstrates, there is a critical difference between genuinely acting together and merely acting in parallel (Bratman, 2013; Gilbert, 1990; Knoblich *et al.*, 2011; Miss *et al.*, 2022; Searle, 1990). Consider two friends walking together versus two strangers randomly walking side by side. In both scenarios, a low-level form of emergent coordination may arise spontaneously, potentially leading to automatic synchronization of their walking paces (i.e., entrainment; Knoblich *et al.*, 2011). However, the key distinction is that the friends share a common goal, whereas the strangers do not. Consequently, a collective goal serves as a fundamental criterion differentiating genuine joint action from mere parallel action (Butterfill, 2015; Butterfill and Sinigaglia, 2023; Sinigaglia and Butterfill, 2020), and lies at the core of higher-level planned coordination (Knoblich *et al.*, 2011). Although the term “joint actions” can be interpreted broadly, in the experiments presented in this thesis, it refers specifically to situations where two or more agents act together and jointly direct at least one shared goal (see Barchiesi *et al.*, 2022).

Core to the understanding of joint actions is how collective goals are represented and how these representations affect action preparation and execution when agents act together. Della Gatta *et al.* (2017) used a two-agent version of the circle-line paradigm (Franz *et al.*, 1991) showing that in the joint condition, participants’ motor outputs were interpersonally coupled, resembling the bimanual circle-line effect known to stem from goal-related motor representations (Garbarini *et al.*, 2014; Garbarini *et al.*, 2013; Garbarini *et al.*, 2012; Jeannerod, 1988; Rizzolatti and Sinigaglia, 2007; Santello *et al.*, 2002; Wolpert *et al.*, 1995). Based on these results, the authors concluded that collective goals could be represented motorically. Several other behavioral studies have indirectly or directly supported the idea that agents’ motor plans may relate to collective goals (Clarke *et al.*, 2019; Dötsch and Schubö, 2015; Meyer *et al.*, 2013; Ramenzoni *et al.*, 2014; Sacheli *et al.*, 2018; Török *et al.*, 2019). On the other hand, direct neurophysiological evidence of whether collective goals are motorically represented remains limited. Previous EEG research focused mainly on how agents plan and monitor their own and others’ actions in joint tasks, suggesting at least some degree of motor involvement in goal representation (Kourtis *et al.*, 2014; Kourtis *et al.*, 2013; Kourtis *et al.*, 2019; Loehr *et al.*, 2013; Novembre *et al.*, 2014).

Importantly, monitoring or representing the other’s action alone does not necessarily indicate a collective goal, as agents can track each other’s actions even when acting in parallel (Atmaca *et al.*, 2011; Baus *et al.*, 2014; Böckler *et al.*, 2012; Sebanz *et al.*, 2005a). In a previous study conducted in our lab, Barchiesi *et al.* (2022) tried to assess collective goal representations by applying a new approach. To identify neural indicators of collective goal representation, the authors compared agents acting together with those acting in parallel or competitively, using TMS to probe motor corticospinal excitability in these different conditions and thereby directly assessing how collective goals might be motorically encoded.

More in detail, the study design implied a turn-based task (the co-actor acted in the first turn, while the participant in the second turn) with four conditions: Joint condition, where a participant and co-actor cooperate to shoot a ball to a common target, winning or losing together; Parallel condition, where each player acts individually on their own target, they win or lose independently; Competitive condition, participants compete to act faster than the other and only one can win; Motor Imagery condition, where the participant played alone and imagined performing the correct response during the first turn, intended as an additional positive control to show that the participant’s motor corticospinal excitability can be manipulated with the experimental setting.

This design contrasts conditions where goals are collective (Joint) vs. individual (Parallel, Competitive), yet participants are compelled to pay attention to the other's actions in all cases (by means of rare catch trials). During the co-actor's turn, a single-pulse TMS was delivered on the participant's left primary motor cortex to measure motor-evoked potentials (MEPs) from the resting right hand over the Extensor Carpi Ulnaris (ECU) and the Flexor Digitorum Superficialis (FDS) muscle, briefly after the co-actor's go-cue presentation (signaling either a finger press or lift action). TMS on M1 directly assesses the engagement of motor processes, allowing the investigation of the content of motoric representations (Cattaneo et al., 2009; Duque et al., 2017). MEP peak-to-peak amplitude served as the primary dependent variable, given prior evidence linking it to action planning, execution, observation, and imagery (Bardi et al., 2015; Cattaneo et al., 2013; Lebon et al., 2019; van Elswijk et al., 2008).

The main prediction was that the participant should covertly implement the co-actor's action plan if the collective goals are motorically represented in the Joint condition. This would manifest in distinct corticospinal excitability modulation in the Joint compared to Parallel and Competitive conditions during the co-actor's cue presentation. In fact, the motor imagery "positive control" showed that MEP amplitude in the ECU muscle increased when participants imagined a finger lift (requiring ECU contraction) compared to imagining a finger press (requiring ECU relaxation), confirming that MEPs could be effectively modulated in the given setting. But contrary to the initial hypothesis, under pre-registered analyses, there was no evidence that participants' ECU MEPs were modulated by the co-actor's action in the Joint condition (Barchiesi et al., 2022). Because of this null result, no further comparison was pursued between the Joint condition and the Parallel/Competitive conditions.

2.1.1 Limitations of Barchiesi et al. (2022)

The null finding of Barchiesi et al. (2022) appears to be in conflict with the above-mentioned body of behavioral (Clarke et al., 2019; della Gatta et al., 2017; Meyer et al., 2013; Sacheli et al., 2018; Török et al., 2019) and electrophysiological (Kourtis et al., 2014; Kourtis et al., 2013; Kourtis et al., 2019; Loehr et al., 2013; Novembre et al., 2014) work suggesting that when acting together, agents represent both their own and their partner's actions as if performing the entire action themselves.

Furthermore, the authors assumed a low sensitivity of the pre-registered dependent variable (ECU MEPs) and devised a new dependent variable to reduce noise from non-specific factors by including the contribution of both ECU and FDS, i.e., the difference between z-scored FDS and ECU MEPs. Ideally, this difference is positive in "lifting" trials (maximum activation of ECU and minimal activation of FDS), while it is negative in "pressing" trials (minimal ECU activation, maximum FDS activation). The comparison between trial types (lift vs. press trials) only revealed a trend in the hypothesized direction ($t = 1.51$, $df = 35$, $p\text{-value} = 0.07$; Cohen's $d = 0.25$). Still, this trend in the postulated direction possibly suggests that the experimental approach, with appropriate modifications, could be valid for demonstrating a motor representation of collective goals.

Consequently, given that the experiment was lengthy, with conditions being motorically identical and administered sequentially, the authors ran further exploratory analyses with a reduced dataset, including only the first block, to control the effect of task-switching and fatigue (at the expense of diminished sample size; $n = 13$). By taking the ECU-FDS difference as a dependent variable (providing a slightly larger effect size), the one-tail paired sample t-test showed a significant difference between press vs. lift trials in the joint condition ($t = 2.30$, $df = 12$, $p\text{-value} = 0.02$; Cohen's $d = .64$). Thus, while this study did not detect, as hypothesized in the pre-registered analysis, a significant MEP modulation driven by the co-actor's action during the joint task, it still offers valuable insights into methodological refinements that future studies could implement.

2.1.2 Design of the new study and aims

To address the limitations identified in Barchiesi et al. (2022), we made substantial modifications to the original paradigm and implemented these in a new experiment, which I was responsible for conducting. Given that the study by Barchiesi et al. (2022) likely suffered from an excessively long experimental session with too many conditions and an overly abstract shared goal in the joint condition, key modification entailed reducing the experimental conditions from four to two (a Solo and a Joint condition) and providing more concreteness to the shared goal among participants. Rather than simply moving balls, in the new task, participants would “assemble” a tandem bicycle or a monocycle, depending on the condition. The aims of Study I are listed below, followed by the corresponding hypotheses and predictions.

1. *Aim 1: The first aim, consistent with the original study, is to determine whether participants engaged in joint actions covertly implement their co-actor's action plan and whether collective goals are represented at the motor level. If this is the case, we hypothesize that by stimulating M1, distinct modulation of corticospinal excitability can be observed in the Joint condition compared to the Solo condition during the co-actor's cue presentation. Specifically, we predict that combining antagonist muscle MEPs (calculated as the difference between ECU and FDS responses) will provide the most robust approach to isolating collective goal representations in the motor system. In this framework, we expected significant differences between “lifting” and “pressing” trials in the Joint condition, whereas no significant differences are anticipated in the Solo condition.*
2. *Aim 2: Given that in Barchiesi et al. (2022) did not utilize neurophysiological markers beyond MEPs, this experiment implemented TMS-EEG co-registration. Accordingly, the second aim of this study is to assess cortical excitability by examining TMS-evoked potentials (TEPs). To do this, we aim to investigate the motor system activity by means of M1 TEPs and the involvement of brain regions associated with more abstract motor processing. Given the supplementary motor area's (SMA) established role in domain-general sequence processing (Cona et al., 2017; Cona and Semenza, 2017) and action outcome monitoring (Bonini et al., 2014), we applied TMS to this region in a separate block to assess its cortical excitability and involvement in joint actions. Thus, the second aim of the study is to also assess TEPs following stimulation of SMA. Due to the absence of specific hypotheses regarding the exact neural circuits involved at the level of M1 and SMA, we adopt an exploratory approach to the TEP analysis and refrain from making precise predictions about TEP characteristics. Furthermore, we refrain from formulating any predictions about its effect on behavior.*

2.2. Methods

2.2.1. Power analysis, participants, and general procedures

We estimated the sample size before starting data collection based on the exploratory analysis (described in section 2.1.1) of the above-mentioned study (Barchiesi et al., 2022). I computed the sample size estimation for a one-tailed paired t-test with G*Power (3.1.9.7, Faul et al., 2007). Using a power of 95% and a statistical significance of 5%, the power analysis resulted in a sample size of 28 participants. In total, we enrolled 34 healthy right-handed volunteers (range: 20-45 years) without any history of neurological or psychiatric disorder. Participants were first screened for conditions incompatible with TMS use (see Rossi et al., 2021; Rossi et al., 2009). Handedness was assessed by the Edinburgh Handedness Inventory (Mean [M] $\pm$ standard deviations [SD]: 92.3 $\pm$ 14.3; Oldfield, 1971). The screened participants subsequently provided written informed consent and received single-pulse TMS to locate the motor hot spot and identify the resting motor threshold (rMT). Three participants had a rMT above 84% of the maximum stimulator output (MSO) and were excluded. Due to technical issues, the electromyographic signal (EMG) of one participant was not recorded. The experiment was comprised of a single session, lasting about 3 h, including about 1.5 h for the session set

up (EEG/EMG montage, hotspot location, and rMT) and 1.5 h for testing (also counting 15 min for instructions and training, plus 15 min for short pauses between each block). No adverse effects due to TMS application were reported. The final sample consisted of 30 participants for the MEP analysis (18 females, $M \pm SD$: 25.2 $\pm$ 4.9 years) and 31 participants for the TMS-EEG analysis (19 females, $M \pm SD$: 25.3 $\pm$ 4.9 years). If applicable, participants received monetary reimbursement for travel expenses. The study has been approved by the Ethical Committee of the IRCCS Istituto Centro San Giovanni di Dio Fatebenefratelli (Brescia 25/2020) and was conducted in accordance with the ethical standards of the Declaration of Helsinki.

2.2.2. Task setup

The task was adapted from Barchiesi et al. (2022). Experiments were conducted in an electromagnetically shielded, dimly lit, and sound-attenuated room to minimize external noise and interference. Upon the participant's arrival, they were explicitly informed that the task involved collaboration with another individual, as it was a joint action task. They were also notified that the co-actor would not undergo TMS stimulation or EMG recordings. The co-actor was a member of the lab who acted as a naïve participant. A total of six lab members alternated as co-actors across experiments (mean age: 24.7 years; all female). Participants and co-actors were seated side by side, with participants on the left and co-actors on the right, as this arrangement corresponded to the sequence of stimuli presented during each turn (see fig. 1). Both individuals each faced identical screens positioned approximately 60 cm away (eye-to-screen distance, ASUS VG248QE; refresh rate: 60 Hz, resolution: 1920 $\times$ 1080, dimensions: 61 cm $\times$ 34.4 cm). Participants rested comfortably on a chinrest to maintain stability during stimulation. Both individuals placed their forearms on the table in a comfortable position, resting their fingers on a flat pressure sensor affixed to the table (4 cm $\times$ 5.5 cm, model RP-S40-ST). They were instructed to make contact with the index, middle, and ring fingers on the sensor, pressing down or lifting their hand in a shovel-like motion. Participants were also instructed to relax their musculature immediately after completing the action to minimize EMG bursts that could interfere with MEP measurements. In the Joint condition, participants alternated actions with a co-actor, pressing or lifting a sensor in sequence with the shared goal of constructing a virtual tandem bike. This was achieved by operating two stylized pinball-like shooters that propelled the right wheel (initiated by the co-actor during the first turn) or the left wheel (initiated by the participant during the second turn). In the Solo condition, participants performed the task independently, as the co-actor's turn was replaced by an automatic turn in which the wheel moved autonomously. The co-actor waited outside the room. Participants responded to identical cues to construct a virtual monocycle, positioned on the left side of the screen. Unlike the previous study (Barchiesi *et al.*, 2022), the co-actor actively performed the task rather than merely pretending to do so. Additionally, both the participant and the co-actor performed the task using their right hand, whereas in the previous study, participants used their left hand. To prevent participants from observing their own or the co-actor's hand movements, both right hands were concealed beneath a cardboard box. As in Barchiesi et al. (2022), catch trials were included during the co-actor's or automatic turn, and participants with commission error rates exceeding 50% in any condition would have been excluded; however, no participants exceeded this threshold. A custom-made script developed in MATLAB® and Psychophysics Toolbox 3 (Brainard and Vision, 1997; Kleiner et al., 2007) was used to display stimuli and control events on the screens.

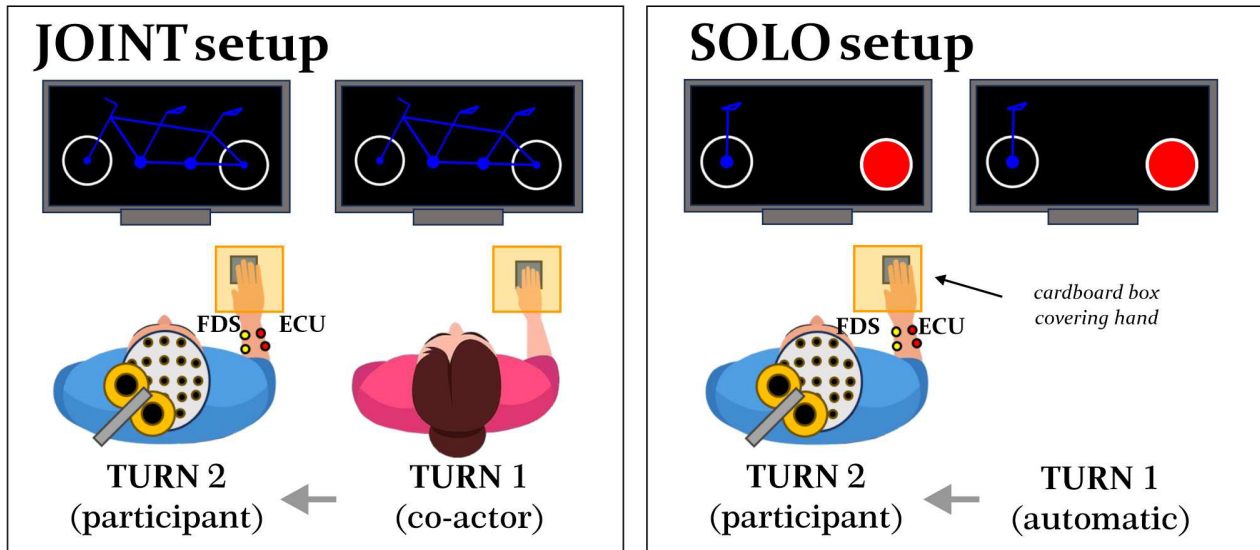
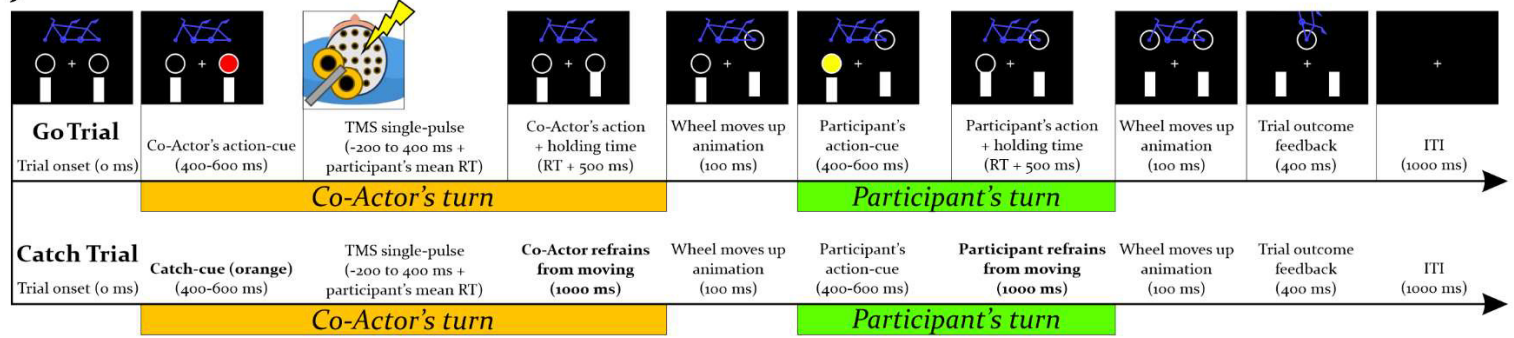


Figure 1: Experimental setup in the Joint condition (left panel) and the Solo condition (right panel). In the Joint condition, the participant (right) and the co-actor (left) sat side-by-side, each viewing the same task scene on separate screens. Both individuals' right hands were covered by a cardboard box to minimize visual distractions. During the co-actor's turn (Turn 1), a single TMS pulse was delivered to the participant's left motor cortex to evoke motor-evoked potentials (MEPs) in the Extensor Carpi Ulnaris (ECU) and Flexor Digitorum Superficialis (FDS) muscles of their right hand. The task involved collaboratively building a tandem bicycle, with the participant taking over during Turn 2. In the Solo condition, the participant performed the task independently while the co-actor was absent. The co-actor's turn (Turn 1) was replaced by an automatic turn, where the system acted autonomously based on preprogrammed timings. The participant's task was to construct a monocycle in the Solo condition, following the same procedures for Turn 2 as in the Joint condition. The experiment included simultaneous co-registration of TMS and EEG, and both conditions shared identical timing and task mechanics to ensure comparability between the Joint and Solo setups.

2.2.3. Trial time-sequence and experiment structure

As previously mentioned, within each trial, the task was performed sequentially by the players in two turns: first the co-actor's turn, followed by the participant's turn. Before the trial onset, sensor pressure was monitored to detect any potential involuntary finger lifting by either individual. If insufficient pressure was detected on one of the sensors, a warning message ("Please, place your fingers on the sensors") was displayed until the fingers were correctly positioned. Once adequate pressure was detected, the trial began with the co-actor's turn.

JOINT TASK



SOLO TASK

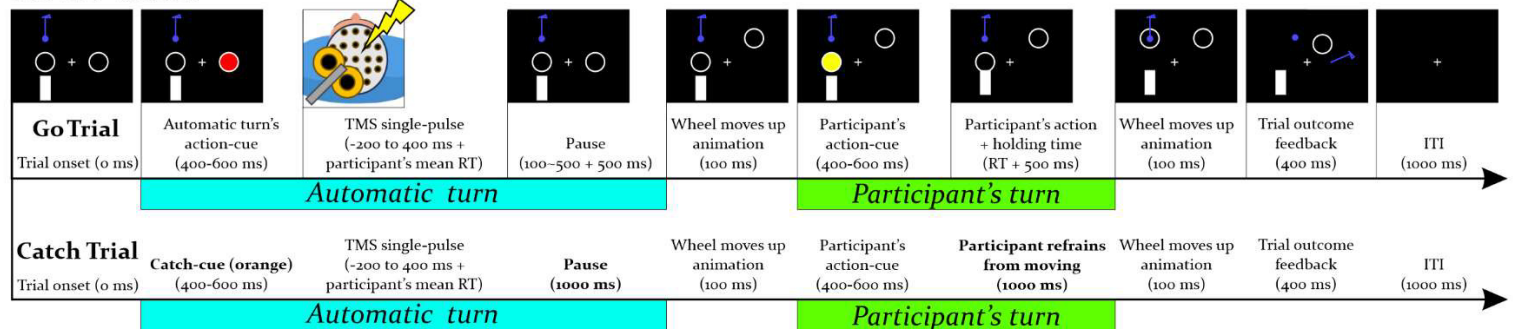


Figure 2: Overview of the trial structure for the Joint and Solo tasks. This figure illustrates each condition's progression and timing of events, highlighting key differences between conditions. In the Joint task (top panel), the trial began with the display of two pinball-like shooters (white rectangles), two wheels (white circles), a blue tandem bike frame (top), and a central white fixation cross. The right shooter was controlled by the co-actor, who always acted first, and the left shooter by the participant, who acted second. After a delay (400–600 ms), the co-actor's wheel (on the right) briefly changed color to red (press), yellow (lift), or orange (catch trial). A single transcranial magnetic stimulation (TMS) pulse was delivered to the participant at a pseudo-randomized interval (-200 to 400 ms) relative to the participant's mean reaction time (RT; computed by tracking their performance in their turn). In catch trials, both the co-actor and participant withheld their actions. Thereafter, the wheel moved and attached to the rear of the bike (regardless of the co-actor's performance). Following a delay (400–600 ms), the participant's action cue (red or yellow) appeared inside the left wheel, signaling their turn. After the left wheel was propelled to the front of the tandem bike, the final feedback animation (400 ms) revealed the trial outcome: successful trials showed the assembled bike moving upward, while failed trials displayed the bike breaking apart. After, a 1 second long black-screen with fixation-cross, served as inter-trial interval (ITI). In the Solo task (bottom panel), the co-actor's turn was replaced by an automatic turn. The wheel moved autonomously following its color change (red, yellow, or orange), mimicking the co-actor's timing. A TMS pulse was delivered with the same timings. Trial feedback was similar to the Joint task, with successful trials showing the monocykle assembling and moving upward, while failed trials depicted it disassembling. The ITI and task mechanics for participant actions remained consistent with the Joint task.

In the joint condition, at the onset of the turn, the screen displayed the following elements: two pinball-like shooters (stylized as white rectangles at the bottom of the screen), two wheels (stylized as white circles in the middle), a blue tandem bike structure (without wheels, at the top), and a central white fixation cross on a black background, as shown in fig. 2 (top panel).

Congruently with their seating position (fig. 1), the co-actor controlled the right pinball-like shooter while the participant controlled the left one. After a variable pseudo-randomized delay of 400–600 milliseconds (ms), the black interior of the co-actor's wheel changed color (red, yellow, or orange) for 67 ms before returning to black. This visual cue indicated what action the co-actor should perform: red signaled a press, yellow signaled

a lift, and orange indicated a catch trial. The task script kept track of the participant's average reaction time (RT). At a pseudo-randomized interval ranging from -200 to 400 ms after the tracked mean RT, a single TMS pulse was delivered to the participant before any animation appeared on the screen. In case of a catch trial, both individuals were required to withhold any movements: the co-actor immediately, and the participant after, during their own turn. Otherwise, the co-actor performed the cued action, triggering the shooter towards the wheel after a 500 ms delay, which also served as the holding time. The shooter's impact on the wheel propelled it toward the tandem bike structure, fitting the wheel onto the rear side of the bike (right side). If the co-actor acted too slowly or did not respond in time, the shooter animation started anyway.

Following a pseudo-randomized delay of 400–600 ms, the participant's action cue appeared inside their designated wheel (on the left side) as a color change to either red (indicating a press) or yellow (indicating a lift) for 67 ms, signaling the start of the second turn. The brief presentation of the color cue in both turns was designed to encourage players to focus closely on the wheels. Unless a catch trial was signaled during the co-actor's turn (requiring the participant to pay attention to the co-actor's cue), the participant performed the corresponding action and maintained it for at least 500 ms (holding time) to trigger the shooter and propel the wheel toward the front position of the tandem bike. As in the previous turn, if the action performed was incorrect or slower than 500 ms, the shooter still pushed the wheel to its position. Unlike Barchiesi et al. (2022), where the response window was set to 1 second, we reduced the upper RT limit to 500 ms to encourage participants to perform actions as quickly and reactively as possible, thereby strengthening the stimulus-response association. The trial concluded with feedback in the form of an animation lasting 400 ms: for successful trials, the tandem bike rotated 90 degrees upward and exited the screen by moving upward; for failed trials, the bike broke apart into two pieces and fell down the screen, indicating that at least one player had made a mistake. A new trial began after a 1-second interval displaying a black screen with a fixation cross.

In the Solo condition, the trial mechanics remained largely the same, with the participant performing the task independently while the co-actor waited in a nearby room. As previously described, the co-actor's turn was replaced by an automatic turn in which the wheel moved autonomously after changing color. Again, the only relevant color for the participant during the automatic turn was orange, indicating a catch trial. Following the visual cue, a TMS pulse was delivered at the same timing as in the joint condition (-200 to 400 ms relative to the participant's tracked mean RT), while the animation started after a pseudo-randomized delay of 100–600 ms, mimicking the average co-actor's timing. In the second turn, participants responded to the same cues to construct a virtual monocycle positioned on the left side of the screen and replacing the tandem bike structure. Similar to the joint condition, failed trials were represented by the monocycle disassembling into various parts, while successful trials were depicted by the monocycle rotating and moving upward off the screen.

Considerable attention was given to providing clear instructions and adequate training, administered to both players jointly. Instructions were delivered using a comprehensive set of 38 slides, providing an exhaustive explanation of the task mechanics to ensure participants were thoroughly prepared. They were instructed to fixate on the white cross all the time during the task. Participants were informed preemptively that if an error occurred during the joint condition, the responsible individual would not be identified, and the trial would be marked as failed due to the collective nature of the task. Emphasis was placed on the distinction between the two conditions: in the solo condition, the goal was individual, with independent performance, whereas in the joint condition, the goal was shared, requiring collaborative performance. Each condition consisted of three blocks of 100 trials, each lasting approximately 10 minutes and corresponding to the three types of stimulation (M1, SMA, and sham). The order of the conditions and blocks was counterbalanced across participants using a Latin square design to minimize potential order effects. Each block consisted of 40 lift, 40 press, and 20 catch trials.

2.2.4. MEPs acquisition and TMS-EEG setup

We acquired EEG signals using 74 TMS-compatible passive Ag/AgCl electrodes (EasyCap, BrainProducts GmbH, Munich, Germany) and a TMS-compatible amplifier system g.Hlamp, g.tec Medical Engineering GmbH, Schiedlberg, Austria) at a sampling rate of 9600 Hz. Recordings were made without applying filters, and skin-electrode impedance was maintained below 5 k Ω . We stimulated the participant's target areas using a Super Rapid2 transcranial magnetic stimulator connected to a 70-mm figure-of-eight coil (Magstim Company, Whitland, UK), eliciting a biphasic waveform (charge delay set at 350 ms). To minimize sensory artifacts contaminating the TEPs, participants were asked to wear noise-canceling earphones producing white noise. EMG signals were amplified alongside the EEG electrodes and recorded from the ECU and FDS muscles on the resting right forearm using pairs of disposable surface electrodes in a bipolar montage. A band-pass filter between 10 and 2500 Hz and a notch filter were applied for visualization purposes only.

The left M1 was functionally identified: The cortical hotspot, defined as the region eliciting the largest MEPs on average in both ECU and FDS, was identified by positioning the coil approximately 3–4 cm lateral to the vertex. Single pulses were delivered at 30% of MSO and gradually increased in ~5% steps up to 70% MSO. This stepwise procedure allowed participants to acclimate to the experimental setup and the sensations of TMS stimulation. We performed a grid search over the left hemisphere to locate the precise hotspot by systematically moving the coil in ~1 cm increments within a circular area approximately 4 cm in diameter. Coil orientation was kept approximately at 45° from the midline such that the current flow direction in the left M1 during the second phase of the biphasic pulse waveform was posterior-to-anterior (Siebner *et al.*, 2022; Sommer *et al.*, 2006). Once the hotspot was identified, we estimated the rMT for the ECU/FDS muscles using the maximum-likelihood threshold-hunting algorithm, a variant of the Parameter Estimation by Sequential Testing (PEST) algorithm (Awiszus, 2003; 2011; Rossi *et al.*, 2021; Rossi *et al.*, 2009). The rMT was defined as the minimum stimulation intensity that elicited an MEP of at least 50 μ V in both muscles. The TMS intensity was set at 120% of the rMT throughout the experiment, and participants were stimulated during each trial.

For SMA stimulation, or more accurately, the SMA-complex (given the low spatial resolution of TMS, we cannot exclude also the partial stimulation of pre-SMA, see Casula *et al.*, 2022), we selected FCz as the stimulation site. This position was sufficiently anterior to avoid current spread to M1, which could otherwise elicit MEPs in shoulder, trunk, or lower limb muscles. Most studies agree that the optimal site for targeting the SMA is between 2 and 4 cm anterior to the vertex (Cona *et al.*, 2017; Cunnington *et al.*, 1996; Hamada *et al.*, 2008; Janssen *et al.*, 2015; Matsunaga *et al.*, 2005; Oliveri *et al.*, 2003; Serrien *et al.*, 2002; Terao *et al.*, 2007; Verwey *et al.*, 2002). Based on the dimensions of our EEG caps, the FCz electrode was positioned between 3.3 cm and 4 cm anterior to Cz. The coil was oriented approximately 0° relative to the midline, ensuring that current flow in the underlying cortex was directed posterior-to-anterior. This orientation is supported by findings that both early and late TEP peaks, as well as local mean field potentials (a measure of cortical excitability), are enhanced when the SMA is stimulated in a posterior-to-anterior direction (Casula *et al.*, 2022). For sham stimulation, the coil was positioned over the Cz electrode at 0° relative to the midline, with a plastic spacer of approximately 3 cm separating the coil from the scalp. The participant's head fiducials were co-registered to a standard 3D head reconstruction, enabling the use of a neuronavigation system (SofTaxic 3.4.3, E.M.S., Bologna, Italy) to ensure precise coil positioning and stability at the identified hotspot throughout the session.

2.2.5. Computation of the muscular engagement index and EMG-accuracy

To evaluate participants' muscular engagement during their turns in response to the action cues, we calculated a muscular engagement index by subtracting the absolute z-scored FDS EMG activity from the absolute z-scored ECU EMG activity. This computation was performed for the time window spanning cue presentation to 1 second afterward. The resulting values were then divided by the sampling rate (9600 Hz) to normalize the index. This index served as an additional behavioral measure, reflecting the movement direction based on muscle activity: lift actions yielded positive values, while press actions resulted in negative values (maximum activation of ECU and minimal activation of FDS and vice versa, respectively). This EMG-based engagement measure directly captures the participant's muscle activation, providing a more accurate reflection of their intended motor response, essential for reinforcing a strong stimulus-response association. Additionally, given the relatively high number of 'no response' trials, we utilized the muscular engagement index to classify also these trials, where participants probably responded to slowly. This approach allowed us to calculate an accuracy parameter based on EMG activity rather than relying solely on sensor output, which was constrained by a strict upper RT limit and a long holding time. Classification thresholds for these 'no response' trials were determined as follows: for each participant, the muscular engagement index was calculated for each trial, and only correctly executed lift and press trials were retained. Correct lift trials were sorted in ascending order, and press trials in descending order. The value corresponding to the 10th percentile (i.e., the trial at the 10% mark) was selected as the classification threshold for each action type, such that 'no response' trials with an index higher than the 10th percentile of correct lift trials were classified as 'lift' and those smaller than the 10th percentile of correct press trials as 'press'. The index was plotted individually for each participant and visually inspected to confirm that the lift and press thresholds were appropriately positioned. Using this classification, we computed adjusted accuracy values (hereafter referred to as EMG-accuracy). In contrast, standard accuracy based on actions executed within the upper RT, defined as the proportion of correct responses relative to the total number of lift and press trials from the sensor output, will hereafter be referred to as behavioral accuracy.

2.2.6. Statistical analysis of behavior

To ensure that participants demonstrated acceptable and comparable performance across all experimental blocks, we conducted a series of analyses on the behavioral parameters. First, to verify that participants were effectively attentive during the co-actor's turn, we conducted a two-way repeated-measures analysis of variance (rm-ANOVA) on catch trial accuracy, with condition (levels: solo, joint) and stimulation-type (levels: M1, SMA, sham) as within-subject factors.

Second, to confirm an adequate stimulus-response association in go trials, we conducted a two-way rm-ANOVA on EMG-accuracy (see section 2.2.5.) with condition (levels: solo, joint) and trial-type (levels: lift, press) as within-subject factors.

Finally, we assessed participants' general movement speed and precision. As the participants' turn always followed the co-actor's turn, we also examined whether trial congruence (both turns involving the same action cue) influenced behavioral performance. Two separate three-way rm-ANOVAs were conducted, with RTs and behavioral accuracy as dependent variables, and congruence (levels: congruent, incongruent), condition, and stimulation-type as within-subject factors.

2.2.7. MEPs preprocessing and statistical analysis

To minimize potential biases, MEPs were analyzed as blinded data. A band-pass filter (10–2500 Hz) and a 50 Hz notch filter were applied offline to reduce artifacts. Peak-to-peak amplitudes were calculated for each MEP within an individualized 10 ms to 50 ms post-TMS pulse window by subtracting the lowest peak from the highest. Artifactual activity was visually checked and corrected. To reduce variability, we ensured that both ECU and FDS were relaxed before TMS pulses, classifying a muscle as relaxed if pre-stimulation EMG activity did not exceed ± 100 μ V peak-to-peak amplitude within 50 ms before the pulse. Trials exceeding this threshold or with MEP amplitudes below 50 μ V were excluded. Mean MEPs were then calculated for each condition (Wilcox, 2009). We stimulated during every trial, resulting in up to 40 trials per action cue (lift and press) per block within each condition. This sample size exceeds typical TMS studies and meets recommendations for high MEP reliability and statistical power (Bastani and Jaberzadeh, 2012; Biabani et al., 2018). As TMS was delivered at a pseudo-randomized interval ranging from -200 to 400 ms relative to each participant's tracked mean RT, we assessed whether stimulation timings were consistent across blocks to rule out any systematic bias. Specifically, we ran two separate repeated-measures ANOVAs on (1) the delay between the visual color cue (the co-actor's go signal) and the TMS pulse, and (2) the latency (positive or negative) between the tracked mean RT and the pulse, with condition (solo vs. joint) and stimulation type (M1, SMA, sham) as within-subject factors.

If collective goals are represented motorically, participants should encode the co-actor's hand actions in accordance with the cues presented during the co-actor's turn. Therefore, we hypothesized greater corticospinal excitability in the FDS and ECU muscles during the co-actor's press and lift trials, respectively. Conversely, MEP peak-to-peak amplitudes were expected to be reduced in the opposing trials (i.e., ECU during press trials and FDS during lift trials). As preliminary control analyses, we conducted three-way mixed-design ANOVAs on ECU-MEPs and FDS-MEPs to examine the effects of condition (levels: solo, joint) and trial-type (levels: lift, press) as within-subject factors. Additionally, participants were divided into two groups based on the order of conditions administered (between-subject factor: joint-first, solo-first) to investigate potential priming or fatigue effects.

As already mentioned, in our lab's prior study (Barchiesi *et al.*, 2022), analyses of the motor imagery condition (used as a positive control) showed a greater effect size when using the difference between ECU and FDS MEPs as the dependent variable, compared to analyzing individual muscles. This approach enhances the likelihood that any positive findings reflect motor representations of collective goals while minimizing confounding effects, such as arousal or other non-specific influences on MEP amplitudes. Accordingly, the difference in MEPs for lift and press trials was used as a measure of selective modulation of the muscles involved in these actions.

To address the primary aim of this study, we conducted a two-way repeated-measures ANOVA with the ECU-FDS MEP amplitude difference as the dependent variable, and condition (levels: solo, joint) and trial-type (levels: lift, press) as within-subject factors. When necessary, Greenhouse-Geisser corrections were applied to account for violations of sphericity, and post hoc analyses were corrected using the Bonferroni method. If the dependent variable was not normally distributed, z-score transformations were applied.

2.2.8. TEP preprocessing and statistical analysis

The preprocessing pipeline was adapted from our previous studies (Bortoletto et al., 2021; Guidali et al., 2023; Zazio et al., 2022). Analyses were performed in MATLAB R2023a (The Mathworks, Natick, MA, USA) using custom scripts with both, EEGLAB v.2023.1 (Delorme and Makeig, 2004), and FieldTrip (Oostenveld et al., 2011) functions (default parameters, unless specified otherwise). Continuous TMS-EEG data was interpolated

for 3 ms around the TMS trigger, high-pass filtered at 1 Hz (using EEGLAB's windowed sync FIR filter function 'pop_eegfiltnew'), down-sampled at 4800 Hz and epoched around the TMS pulse from 700 ms before to 800 ms after the stimulation. Then, for each participant, we merged all blocks and applied the source-estimate-utilizing noise-discarding (SOUND) algorithm (spherical 3-layer model, regularization parameter: $\lambda = 0.1$; Mutanen et al., 2018) to discard noise measurement. A first automatic artifact rejection was performed (EEGLAB function 'pop_jointprob') with global and local limits set to 5 SD deviations to discard highly artifactual trials. Thereafter, we run an independent component analysis (ICA) for ocular artifact correction and components relative to horizontal and vertical ocular movements were visually inspected and discarded by two independent researchers (EEGLAB function 'pop_runica', infomax algorithm, 73 channels included with an equal number of computed components). To remove TMS-evoked muscular artifacts in the first 50 ms after pulse from the M1 blocks, we separated only these two blocks from our merged data and applied a signal-space projection and source-informed reconstruction algorithm (SSP-SIR, Mutanen et al., 2016). The computed principal components were visually inspected by two independent researchers and discarded if they showed a high-frequency signal time-locked the TMS pulse (3.9 ± 1.0 SSP-SIR components were removed on average). Finally, we split our data back to the original blocks, removed the signal from 0 to 8 ms after the TMS pulse, and, after a low-pass filter at 100 Hz (IIR Butterworth filter, order 4, using the EEGLAB function 'pop_basicfilter'), we performed a second automatic artifact rejection with limits set to 3 SDs. Data was off-line re-referenced to the average of the left and the right mastoids (TP9/10), epoched from -100 to 400 ms, baseline corrected in the 100 ms to 5 ms preceding the pulse and averaged according to the experimental conditions. No channels were excluded, and after preprocessing, an average of $6.9 \pm 2.2\%$ of the trials in each condition were discarded from further analyses. TEPs were compared using cluster-based permutation tests for dependent samples (FieldTrip function 'ft_timelockstatistics') approximated with a Monte Carlo procedure using 1000 permutations (Maris and Oostenveld, 2007).

2.3. Results

2.3.1. Behavioral results

Our behavioral parameters were primarily used to assess performance and confirm consistency across all experimental conditions. Participants' behavioral performance was generally good. No participant was excluded due to insufficient accuracy in catch trials (0.88 ± 0.07 , $M \pm SD$). Only two participants scored below 70% accuracy in one of the two conditions (62% and 67%). To ensure homogeneity across blocks, we conducted a two-way non-parametric aligned rank transform analysis of variance (ART-ANOVA, Leys and Schumann, 2010) on catch trial accuracy (0.88 ± 0.13 , $M \pm SD$) with Condition (levels: Joint, Solo) and Stimulation Type (levels: M1, SMA, Sham) as within-subject factors. No significant differences were found (see Table 1).

**Repeated Measures Aligned Rank Transformed ANOVA on catch accuracy:
Condition (Joint, Solo) $\times$ Stimulation Type (M1, SMA, Sham)**

	Df	Residual Df	F-value	p-value
Condition	1	150	1.11412	0.29289
Stimulation	2	150	1.57706	0.20999
Condition:Stimulation	2	150	0.24058	0.78648

Table 1: Results of the non-parametric repeated measures Aligned Rank Transformed analysis of variance (ART-ANOVA, Leys and Schumann, 2010) on Catch Trial Accuracy, with Condition (Levels: Joint, Solo) and Stimulation Type (Levels: M1, SMA, Sham) as within-subject factors. Df, degrees of freedom.

Due to the intentionally fast task pace (with a 500 ms upper RT limit) and the extended holding time (500 ms), several trials were recorded as ‘no response,’ even when participants may have attempted the correct action. To assess consistent muscular engagement across blocks, we conducted a two-way ANOVA (with Condition and Stimulation Type as factors) on EMG-accuracy (0.86 ± 0.13 , $M \pm SD$), which also revealed no significant differences. All participants achieved at least 65% EMG-accuracy.

We performed three-way repeated-measures ANOVAs on mean reaction times (RTs) and behavioral accuracy, by including an additional Congruence factor (action-cue congruence between participants and co-actors within the same trial; levels: Congruent, Incongruent). Significant effects emerged only in the analysis of behavioral accuracy (fig. 3).

First, a significant main effect of Stimulation Type was observed ($p = 0.021$, $\eta^2 = 0.122$), though none of the post hoc comparisons survived Bonferroni correction. Second, a significant main effect of Condition was found ($p = 0.030$, $\eta^2 = 0.147$, fig. 3A), with participants performing less accurately in the Joint condition compared to the Solo condition (0.71 ± 0.11 vs. 0.75 ± 0.10 , $M \pm SD$). Lastly, a significant main effect of Congruence ($p = 0.020$, $\eta^2 = 0.168$) indicated higher accuracy in congruent trials compared to incongruent ones ($M_{diff} \pm SD = 0.03 \pm 0.13$, fig. 3B).

Given that the co-actors, who acted to be a naïve participants but were actually lab members, we also examined their behavioral performance during the joint condition. As expected, the co-actors demonstrated high accuracy during catch trials (0.89 ± 0.05 , $M \pm SD$). Additionally, their behavioral accuracy during lift and press trials was significantly higher (0.86 ± 0.07 , $M \pm SD$) compared to the participants (0.71 ± 0.10 , $M \pm SD$; $t(50.87) = -6.41$, $p < .001$). To assess whether the co-actor's performance influenced participant performance, we computed block-wise correlations between the co-actors' and participants' accuracies. The results indicated no statistically significant relationships in the M1 block ($r = 0.06$, $t(29) = 0.33$, $p = 0.742$), sham block ($r = 0.04$, $t(29) = 0.20$, $p = 0.842$), or SMA block ($r = 0.20$, $t(29) = 1.10$, $p = 0.281$).

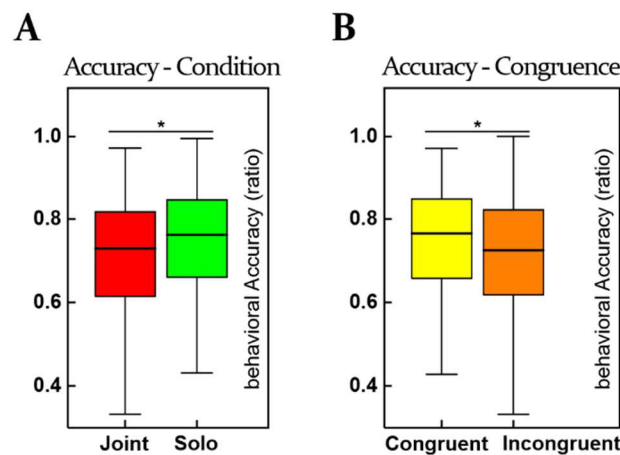


Figure 3: Significant results for behavioral accuracy (ratio), i.e., standard accuracy based on actions executed within the upper RT, defined as the proportion of correct responses relative to the total number of lift and press trials as recorded from the sensor output. (A) Behavioral accuracy by Condition, showing significantly lower accuracy in the Joint condition compared to the Solo condition. (B) Behavioral accuracy by Congruence, with significantly higher accuracy observed in Congruent trials compared to Incongruent trials. For all panels, the box plots represent the median (horizontal line within the box), the interquartile range (IQR; the height of the box), and the whiskers extend to 1.5 times the IQR or the furthest data point within that range. Outliers are represented as individual points outside the whiskers. Asterisks (*) indicate statistically significant differences.

2.3.2. MEPs

As a preliminary analysis, we examined whether delivering TMS at a randomized latency relative to each participant's mean RT introduced any systematic bias. We tested for any effect of condition or stimulation type on the cue-TMS delay and RT-TMS latency but found no significant differences in either measure (see Table 2).

Repeated Measures ANOVA on Cue-TMS Delay: Condition (Joint, Solo) × Stimulation Type (M1, SMA, Sham)						
	Df	Residual Df	MSE	F-value	Partial η^2	p-value
Stimulation	1.96	58.74	0.00048	0.38	0.012	0.683
Condition	1.00	30.00	0.00032	0.39	0.013	0.535
Stimulation:Condition	1.95	58.59	0.00035	1.91	0.060	0.159

Repeated Measures ANOVA on participants' mean RT-TMS Latency: Condition (Joint, Solo) × Stimulation Type (M1, SMA, Sham)						
	Df	Residual Df	MSE	F-value	Partial η^2	p-value
Stimulation	1.66	49.73	0.000170	1.35	0.043	0.266
Condition	1.00	30.00	0.000025	0.20	0.006	0.662
Stimulation:Condition	1.66	49.94	0.000153	0.94	0.031	0.381

Table 2: Results of the repeated measures ANOVA on Cue-TMS Delay and mean RT-TMS Latency. The analysis includes Condition (Levels: Joint, Solo) and Stimulation Type (Levels: M1, SMA, Sham) as within-subject factors. ANOVAs did not yield any significant effect. Reported values include degrees of freedom (Df), residual degrees of freedom (Residual Df), mean squared error (MSE), F-value, partial eta squared (Partial η^2), and p-value for each main effect and interaction.

After excluding trials with excessive pre-TMS muscle contraction or MEP amplitudes smaller than 50 μ V, at least 77.5% of trials were retained in each condition (i.e., a minimum of 31 out of 40 trials), with an average of 39.2 ± 1.5 trials per condition, resulting in the removal of 1.96% of trials. Since no participant was excluded due to poor behavioral performance, the final sample consisted of 30 participants (18 females; mean age: 25.2 ± 4.9 years; handedness: $92.0\% \pm 0.2\%$; TMS stimulation intensity: $76.8\% \pm 8.9\%$ MSO; all values presented as $M \pm SD$).

First, as a control analysis, to assess corticospinal excitability individually in the ECU and FDS muscles while participants observed the co-actor's action cues, we conducted two separate three-way mixed-design ANOVAs on mean peak-to-peak ECU and mean peak-to-peak FDS MEP amplitudes. Condition (Solo, Joint) and Trial Type (Lift, Press) were tested as within-subject factors, and Order (Joint-first, Solo-first) as a between-subjects factor. Due to non-normal distribution, MEP values were z-scored prior to analysis.

The ANOVA on ECU MEPs showed a significant Condition $\times$ Trial Type interaction ($p = 0.020$, $\eta^2 = 0.177$, fig. 4A). Bonferroni-corrected post hoc analysis indicated that in the Solo condition, MEP amplitudes during lift trials were significantly larger than during press trials ($M_{\text{diff}} \pm SD = 0.11 \pm 0.21$, fig. 4A). Whereas the ANOVA on FDS MEPs revealed a significant main effect of Condition ($p = 0.049$, $\eta^2 = 0.131$, fig 4B), revealing larger cortico-spinal excitability in the joint condition, with respect to solo condition ($M_{\text{diff}} \pm SD = 0.180 \pm 0.267$).

Finally, to address Aim 1 and investigate our primary hypothesis, we conducted a two-way repeated-measures ANOVA on the difference between z-scored ECU and FDS MEP amplitudes (ECU–FDS) with Condition (Solo, Joint) and Trial Type (Lift, Press) as within-subject factors. This analysis did not reveal any significant effects.

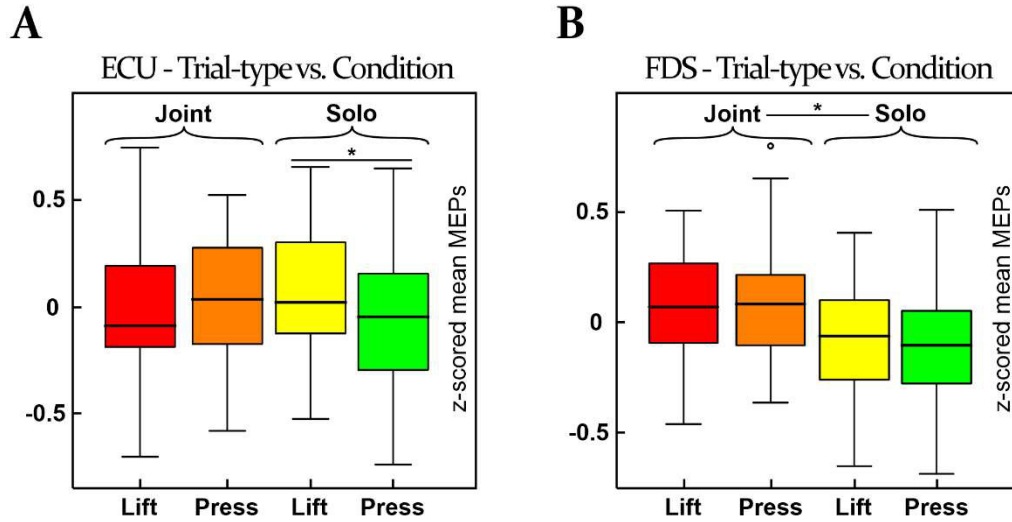


Figure 4: Significant results of motor-evoked potentials (MEP). (A) Z-scored mean MEP amplitudes were recorded from the ECU muscle for Lift and Press trial types in both conditions, with a significant Condition $\times$ Trial Type interaction indicating larger MEP amplitudes during Lift trials compared to Press trials in the Solo condition. (B) Z-scored mean MEP amplitudes recorded from the FDS muscle, showing a significant main effect of Condition with higher amplitudes in the Joint condition. For all panels, the box plots represent the median (horizontal line within the box), the interquartile range (IQR; the height of the box), and the whiskers extend to 1.5 times the IQR or the furthest data point within that range. Outliers are represented as individual points outside the whiskers. Asterisks (*) indicate statistically significant differences.

2.3.3. TEPs

To examine cortical response differences between the Joint and Solo conditions, TMS-evoked potentials (TEPs) were compared using cluster-based permutation tests for dependent samples (implemented in FieldTrip using the Monte Carlo method with 1,000 permutations). Comparisons were made across all channels and time points from 5 to 350 ms post-TMS pulse within each stimulation site: M1 (fig.4), SMA (fig.5), and Sham. A significant positive cluster was identified in the M1 condition between 285 and 350 ms (cluster-corrected $p = 0.032$; fig. 6). To control for non-specific effects (e.g., sensory or auditory artifacts) and isolate M1-specific activity, we subtracted the sham condition activity from the M1 and SMA TEPs. The previously observed positive cluster in M1 was no longer significant in the M1–Sham comparison (cluster-corrected $p = 0.157$). No other significant effects were detected.

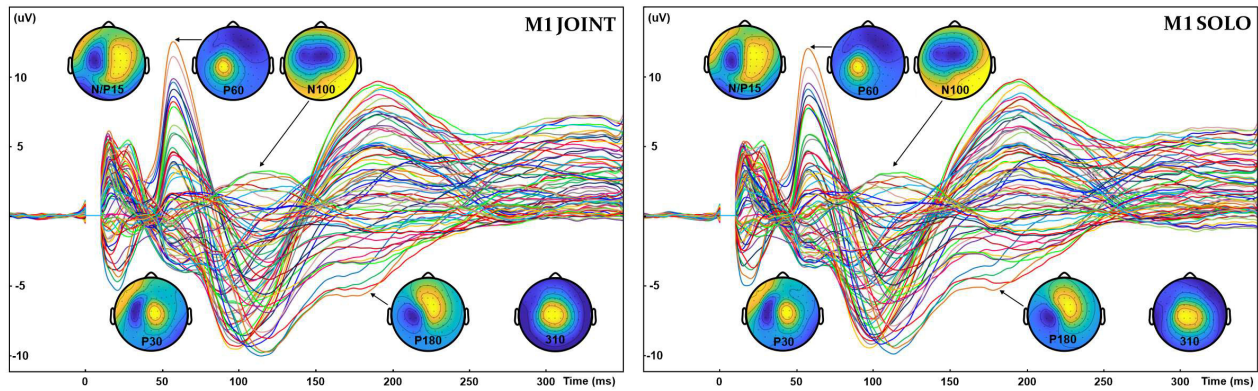


Figure 5: TMS-evoked potentials following M1 stimulation during the Joint condition (left) and Solo condition (right). Each trace represents the EEG response from a single electrode, and the overlaid topographical maps illustrate the characteristic components of M1 stimulation at 15 ms, 30 ms, 60 ms, 100 ms, 180 ms, and 310 ms, highlighting the spatiotemporal dynamics of cortical activation in both conditions.

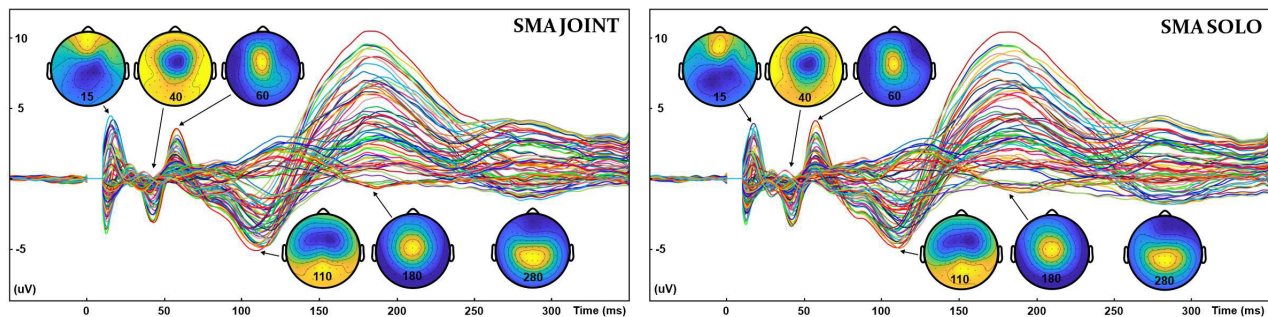


Figure 6: Butterfly plots of TMS-evoked potentials following SMA stimulation during the Joint condition (left) and Solo condition (right). Each trace represents the EEG response from a single electrode, with overlaid topographical maps illustrating the characteristic components of SMA stimulation at 15 ms, 40 ms, 60 ms, 110 ms, 180 ms, and 280 ms.

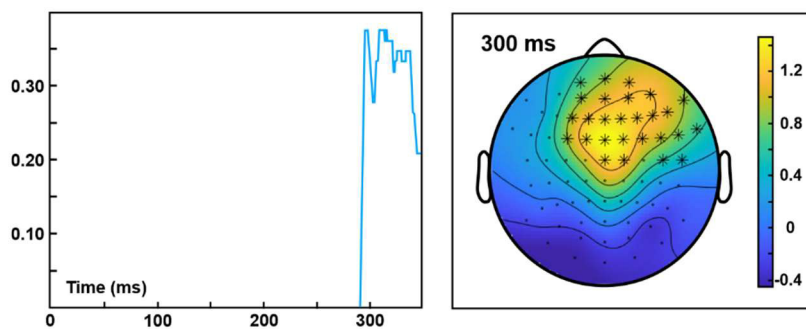


Figure 7: Time course of the significant cluster from the comparison of Joint vs. Solo conditions in M1 TMS-evoked potentials (left) and corresponding topographical map at 300 ms (right), showing the spatial distribution of the effect. Asterisks mark significant electrodes, with warmer colors indicating positive effects and cooler colors indicating negative effects.

2.4. Discussion

Our study investigated the neural basis of joint actions, specifically whether collective goals are motorically represented. We hypothesized that when acting together, individuals engage motor processes for their own actions and those of their co-actor, effectively processing the entire action sequence required to represent the collective goal. This motor representation would reflect an integrated understanding of both self-generated and the co-actor actions as part of a shared objective. To test this, we conducted the first-ever TMS-EEG experiment in Joint Action research, measuring motor-evoked potential (MEP) amplitudes as an index of motor cortex activation and TMS-evoked potentials (TEPs) to assess cortical excitability and effective connectivity (Farzan and Bortoletto, 2022). We expected that if participants represented the collective goal motorically, their MEP amplitudes would vary in response to the action cues in the co-actor's turn.

In line with our laboratory's previous pre-registered study (Barchiesi *et al.*, 2022), we implemented specific criteria to ensure reliable task execution. First, participant performance on catch trials was monitored to confirm attentiveness during the co-actor's turn and adherence to task instructions. Second, participants were evaluated based on RT and accuracy to verify that they had learned the stimulus–action associations and remained engaged throughout the task by maintaining consistent performance across blocks. Additionally, unlike Barchiesi *et al.* (2022), we introduced an upper RT limit of 500 ms to encourage reactive rather than deliberative responses and increased the holding time (to 500 ms), which inevitably increased “no response” trials. Thus, to ensure proper muscular engagement, we also assessed EMG-based accuracy showing proper behavior even during most of these “no response” trials. Despite task constraints, the relatively low error rates suggest that participants followed the instructions carefully and that the task demands were appropriate and not overly difficult.

Using MEPs as a dependent variable was justified by previous literature showing that the representation of actions in motor areas is related to muscle-specific increases in MEP amplitude. Specifically, modulation of MEP amplitude has been observed during motor processes such as action planning and execution (van Elswijk *et al.*, 2008), action observation (Bardi *et al.*, 2015; Cattaneo *et al.*, 2013), and motor imagery (Lebon *et al.*, 2019). In line with this research, Barchiesi *et al.* (2022) incorporated two motor imagery blocks (one in the pilot experiment and one in the main experiment) in their design, providing fundamental evidence that MEPs could be modulated within our type of experimental framework. Following Barchiesi *et al.* (2022), after significant changes in the experimental design, we used ECU-FDS MEP amplitude difference to test the hypothesis of motor representations of collective goals. However, we did not find evidence of a specific modulation at the motor level for the co-actor's action representation in the Joint condition. However, contrary to our hypothesis, we observed a significant modulation between lift and press trials in the Solo condition within ECU. Furthermore, we did not find a similar modulation in FDS, instead we observed that MEPs were larger in the Joint condition. Our primary dependent variable, ECU–FDS difference, showed no significant modulation.

The larger FDS-MEPs in the Joint condition, however, are in line with recent evidence that corticospinal excitability is modulated by attentional focus in dynamic action (Matsumoto *et al.*, 2024). Specifically, in a ramp-and-hold contraction task, the authors reported larger MEPs under an external focus (i.e., directing attention to the pressure applied to an object) compared to an internal focus (i.e., attending attention to one's own finger). A comparable effect may have occurred in our study, such that participants might have been more externally focused on the co-actor during the joint condition, whereas acting alone in the solo condition might have led to a more internally oriented focus.

This self-directed attention could also suggest why we found a significant modulation in ECU-MEPs. Participants in the Solo condition may have covertly imagined or prepared their (lift) actions during the automatic turn. In contrast, during joint actions, the (externally triggered) representation of collective goals—or more broadly, the co-representation of another individual's action—might have still engaged motor

processes but could simultaneously have interfered with the motor representation (or preparation) of one's own action that. Such conflicting self-other motor processing could suggest that MEPs may not be an ideal measure for probing collective goal representation or action co-representation.

One might wonder why MEPs were modulated differently across the two muscles. One possible explanation is the fact that proprioceptive and visual inputs can differentially alter the corticospinal excitability of reciprocal forearm muscles, implying distinct neural control mechanisms for flexors versus extensors (Quinn et al., 2018; Suzuki et al., 2019). Thus, it should not be assumed that extensors and flexors (or antagonistic muscle groups in general) will respond equivalently to TMS, as each may be governed by distinct cortical and subcortical pathways.

Unlike Barchiesi et al. (2022), we applied TMS over a broader time window, from -200 ms to 400 ms relative to the participant's mean RT. This raises a second critical point: the uncertainty regarding the optimal timing to effectively probe corticospinal excitability for action co-representation in joint tasks. If the most sensitive window for detecting these effects occurs earlier or later than our chosen timeframe, we may have unintentionally diluted any potential effects.

Another limitation of our experiment concerns task design. Unlike other joint action tasks that require precise coordination, our task was specifically designed to minimize the need for fine synchronization with the co-actor. Despite this, participants were still influenced by the co-actor's cues. This was evident in the lower accuracy observed in the Joint condition compared to the Solo condition. Further supporting this, we found a significant main effect of Congruence, with participants performing more accurately in congruent trials than in incongruent ones. However, when roles are clearly divided—as in our turn-based task design—achieving shared goals may not necessitate a motor representation of the co-actor's actions (Kutz, 2000), explaining the absence of significant modulation in the Joint condition. This interpretation aligns with the perspective that collective goal achievement can rely on various cognitive and motor processes rather than solely on motor representations of others' actions (Sinigaglia & Butterfill, 2020).

Alternatively, as suggested by Barchiesi et al. (2022), it is possible that the joint nature of the task modulates activity in action-related regions outside the primary motor cortex (M1), such as the premotor cortices. These regions may be modulated in a way that suppresses their output to M1, preventing it from receiving afferent input. Supporting this idea, a recent study demonstrated that reactive inhibition is slowed during joint actions; however, applying continuous theta burst stimulation (cTBS) to disrupt activity in the left dorsal premotor cortex (IPMd) eliminated the joint action-induced slowing of response inhibition (Cardellicchio *et al.*, 2021a).

Regarding TEPs, we did not propose any specific hypothesis for either M1 or SMA stimulation, given that, to the best of our knowledge, no prior TMS-EEG experiment has been conducted within a joint action paradigm. After collecting TEPs from the SMA, we computed the grand-average signal across all participants and conditions and identified five main peaks at approximately 20, 30, 60, 110, and 180 ms, consistent with previous reports (Casula *et al.*, 2024; Casula *et al.*, 2022; Leodori *et al.*, 2024). Likewise, TEPs elicited by M1 stimulation exhibited the characteristic temporal components extensively described in the literature (Farzan and Bortoletto, 2022). However, when comparing the Solo and Joint conditions via cluster-based analyses, after subtracting the sham condition, no significant differences emerged in either region.

These null findings converge with the lack of evidence for a motoric representation of shared goals, as previously noted for the behavioral and MEP data. Several factors could explain why TEPs remained inconclusive. One possibility is that joint action does not substantially affect early cortical TEP components in SMA or M1. Indeed, previous studies indicate that TEP components, particularly those before 100 ms, can be highly site-specific (Freedberg et al., 2020; Garcia et al., 2011; Ozdemir et al., 2021; Rogasch et al., 2020). Such topographical specificity may obscure any subtle modulation arising from joint actions, making it difficult to detect under the current experimental design.

Regarding later TEP components such as the N100, P180, and N280, they tend to be influenced by multiple overlapping sources (Farzan and Bortoletto, 2022). The N100, for example, often exhibits a broad topography and has been linked to multiple generators (Roos et al., 2021). It can also be confounded by auditory and somatosensory responses evoked by the coil click or skin stimulation (Farzan and Bortoletto, 2022). The subsequent P180 and N280 peaks are still poorly characterized, though they may arise from a mixture of cortical sources and auditory evoked responses (Ahn and Fröhlich, 2021; Ter Braack et al., 2015).

The inherent variability of EEG data, compounded by the dynamic nature of joint-action paradigms, can reduce sensitivity to subtle effects, particularly given intersubject and trial-by-trial variability. To mitigate non-task-related artifacts, we conducted the experiment in a sound-attenuated room, employed active noise-canceling earphones with white noise, and introduced a sham condition for subtraction. This approach, commonly used in TMS-EEG studies (Conde et al., 2019; Gordon et al., 2018; Rocchi et al., 2021), helps control for the auditory clicks and scalp sensations that could contaminate TEP waveforms. Nonetheless, it remains unclear whether these precautions fully eliminate all extraneous confounds.

A critical question is whether the joint condition by itself is sufficient to produce a detectable state-dependent modulation of TEPs in SMA or M1. Previous work shows that TEPs can indeed vary across different brain states—such as distinct levels of consciousness or different cognitive loads (Ferrarelli et al., 2010; Massimini et al., 2005; Noreika et al., 2020). However, our results suggest that the joint condition tested with our paradigm may not have generated a sufficiently distinct brain state to alter TEPs in a measurable way.

Future investigations should consider refined experimental designs (e.g., stronger manipulation of joint-action contexts), higher statistical power, and possibly more advanced source-localization techniques. These steps may help clarify whether TEPs can reveal subtle cortical changes in response to collective goals in SMA, M1, or other relevant cortical areas.

2.5. Conclusion

This study represents a preliminary effort to investigate whether collective goals are represented at the motor level by employing TMS-EEG co-registration in participants acting alongside a co-actor or alone. In addition, we revisited the MEP measures from Barchiesi et al. (2022) under comparable experimental conditions, while simultaneously attempting to address the limitations identified in that previous work. Although we hypothesized that MEPs would be modulated in joint action contexts according to the confederate's intended action, no significant modulation emerged; on the contrary, we found significant modulation in the Solo condition, but only in ECU-MEPs. Even after accounting for the methodological constraints outlined by Barchiesi et al. (2022), we found no evidence to support our initial conjecture. Likewise, the TEP results also point away from a motoric representation of shared goals: TEP recordings in both the SMA and M1 were inconclusive, as the cluster-based analysis—after subtracting the sham condition—revealed no significant effects. Despite these null findings, our study provides valuable insights and methodological guidance for future investigations of collective goal representation in both healthy and clinical populations.

3. STUDY II

3.1. Background

3.1.1. *Slower Inhibition in Joint Actions: Co-Representation, Referential Coding, or Attentional Bias?*

An important observation from the joint action literature (see section 1.3.4.) is the pivotal role of inhibitory control. However, as noted in the introduction, only two studies (Cardellicchio *et al.*, 2021a; Cavallo *et al.*, 2014) have implemented a joint variant of the SST, the most commonly used paradigm for studying inhibition, particularly action cancellation (Raud *et al.*, 2020b; Verbruggen *et al.*, 2019). Both studies reported longer SSRTs under the Joint condition compared to the Solo condition, as well as neurophysiological evidence indicating the engagement of a more selective, and consequently slower, stopping mechanism (Aron and Verbruggen, 2008; Majid *et al.*, 2012). This aligns with the concept of co-representation: in the Joint condition, both the participant's and co-actor's actions remain active, yet only the participant's own action must be selected for inhibition. In other words, the parallel motor plans elicited by co-representing the partner's action must be bypassed, necessitating the recruitment of a more targeted inhibitory mechanism during joint actions.

However, relying solely on co-representation to explain this slower inhibition may not be the only possible interpretation. Alternatively, referential coding effects (Dolk *et al.*, 2014; Dolk *et al.*, 2013) could result from purely perceptual and attentional processes, in which spatial codes for both one's own and the other's actions are integrated into the participant's task set to distinguish each person's actions. If the relevant stimulus attribute appears on the co-actor's side, spatial response codes linked to that side are automatically activated and conflict with the participant's own response, potentially leading to disinhibition, as observed in the two studies. Indeed, Cavallo *et al.* (2014) themselves acknowledge the possibility of this "non-social" explanation, noting that their setup may have elicited referential coding effects at the cost of increased motor control demands (Dolk *et al.*, 2011; Dolk *et al.*, 2014; Hommel *et al.*, 2001; Maier *et al.*, 2023).

Cardellicchio *et al.* (2021a) do not discuss alternative interpretations, but given that participants reached for a bottle held either by a co-actor (joint) or a mechanical holder (solo), the mere presence of the co-actor's hand may have shifted, and thus biased, attentional priorities toward the target location (Garza *et al.*, 2013; Reed *et al.*, 2010; Reed *et al.*, 2006). Furthermore, Cardellicchio *et al.* (2021a) used continuous theta burst stimulation (cTBS) to investigate the role of the left dorsal premotor cortex (IPMd), demonstrating that this region modulates joint action stopping performance. Their interpretation is that IPMd, driven by co-representation, recruits a more selective mechanism to control joint action responses while suppressing parallel, interfering motor plans. However, during their experiment, countermanding movements were requested while participants were moving toward the co-actor's hand, thus requiring them to stop after movement onset and after target fixation (i.e., the co-actor's hand holding the bottle).

Previous work shows that neural correlates of potential reaching actions coexist in the premotor cortex during periods of uncertainty, but once an unambiguous cue appears, the chosen motor plan is reinforced while alternative plans are inhibited (Cisek and Kalaska, 2005). Yet, this selective weighting of representations is biased (Klaes *et al.*, 2011) and possibly mediated, among others, by attentional processes (Cisek and Kalaska, 2010). Consequently, disrupting PMd activity, as in Cardellicchio *et al.* (2021a), could impair this motor-plan competition, diminishing the hand-induced attentional prioritization effect. Such a "downregulated competition" account is consistent with observed reductions in response times (Cattaneo and Parmigiani, 2021) and enhanced procedural motor skills (Stephan *et al.*, 2016) when PMd activity is suppressed. Hence, even in Cardellicchio *et al.* (2021a), there may be an alternative, non-social, but rather attentional interpretation of the behavioral and neurophysiological outcomes, not strictly requiring the co-representation framework.

3.1.2. *Selective Inhibition: Measurement, Mechanisms, and Implications for Joint Actions*

If we, however, accept the hypothesis that selective inhibition is key to joint actions, regardless of a social or non-social interpretation of slower stopping latencies in joint actions, it is essential to understand how selective inhibition is typically measured and how it manifests outside a joint action context. This consideration is crucial for designing any new joint paradigm aimed at testing whether inhibitory modulation truly stems from co-representation (i.e., a social effect) rather than nonsocial accounts.

In a standard single-effector SST, participants make a speeded response (e.g., pressing a button) to go signals and then attempt to inhibit that response when a stop signal appears, a process predominantly driven by reactive processes. The primary measure of interest is the SSRT, which provides an estimate of the covert latency of this reactive inhibitory process, i.e., reactive inhibition. In contrast, a selective SST with two effectors (e.g., right and left hands) introduces selective inhibition: participants must inhibit the hand signaled to stop while continuing any required response with the other hand. This entails additional cognitive demands, as inhibition is no longer global but instead requires suppressing one action while allowing another to proceed. Consequently, participants must also discriminate whether to inhibit one hand, the other, or neither, thereby increasing task complexity.

Proactive control, on the other hand, refers to a strategic, anticipatory mechanism in which individuals modify their behavior in advance (e.g. strategic slowing) based on contextual cues, prior experience, or learned probabilities. This stands in contrast to reactive control, which is engaged only after a stop signal or unexpected event occurs. In both types of SST, the interplay between reactive and proactive control is critical, the latter often manifesting as strategic slowing of response times to improve the likelihood of successful stopping. Moreover, proactive control can be experimentally manipulated, for example, by providing pre-trial cues about the probability of a stop signal, allowing participants to anticipate and adjust their behavior accordingly. Early influential work on selective stopping, employing a bimanual variant of the SST (Aron and Verbruggen, 2008), demonstrated that foreknowledge of the stopping location, via informative cues, significantly slows the stopping latencies, albeit at the advantage of reducing the stopping-interference effect, thereby indicating that stopping can be mechanistically selective. Aron and Verbruggen (2008) posited that the recruitment of selective or global stopping mechanisms is mutually exclusive and context-dependent. However, while subsequent studies supported these findings (Claffey et al., 2010; Majid *et al.*, 2012), others reported null or opposing results regarding SSRT differences, in bimanual SSTs, between informative and noninformative cues (Cirillo et al., 2018; Lavalley et al., 2014; Raud and Huster, 2017; Smittenaar et al., 2013).

To investigate whether stopping only one component of multiple actions (i.e., selective inhibition) involves abruptly activating a single global inhibitory mechanism, followed by reinitiating any ongoing actions, or whether it relies on balancing distinct global and selective inhibitory processes, Raud et al. (2020a) designed a multimodal experiment incorporating behavioral and physiological markers of proactive control, motor preparation, and response inhibition. They administered two versions of an SST containing proactive cues, i.e., a standard unimanual paradigm and a bimanual task for selectively stopping one of two prepared responses, as done similarly before (Aron and Verbruggen, 2008).

Contrary to the dual-mechanism model, which predicts distinct global versus selective inhibition, they found no significant differences in SSRTs, stopped-hand MEP amplitudes, or frontal β power (13–20 Hz) between the two tasks. However, the authors did observe evidence of selective proactive control before the actual inhibition in the bimanual condition. Taken together, these findings suggest the recruitment of a single inhibitory stopping mechanism, with some indications of selective stopping where net behavioral outcomes depended on action-specific motor preparation. The authors propose that a rapid, reactive inhibition

mechanism is likely activated whenever a stop signal is detected, while the success of stopping may depend on perceptual speed and the concurrent state of the motor cortex.

In conclusion, the inconsistencies in the literature challenge the notion that selective inhibition is a distinct process and, by extension, whether it actually operates during joint actions as originally proposed (Aron and Verbruggen, 2008). Findings of Raud et al. (2020a) suggest that what appears to be selective inhibition may stem from changes in motor preparation rather than from two separate inhibitory mechanisms. This aligns with other neurophysiological evidence suggesting that proactive control biases sensorimotor and attentional systems in anticipation of a stop signal (Elchlepp et al., 2016; Langford et al., 2016). The same principle could extend to joint actions, where a proactive biasing of motor preparation, possibly driven by co-representation, might offer a more plausible explanation rather than switching the underlying inhibitory mode.

3.2. Aims of Study II

Two main issues arise from previous work on joint action stopping and, by extension, on selective inhibition. First, it remains unclear whether the slower reactive inhibition reported in prior joint SST studies genuinely stems from co-representation or could instead be explained by non-social mechanisms (e.g., referential coding, attentional shifting). Second, the literature does not conclusively show that selective inhibition is a distinct and slower process compared to global inhibition. Indeed, as Raud and colleagues suggest, what appears to be selective inhibition may simply reflect changes in motor preparation rather than a separate inhibitory mechanism.

Consequently, we do not know whether the processes involved in joint actions, leading among them co-representation, truly invoke an independent selective inhibition mechanism, or simply induce a proactive bias in motor preparation. To address these uncertainties, Study II aims to clarify these issues through two main steps:

1. **Positive Control Experiment:** Devise and administer a control paradigm that substitutes co-representation (as evoked by joint actions) with the co-engagement of a second effector in a selective bimanual inhibition task. This bimanual selective inhibition serves as a proxy for joint action, given that coordinating two effectors in one individual can mirror some of the demands of coordinating actions between two people.
2. **Joint Experiment:** Employ the same task in its unimanual form under a joint condition and compare it with the corresponding solo condition. The hypotheses for this joint experiment will be guided by the findings from the positive control.

Two guiding principles shape the design of the new paradigm, as will be detailed in the next chapter. First, we will use a Stop-Change Task (SCT) that robustly engages motor preparation and action re-engagement after inhibition, examining both reactive inhibition and proactive control. This approach enables us to investigate how selective stopping, and, by extension, joint actions, affect various facets of motor control. Second, the paradigm will strive to maximize co-representation by emphasizing collective goals, while minimizing non-social confounds.

Thus, the rationale behind the positive control is straightforward. If we fail to observe longer SSRTs in a selective bimanual SCT (as Raud et al., 2020a, did with their bimanual SST), it becomes increasingly unlikely that the prolonged stopping latencies reported in the joint SST by Cavallo et al. (2014) and Cardellucchio et al. (2021a) result from co-representation. In that case, other positive control outcomes may point to differences in proactive control or action re-engagement, thereby shaping the hypotheses for the Joint Experiment. Conversely, if we do find lengthened SSRTs in the bimanual condition, it would, with due caution, suggest that

co-representation-like processes, rather than merely non-social confounds, play a central role in slowing reactive inhibition in joint action stopping.

Accordingly, the primary aim of the Positive Control Experiment is to indirectly assess whether co-representation truly accounts for the extended stopping latencies reported in joint SST studies, by using bimanual selective inhibition as a proxy. In parallel, the main aim of the Joint Experiment is to disentangle the various facets of motor control involved in joint action stopping and re-engagement, while simultaneously highlighting co-representation and limiting non-social confounds (such as referential coding).

4. STUDY II: POSITIVE CONTROL EXPERIMENT

4.1. Background

4.1.1. *The bimanual selective Stop-Change Task as a positive control*

Biased motor preparation appears to be involved in selective stopping (Raud *et al.*, 2020a), while a slower, more selective inhibition mechanism has been proposed to account for prolonged joint action stopping (Cavallo *et al.*, 2014). However, it remains unclear whether, and how, these two processes might be connected. If motor preparation does contribute to a longer inhibition process, then an inhibition task that places greater demands on motor planning should, in principle, amplify the slowing of stopping latencies.

In the bimanual SST, selective stopping does not require substantial motor re-engagement, thus imposing only a minimal load on motor preparation, potentially explaining, among other factors, the mixed results reported in the literature. By contrast, a bimanual SCT demands more extensive motor preparation during selective stopping, as participants must also selectively re-engage in an alternate action. One possibility is that co-representation biases motor preparation, thereby prolonging stopping latencies. If this link holds true, then a bimanual selective SCT, by virtue of its greater demands on motor preparation, would serve as an ideal positive control paradigm. Building on the task design of Raud *et al.* (2020a), I therefore devised a positive control paradigm intended for a future joint SCT.

Specifically, I devised a unimanual two-choice SCT, in which two possible responses are initiated or reprogrammed using the right hand, alongside a bimanual variant that similarly requires selective stopping of the right hand to cancel one of two prepared responses before switching to an alternative movement. Unlike Raud *et al.* (2020a), however, both versions of the task exclusively involve right-hand stops (and following changes).

The reason for this setting is that the bimanual condition effectively “simulates” co-representation: the unselected effector (the left hand) always completes its initiated movement, acting as a stand-in for a co-actor’s action. The participant must selectively inhibit and re-engage only the selected (right-hand) effector, mirroring what would occur in an unimanual joint SCT. Analogous to how participants in a joint Simon task co-represent a partner’s action as if performing a solo task, a bimanual SCT here serves as a potential substitute for a purely unimanual joint version. Ideally, the latter prompts co-representation and thus induces delayed inhibition, stemming from biased motor preparation.

Simplifying the design from Raud *et al.* (2020a), I separated certain-go and maybe-stop trials into different blocks. This eliminated the need for informative cues and shortened the trials while still allowing for the assessment of proactive control by contrasting certain-go and maybe-stop trials. Instead of pressing keyboard keys with thumbs, participants performed lift and press actions with either one hand or both hands (unimanual vs. bimanual conditions). To minimize working memory load in the bimanual version (and to avoid complex action combinations) movements performed with one hand were matched by the opposite movement in the other hand. Consequently, there were only two go cues and corresponding action sets: pressing with the right hand (red cue) required a simultaneous lift of the left hand, whereas lifting with the right hand (yellow cue) required a simultaneous press of the left hand (see Methods for more details).

Several considerations motivated this design. First, to “simulate” co-representation in the bimanual condition, the left hand always performed a predictable action, while the right hand carried the same responsibility for acting or changing as in the unimanual version. Second, choosing opposite actions (press vs. lift) is reminiscent of push–pull joint coordination (e.g., moving furniture or operating a lever with another person), thereby offering some ecological validity. Third, avoiding identical frequent go actions in both hands circumvented

mirroring effects, ensuring that participants had to prepare both potential action sets. Fourth, in change trials, the action sets became congruent, reducing the complexity of re-engagement.

Since the SCT is effectively an extension of the SST (Boecker *et al.*, 2013), it also offers additional benefits. Specifically, it enables the measurement of action re-engagement times (change-RT) and differentiates between correct inhibitory control and simple inattentiveness in stop-change trials—whereas, in the SST, withholding a response could equally be due to effective stopping or failure to notice the go signal.

4.1.2. Gamification of the Stop-Change Task for the Joint and Bimanual Positive Control Task

A range of social factors significantly affect the strength of co-representation. Notably, well-defined collective goals are crucial for eliciting co-representation in social task contexts, whereas purely perceptual factors tend to drive referential coding when no explicit joint outcome is involved (see section 1.2.4.). Numerous studies demonstrate how task design and instructions can emphasize a cooperative goal, for instance, by establishing shared intentions, introducing common rewards, or providing mutual feedback, thereby enhancing co-representation (Miss *et al.*, 2022). This effect is most pronounced in scenarios that highlight a common outcome, supporting the principle that shared goals are key to generating a truly social effect (Sebanz *et al.*, 2006a). Although a simple instruction to “cooperate” often suffices for adults, a salient joint reward structure with well-defined shared objectives can further strengthen interdependence and co-representation.

One strategy is to integrate game-design elements, a process known as gamification, into the experimental paradigm. Gamification involves using principles like point systems, badges, leaderboards, challenges, progressive levels, and immersive storytelling to boost engagement and motivation. However, such strategies should be carefully designed to avoid undesirable outcomes, such as excessive competition or elevated stress. The SCT (like the SST) demands sustained cognitive effort and can feel repetitive or frustrating. Because the staircase algorithm ensures a roughly 50% failure rate on stop trials regardless of participants’ effort, motivation can diminish, potentially leading to increased go omissions and more stop-process trigger failures. This not only undermines task adherence but also hinders a reliable SSRT estimate (Verbruggen *et al.*, 2019).

Gamifying the SCT/SST may alleviate these issues by maintaining higher levels of motivation, as demonstrated in a study where a gamified SST improved participants’ enjoyment without compromising execution or performance (Friebs *et al.*, 2020). Although there is some concern that introducing more complex visuals and rules could detract from cognitive resources like attention and working memory, evidence from a gamified visual search task suggests the opposite: performance increased with no change in search or fixation strategies (James *et al.*, 2019). Given no differences in strategies, the authors interpreted the results in terms of higher levels of attention and effort. Likewise, an n-back working memory task, when gamified, produced more positive subjective experiences without adversely affecting task load or performance (Scharinger *et al.*, 2023).

However, the literature on gamified cognitive tasks remains limited, and potential drawbacks are not yet well understood. Consequently, to probe the feasibility of a gamified joint SCT and assess the effect of gamification, I also developed a gamified version of the bimanual positive-control SCT to examine whether any behavioral differences emerge between the two formats.

4.1.3. Aims and Hypotheses of the Positive Control Experiment

Building on earlier investigations of selective inhibition, this positive control experiment extends the SC paradigm to a bimanual context to examine how proactive and reactive control mechanisms interact under conditions of heightened motor preparation, conditions that may arise during co-representation while engaged in joint actions. Outlined below are the primary aims of the Positive Control Experiment, followed by the core hypotheses derived from these objectives.

1. *Validate the bimanual SCT as a positive-control task for joint action stopping*

Building on the findings and task design of Raud et al. (2020a), the first aim is to develop and validate a bimanual SCT that likely imposes higher demands on motor preparation due to the need for rapid action re-engagement after selective stopping. We predict that No-Change trials (i.e., go-trials in the Stop-Change blocks) will have longer RTs in the bimanual version than in the unimanual version, reflecting a stronger reliance on proactive control. We also expect these heightened demands to directly influence SSRT, which should be significantly longer in the bimanual variant. Further, to assess reactive inhibition more thoroughly, we will measure prEMGs (see Section 1.5.2), which we likewise predict to be prolonged under bimanual conditions. Crucially, our goal is to determine whether this bimanual SCT can function as a positive-control paradigm for examining joint action stopping. By requiring the selective inhibition of one hand while the other continues moving, the task mirrors key elements of co-representation seen in joint action contexts. Should the bimanual SCT consistently elicit extended stopping latencies, attributable to biased or more demanding motor preparation, it would serve as a vital benchmark for future joint SCT studies.

2. *Investigate the effects of gamification on task performance and engagement*

Recognizing that standard inhibitory control tasks can be both repetitive and cognitively taxing, and that joint tasks benefit from emphasizing collective goals to reliably induce co-representation, our second aim is to explore how gamification influences task performance and participant engagement. Ideally, we anticipate that our behavioral outcomes will not differ significantly between a standard SCT and a gamified SCT, indicating that gamification does not compromise the core measures of inhibitory control.

4.2 Methods

4.2.1. Participants, sample size estimation, and exclusion criteria

Sample size estimation was based on the effect size reported by Aron and Verbruggen (2008) and was calculated via G*Power (3.1.9.7, Faul et al., 2007) for a two-tailed paired t-test. With 90% power and a 5% significance level, the power analysis indicated a required sample size of 23 participants. Accordingly, 27 right-handed participants with no history of neurological or psychiatric disorders (9 males, age range 20–36 years) were enrolled after providing written informed consent. One subject did not complete the experiment and was excluded.

Exclusion criteria addressed potential violations of the independent race model assumption and the reliability of SSRT estimation. The SSRT was estimated based on the independent race model, which assumes an independent race between the go and stop processes; any violation of this assumption yields unreliable SSRT estimates (Band et al., 2003).

To check for such violations at the individual subject level, we compared each participant's mean RT on unsuccessful change trials with their mean RT on No-Change trials (including choice errors and premature responses) for both response modes (bimanual and unimanual conditions, Verbruggen et al., 2019).

If the mean RT on unsuccessful change trials was numerically longer than the mean RT on No-Change trials in at least one response mode, SSRT was not estimated. Three participants were excluded for this reason, all for violations of the bimanual condition.

Because SSRT estimation is also sensitive to the percentage of go omissions (omissions in No-Change trials), we used the integration method with replacement of go omissions, which simulations indicate is robust even when omission rates are high (Verbruggen *et al.*, 2019). Nonetheless, SSRT tends to be underestimated as the percentage of go omissions increases, so we excluded participants with more than 15% omission errors in No-Change trials. Two participants exceeded this threshold in the bimanual condition and were therefore excluded. A further exclusion criterion targeted the probability of unsuccessful change trials, since SSRT estimates are most reliable when this probability is near 0.50 (Band *et al.*, 2003). We set thresholds at 0.75 and 0.25, meaning participants with probabilities above 0.75 or below 0.25 in any condition were subject to exclusion; however, no participants met this criterion.

After applying these exclusion criteria, the final sample for behavioral analysis comprised 21 participants (7 males, $M \pm SD = 24.3 \pm 3.5$ years). For prEMG analysis, one subject's EMG data became corrupted and was unusable, resulting in a prEMG sample of 20 participants (6 males, $M \pm SD = 24.4 \pm 3.6$ years). Handedness was confirmed via the Edinburgh Handedness Inventory ($M \pm SD: 94.9 \pm 12.8$; Oldfield, 1971). All participants were naïve to the purpose of the study and completed the experiment in a single session lasting approximately 2 hours. This included about 30 minutes for informed consent procedures and EMG setup, followed by 90 minutes for instructions, practice, testing, and short breaks between blocks. Participants received monetary reimbursement for travel expenses, if applicable. The study was approved by the Ethical Committee of the IRCCS Istituto Centro San Giovanni di Dio Fatebenefratelli (Brescia e 25/2020) and was conducted in accordance with the Declaration of Helsinki.

4.2.2. Procedure

Experiments were conducted in an electromagnetically shielded, dimly lit, and sound-attenuated room (the same as in Study I) to minimize external noise and interference. Upon arrival, participants were fully informed about the experimental procedures and provided informed consent. Surface EMG signals were recorded using disposable Ag/Cl electrodes (Delsys) connected to a g.Hlamp amplifier system (g.tec Medical Engineering GmbH, Schiedlberg, Austria), sampled at 9,600 Hz. Following the protocol of the first study, electrodes were placed in a bipolar montage over the extensor carpi ulnaris (ECU) and flexor digitorum superficialis (FDS) on both the right and left forearms. Although only right-forearm EMG data were analyzed, the symmetrical placement ensured comparable proprioceptive feedback across both arms. No online hardware filters were applied during acquisition; however, for visualization purposes only, a band-pass filter (10–2,500 Hz) and a notch filter were applied.

Two USB-controlled hand levers recorded each hand's press actions. For lift actions, pressure sensors (RP-S40-ST, 4 cm × 5.5 cm) were affixed to each lever and connected to an Arduino-based circuit for data collection and processing. Participants rested their forearms on two black wooden platforms (approximately 3 × 40 × 10 cm), designed to keep the hand at the same level as the lever attached at the platform's distal end. This arrangement prevented the hand from being held at an incline and ensured a neutral wrist position, thereby promoting muscle relaxation and allowing a downward (negative) excursion of the hand during press actions (Fig. 9A). The hand levers themselves were repurposed commercial USB footswitches (FS221-P, PCsensor, Shenzhen, China; 42 × 63 × 100 mm), each triggered by a low-noise photoelectric switch. In response to on-screen cues, participants either pressed the lever or lifted the hand while maintaining a stable and horizontal forearm position on the platform.

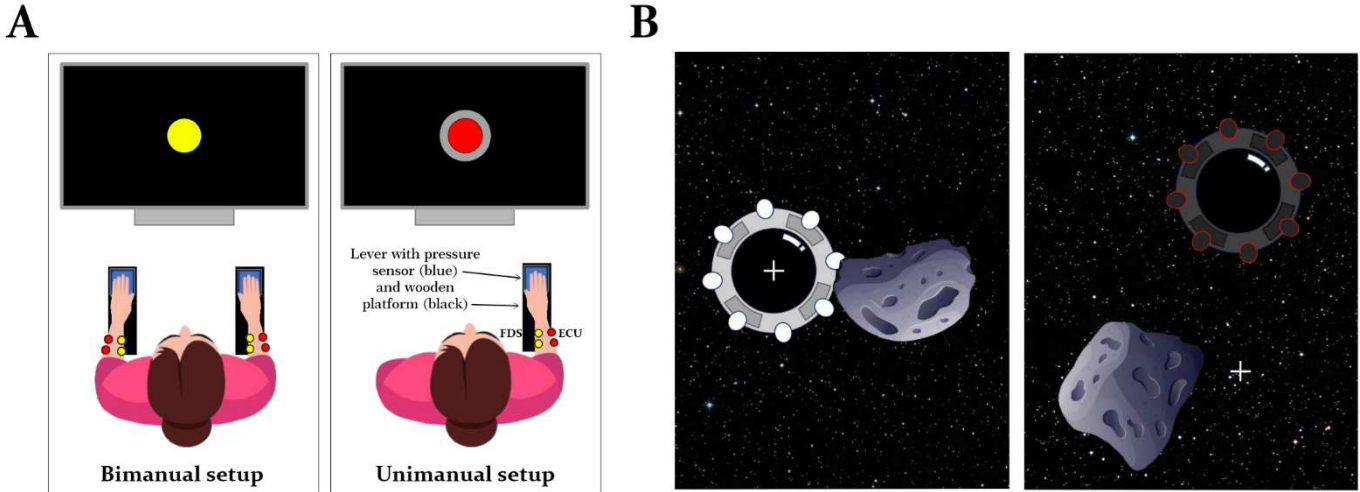


Figure 9: Experimental setup of both response modes and screenshots of the feedbacks in the gamified format. (A) Task setup for the bimanual (left) and unimanual (right) conditions (see section 4.2.5. for task mechanics). The left side illustrates the standard format, where a simple yellow circle represents a "lift" cue. The right side presents the gamified version, in which the cues (in this case, a red "press" cue) have a gray border that later transitions into the hull of a flying saucer (UFO), maintaining a structured transition between the task's cue in the execution phase and the feedback phase. EMG electrodes for the flexor digitorum superficialis (FDS) and extensor carpi ulnaris (ECU) muscles are indicated, along with additional components such as the lever with a pressure sensor (blue) and the wooden support platform (black) for resting the forearm. (B) Cropped screenshots depicting feedback in the gamified version (see section 4.2.5.). The left panel shows negative feedback (a collision with an asteroid), indicating an incorrect response; in this case, the light gray hull with white lights indicates trials in the SCT blocks (either No-Change or Change trials). The right panel shows positive feedback, where the UFO successfully avoids the asteroid, indicating a correct response. The hull is dark gray with no lights, indicating Go-Only block trials.

Participants sat facing a computer monitor approximately 60 cm away (eye-to-screen distance, ASUS VG248QE; 60 Hz refresh rate, 1920 × 1080 resolution, 61 cm × 34.4 cm). They were instructed not to grip the lever or adopt a rigid posture, but instead to perform shovel-like motions for both hand lifts and presses. To reduce excessive muscle tension in the ECU and FDS, the thumb and pinky finger on each hand were gently secured with a small strip of medical micropore tape (3M, Minnesota, U.S.), preventing rigid finger extension or inadvertent lever gripping. A custom-script in MATLAB® combined with Psychophysics Toolbox 3 (Brainard and Vision, 1997; Kleiner *et al.*, 2007) controlled the presentation of visual stimuli and the events of the SCT.

4.2.3. Bimanual and unimanual Stop-Change Task

Programming of the paradigm strictly followed the guidelines of Verbruggen *et al.* (2019). As described in the Background (4.1.), the two-choice SCT always required changing the right-hand response to its alternative in both task versions. In the bimanual version, participants were instructed to selectively change only the right-hand response while additionally continuing the left-hand action as planned.

Two block types were administered: Go-Only blocks (all certain-go trials) and Stop-Change (SC) blocks (pseudo-randomly intermixed No-Change and Change trials). Change trials constituted 33% of the trials in each SC block. To minimize fatigue, each response mode (bimanual or unimanual) featured four 90-trial SC blocks and four 20-trial Go-Only blocks, for a total of eight blocks per response mode. The order of these blocks was alternated so that participants could take a short pause after a cognitively more demanding SC block, before proceeding to a comparatively simpler, albeit repetitive, albeit very short Go-Only block. Half of the blocks employed a gamified format and the other half a standard format, yielding 720 SC trials and 160 Go-Only trials overall. Block type, task format, and response mode were counterbalanced in a Latin-square arrangement. Although task types alternated on a block-by-block basis, Go-Only and SC blocks that shared

the same format were presented in pairs. Participants always completed the entire set of blocks for one response mode before switching to the other.

At the beginning of the experiment, and again after finishing the first response mode, participants completed 130 practice trials to familiarize themselves with that mode. The practice phase comprised two Go-Only blocks of 20 trials each and two SC blocks of 45 trials each, arranged in one gamified pair and one standard pair. During practice blocks, trial-end feedback indicated the specific error type (too slow, commission, omission, or no response). In contrast, feedback during the main experimental blocks was only positive or negative. Participants who felt they needed more practice were permitted an additional training block. In total, counting both practice and experimental trials, participants performed 900 SC trials and 240 Go-Only trials.

In No-Change trials of the bimanual task, movements performed with one hand were paired with the opposite movement in the other hand: pressing with the right hand (red cue) required a simultaneous lift of the left hand, while lifting with the right hand (yellow cue) required a simultaneous press of the left hand. Errors were recorded individually for each hand. However, negative feedback was given if the participant made a mistake with either effector.

Similarly, in the unimanual task, the red cue indicated a press, and the yellow cue indicated a lift, both executed with the right hand. At the end of each trial, participants received feedback indicating whether their response was correct or incorrect. Trials in the Go-Only blocks were identical to the No-Change trials.

In Change trials, participants who had already initiated or were in the process of initiating a right-hand movement (e.g., pressing down in response to the initial go-cue) were required to switch to the alternative action (e.g., lifting up) upon presentation of the change cue. Change-Success trials were those in which participants successfully altered the right-hand action upon presentation of the change cue, as confirmed by positive feedback. By contrast, if the system had already registered the initial go action, the trial was deemed a failure, and negative feedback was presented to indicate the unsuccessful change, despite changing action afterward. A staircase algorithm governed the stop-signal delay (SSD): after each successful change, 50 ms was added to the SSD (Change trials became more difficult), whereas 50 ms was subtracted following a failed change (Change trials became easier, but SSD never dropped below 50 ms), thereby maintaining an approximate 50% failure rate for Change trials.

Notably, in the bimanual task, for the purpose of determining a successful or failed change (and thus updating the staircase), only the right-hand action was taken into account. Consequently, a trial could be designated as change-success even if the left hand committed a commission error. However, in such a scenario, participants still received negative feedback to reflect the error on the left side. The initial SSD was set to 150 ms.

The feedback at the end of the trial was especially important in the SC blocks because it motivated participants to respond as quickly as possible in No-Change trials, where the upper RT limit for positive feedback was set to 700 ms. However, RTs were recorded up to 1000 ms, at which point the trial was marked as a “no response.” Thus, participants were aware if their response was too slow. Following the guidelines of Verbruggen et al. (2019), participants were instructed not to wait for the change cue, and the experimenter gave block-based feedback if they noticeably slowed down.

4.2.4. Task instructions and formats

For the standard format, participants were instructed to prioritize both speed and accuracy and explicitly cautioned against delaying their response to the go signal in anticipation of a possible change signal. They

were also informed that, due to the tracking algorithm, the task would become increasingly challenging, resulting in a failure to inhibit the initiated go response on approximately 50% of all change trials.

In contrast, the gamified format introduced a simple storyline, where participants controlled a stylized alien “flying saucer” spacecraft flying through space (see section 4.2.5.) and had to execute the correct actions to avoid incoming asteroids (Fig. 9B). While the sequence of events, timings, and fundamental mechanics remained identical across both formats and response modes, the gamified version differed in its cue appearances, feedback aesthetics, and narrative elements. In the standard format, participants were given no specific goal beyond meeting the core task requirements.

4.2.5. Stimuli and trial time-sequence in gamified and standard-format versions

Before each trial, the system monitored pressure on the sensor(s) to ensure that participants’ hands were correctly positioned. If insufficient pressure was detected, a warning message (“Please place your fingers on the sensors”) appeared until proper contact was restored. Once adequate pressure was registered, the trial began.

In the standard format (Fig. 10), each trial began with a black background and a central white fixation cross ($\sim 1.9^\circ$ of visual angle [dva]) that was always visible in the foreground. Participants were instructed to maintain fixation on this cross throughout the experiment. In the gamified format (Fig. 11), in addition to the fixation cross, a black circle ($\sim 5.7^\circ$ dva) with a 1° thick gray border was present. Depending on the block type, the border could be a dark gray with a deep-blue edge (Go-Only blocks), enhancing contrast against the black background, or a light gray with a white edge (SC blocks). The total diameter of the circular stimulus in the gamified format was $\sim 6.8^\circ$ dva.

After a variable pseudo-randomized delay of 500–700 ms, a red or yellow full circle ($\sim 5.7^\circ$ dva) appeared in the standard format, corresponding to press (red) or lift (yellow) actions. In the gamified format, the previously black circle was replaced by this colored circle while retaining the same border.

In No-Change trials, participants responded as quickly as possible with the correct action (or the correct action-set in the bimanual task). In change trials, following the SSD governed by the staircase algorithm, the circle switched color, indicating the need to change the right-hand action from press to lift (red to yellow) or lift to press (yellow to red). Participants had 1,000 ms from the onset of this color change to execute the alternative action. The action cue disappeared after this time limit, at which point the feedback phase began.

Feedback in the standard format appeared as a simple red “X” (negative feedback) or a green “OK” (positive feedback), each $\sim 2.9^\circ$ dva, and was displayed for 1,670 ms (Fig. 10). This interval also served as the intertrial interval (ITI). In the gamified format, over the same 1,670 ms interval, the black circle with a gray border transitioned into a stylized alien “flying saucer” (UFO) viewed from above, with the black center representing the UFO’s canopy and the gray border its hull (see Fig. 9B). If the trial was successful, the UFO quickly dodged an incoming asteroid, if unsuccessful, it collided with the asteroid. To enhance the sense of motion, a background of moving stars gradually appeared at the onset of this animation and then faded out before its conclusion.

The Go-Only blocks were identical to the SC blocks except that they contained no change trials. The go trials in these blocks were structurally the same as the No-Change trials, with the same cue, timing, and feedback arrangements.

STANDARD format (bimanual)

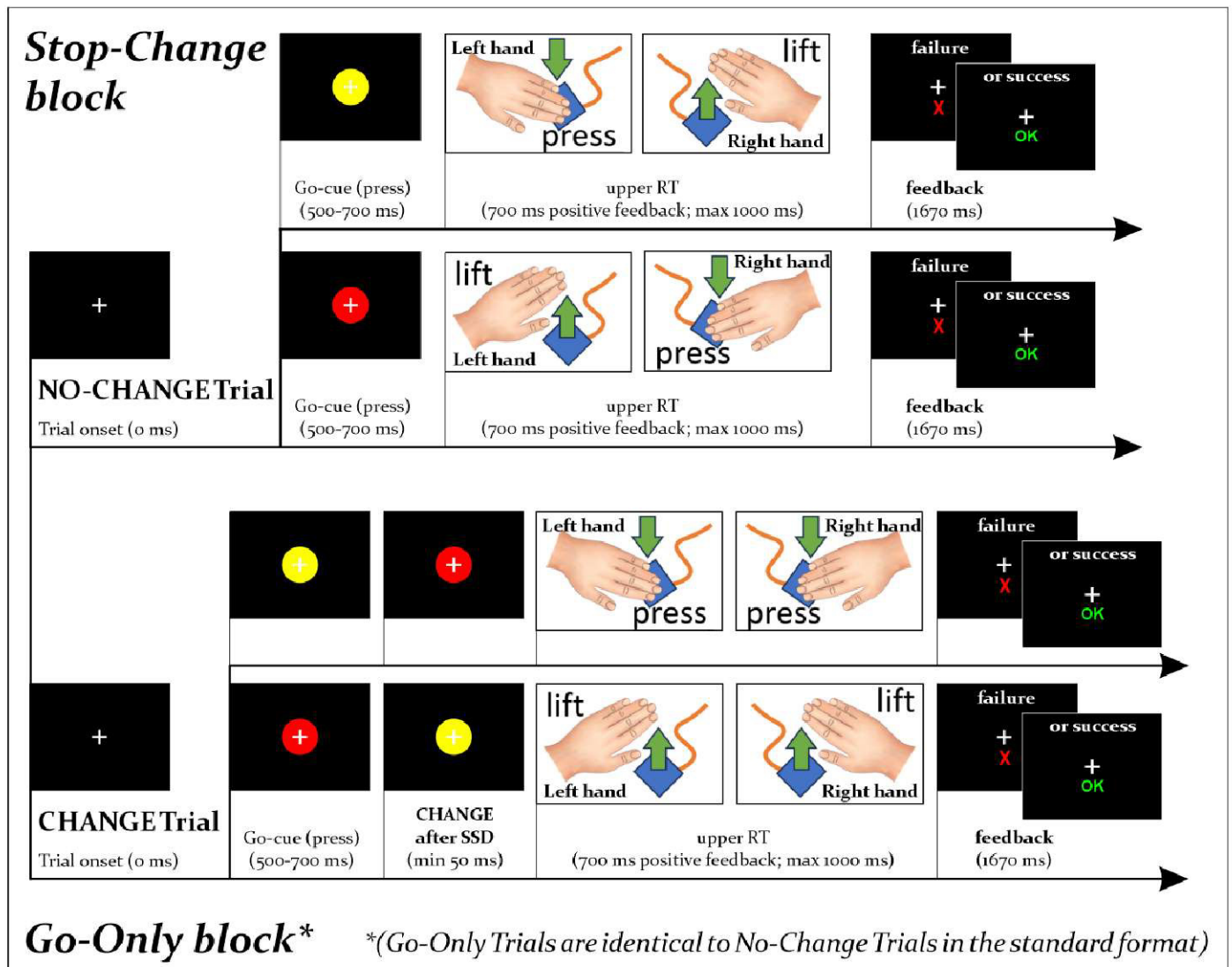


Figure 10: Task sequence for the standard format, illustrating the trial structure for Change and No-Change trials. As an example, the bimanual condition is shown, however timings are identical between the two response modes. In a Change trial (top row), the trial begins with a fixation cross, followed by a Go-cue (press). After a variable stop-signal delay (SSD), a Change signal (yellow circle) appears, requiring participants to lift both hands instead of pressing with the right hand and lifting with the left hand (always opposite actions in bimanual go trials, see Methods). If the response is correctly executed within the time limit (700 ms), positive feedback (green "OK") is displayed (response are recorded within 1000 ms). In a No-Change trial (bottom row), participants receive a Go-cue (press), but no Change signal follows. If participants fail to comply with the instructed action, they receive negative feedback (red "X"). Go-Only trials (not explicitly shown) follow the same structure as No-Change trials, requiring only the initially cued press without any stopping or changing.

GAMIFIED format (unimanual)

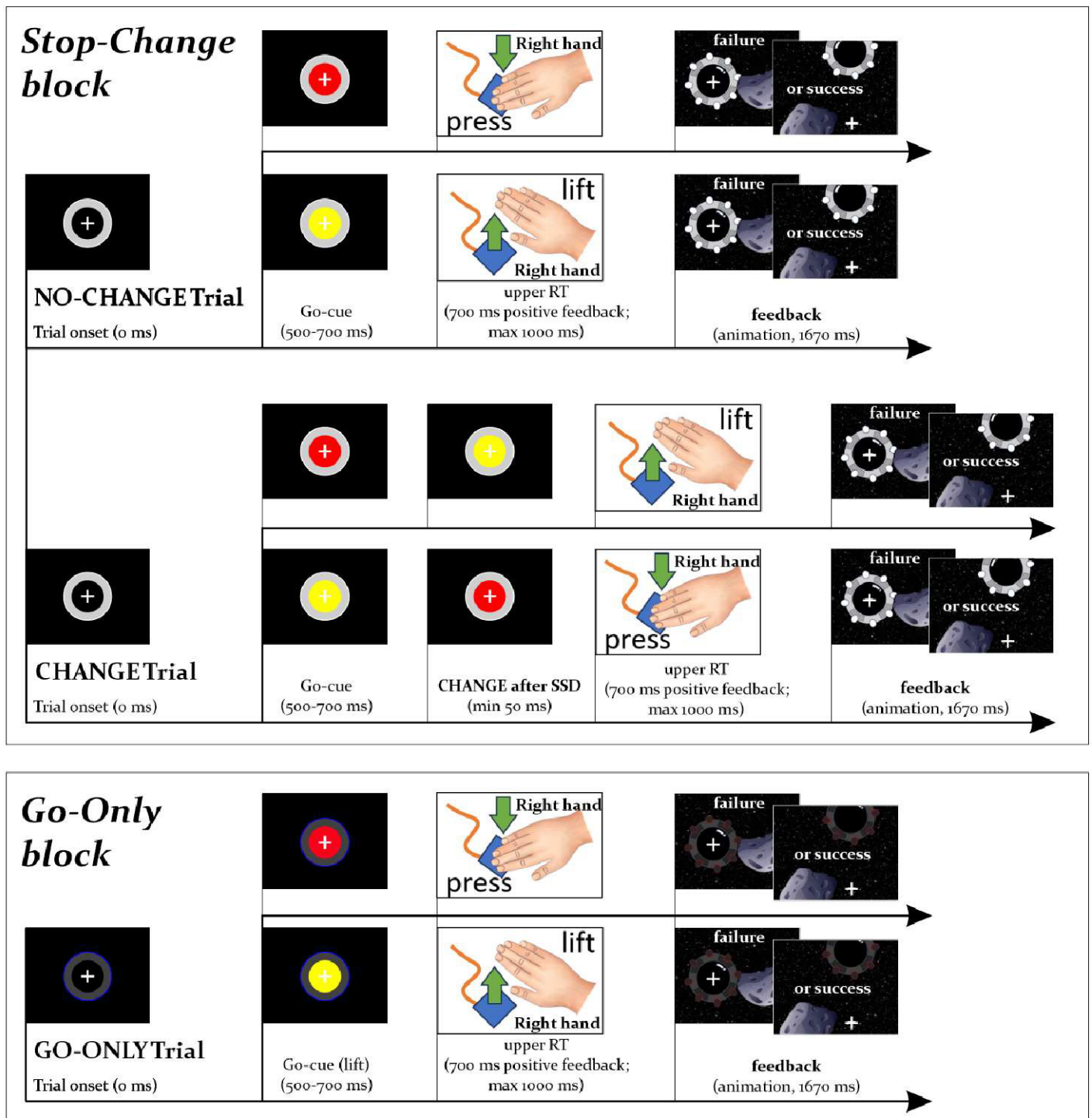


Figure 11: Task sequence for the gamified format, illustrating the trial structure for Change, No-Change, and Go-Only trials (as an example the unimanual condition is shown). In a Change trial (top row), the trial starts with a fixation cross embedded in a gray-bordered cue representing the hull of the UFO. A Go-cue (lift in this example) is presented, requiring the participant to act as fast as possible. After a variable stop-signal delay (SSD), the cue changes to a red circle, signaling the required response change. The participant must cancel the initiated lift action and press. Incorrect execution results in negative feedback in the form of a collision with an asteroid, shown with UFO hull lights active (failure). In a No-Change trial (middle row), the Go-cue (lift) appears, but no Change signal follows, requiring the participant to continue the action as initiated. In a Go-Only trial (bottom row), the cue has a dark gray hull with a blue outline. Correct responses results in a positive feedback, where the UFO successfully avoids the asteroid. The upper RT for positive feedback is 700 ms, while responses are recorded for a maximum of 1000 ms. This gamified format integrates space-themed visual cues and feedback animations to enhance engagement while maintaining identical timings with the standard format.

4.2.6. Statistical analysis of behavioral data

We used RTs and SSRTs as our primary behavioral measures. Normality of each parameter's distribution was tested using the Shapiro-Wilk test, and homogeneity of variances was assessed using the Levene test. Whenever the assumptions for standard ANOVA were violated, we applied aligned rank transform analysis of variance (ART-ANOVA, Leys and Schumann, 2010) and the aligned rank contrast for Post-Hoc testing. For simplicity, lift and press actions were collapsed and not analyzed separately. All Post-Hoc comparisons were corrected using the Bonferroni method. To confirm the validity of our SSRT estimates, we additionally verified the basic assumptions of the independent race model (horse-race model) at the group level (see section 4.2.1. for an individual subject approach). To do this, we conducted a repeated-measures ANOVA on RTs with Trial Type (levels: change-failure, no-change), Response Mode (levels: bimanual, unimanual), and Task Format (levels: gamified, standard) as within-subject factors, on the premise that change-failure trials should have shorter RTs than no-change trials.

In addition, we ran a repeated-measures ANOVA on p-failure (the proportion of failed change trials), with Task Type (bimanual, unimanual) and Task Version (gamified, standard) as within-subject factors, to verify that the staircase algorithm maintained a ~50% failure rate appropriately across conditions.

However, the primary goal of this study was to evaluate proactive control (e.g., strategic slowing) and reactive control (prEMG measures and SSRTs). To examine how response modes influenced RTs across blocks (go-only vs. stop-change) and how these interacted with Trial Type and Task Format, we conducted a three-way rm-ANOVA with Trial Type (go-only, no-change, change-success), Task Format (gamified, standard), and Response Mode (bimanual, unimanual) as within-subject factors. Finally, we performed a two-way repeated-measures ANOVA on SSRT with Response Mode (bimanual, unimanual) and Task Format (gamified, standard) as the within-subject factors.

4.2.7. Partial response EMG preprocessing and analysis

EMG preprocessing and variable extraction were based on publicly available scripts shared by Raud et al. (2021; <https://osf.io/rqnuj/>) in conjunction with their guidelines for prEMG analysis (Raud et al., 2022). Unless otherwise specified, the parameters used strictly followed those in the original scripts. The adapted routines were implemented in MATLAB (MathWorks, version 2023a) and EEGLAB (Delorme & Makeig, 2004; version 24.2.1).

First, raw EMG signals were bandpass filtered between 20 and 250 Hz using a second-order Butterworth filter and then resampled to 500 Hz. Epochs were extracted from -200 ms to 2,000 ms relative to the onset of the go signal. As per Raud et al. (2022), any trial whose mean baseline activity exceeded 100 μ V would be discarded, although in this dataset no prEMGs were actually rejected under this criterion. The EMG signals were then root-mean-square transformed over a ± 5 -point moving average window and baseline-corrected. For each participant and each right-hand muscle, the resulting epochs were concatenated and z-scored on a block-by-block basis.

Following Raud et al. (2022), an EMG burst was considered present in a trial if any data point exceeded a threshold of 1.2 (expressed in standard deviation units across all trials). This threshold, also used consistently in recent studies (Huster et al., 2020; Raud et al., 2020a; Raud et al., 2020b), was verified visually and found to perform well. Peak latency was defined as the time point at which the amplitude reached its maximum. Onset latency was determined by searching backward in time from the peak, stopping when a continuous 8-ms window of data points fell below the amplitude threshold. Finally, peak and onset latencies were recalculated relative to the stop-change onset by subtracting the respective SSD.

A critical question is how many prEMG trials are needed to obtain reliable estimates. Raud et al. (2022) addressed this by iteratively reducing the number of subjects with the lowest counts of prEMGs (starting at six) in a relatively large dataset ($n = 46$). They found that reliability for prEMG onset latency remained high regardless of reductions in either trials or participants, whereas peak latency reliability improved with the number of trials and plateaued at around 13 trials. They concluded that having approximately 15 (or more) prEMG trials is optimal, yet reliability estimates at the group level remained high even when including participants with fewer than 10 trials, indicating an overall strong reliability of prEMGs.

Based on these findings, we analyzed prEMGs inclusively, retaining all participants regardless of their prEMG counts. We then reanalyzed the data by excluding participants with low numbers of prEMGs, as a control, using paired-sample t-tests on onset and peak latencies. Finally, we used Pearson's correlation to examine relationships among prEMG onset latency, prEMG peak latency, and SSRT.

4.3. Results

4.3.1. Horse race model assumptions

Table 3 provides an overview of all behavioral parameters across both response modes and task formats

	Bimanual		Unimanual	
	Gamified	Standard	Gamified	Standard
p(failure)	0.47 ± 0.03	0.48 ± 0.08	0.48 ± 0.04	0.48 ± 0.05
SSD	310.6 ± 84.4	310.6 ± 81.4	281.7 ± 100.5	320.3 ± 95.9
SSRT	295.6 ± 59.3	299.9 ± 56.4	263.7 ± 36.4	249.8 ± 36.5
Change RT	549.6 ± 93.0	552.5 ± 96.6	438.5 ± 77.7	452.7 ± 71.5
Change-Failure RT	556.5 ± 54.3	566.3 ± 86.0	482.7 ± 61.0	509.7 ± 64.4
No-Change RT	612.9 ± 55.6	614.3 ± 67.0	553.0 ± 79.5	580.7 ± 77.8
p(No-Change omission)	0.03 ± 0.04	0.03 ± 0.04	0.01 ± 0.02	0.01 ± 0.02
p(No-Change choice error)	0.05 ± 0.05	0.08 ± 0.09	0.04 ± 0.03	0.04 ± 0.03
No-Change Accuracy	0.91 ± 0.07	0.87 ± 0.11	0.94 ± 0.04	0.94 ± 0.04
Go-Only RT	473.2 ± 45.9	469.5 ± 45.8	433.9 ± 32.8	437.7 ± 42.1
p(Go-Only omission)	0.02 ± 0.05	0.02 ± 0.05	0.01 ± 0.04	0.01 ± 0.02
p(Go-Only choice error)	0.04 ± 0.08	0.06 ± 0.07	0.05 ± 0.03	0.05 ± 0.05
Go-Only Accuracy	0.94 ± 0.09	0.93 ± 0.08	0.94 ± 0.05	0.94 ± 0.05

Table 3. Behavioral parameters across response modes (Bimanual, Unimanual) and task formats (Gamified, Standard). The table presents mean values $\pm$ standard deviations for change-failure rates ($p(\text{failure})$), Stop-Signal Delay (SSD), Stop-Signal Reaction Time (SSRT), successful change-action reaction times (Change RT), and Change-Failure RT. Additionally, RTs, error rates, and accuracy scores (correct trials over total trials) for No-Change and Go-Only trials are provided.

Results of the rm-ANOVA on RTs with Trial Type (levels: Change-Failure, No-Change), Response-Mode (levels: Bimanual, Unimanual), and Task Format (levels: Gamified, Standard) as within-subject factors (Table 4), supported the assumption of the race-model by showing a significant main effect of Trial Type, with RTs in change-failure trials being shorter than in No-Change trials ($M_{\text{diff}} \pm SD = -61.4 \pm 74.3$). We also found a significant main effect of Response-Mode, revealing that participants were slower in the Bimanual task ($M \pm SD = 587.5 \pm 70.9$) compared to the Unimanual task ($M \pm SD = 531.5 \pm 79.6$).

These two main effects were qualified by their significant interaction. Post hoc analysis with Bonferroni correction showed that, besides all within-condition comparisons being significant, the between-condition cross-comparison of bimanual No-Change vs. unimanual change-failure was also significant ($t(20) = 4.14$, $p = 0.003$, estimate $\pm$ SE = 46.8 ± 11.3). This outcome is expected, as bimanual No-Change trials were the slowest overall, while unimanual Change-Failure trials were the fastest. Finally, we found a significant main effect of Task Format, as participants were slightly faster, on average, in the Gamified version ($M \pm SD = 551.3 \pm 77.7$) than in the Standard version ($M \pm SD = 567.7 \pm 82.3$). No other significant effects were found.

**Repeated Measures ANOVA on Response Time:
Response Mode (Bimanual, Unimanual) $\times$ Task Format (Gamified, Standard)
 $\times$ Trial Type (change-failure, no-change)**

	Df	Residual Df	MSE	F-value	Partial η^2	p-value
Response Mode	1.00	20.00	4835.8	27.25	0.577	<0.001
Task Format	1.00	20.00	1859.2	6.15	0.235	0.022
Trial Type	1.00	20.00	1104.8	143.37	0.878	<0.001
Res. Mode:Task Format	1.00	20.00	1883.2	2.62	0.116	0.121
Res. Mode:Trial Type	1.00	20.00	806.6	4.44	0.182	0.048
Task Format:Trial Type	1.00	20.00	453.1	0.34	0.017	0.566
Res. Mode:Task Format:Trial Type	1.00	20.00	291.5	0.75	0.036	0.396

Table 4. Results of the repeated measures ANOVA on response times in change-failure and No-Change trials to confirm stochastic independence of the go and stop processes. Significant effects ($p < 0.05$) are highlighted in bold. Reported values include degrees of freedom (Df), residual degrees of freedom (Residual Df), mean squared error (MSE), F-value, and p-value for each main effect and interaction. Partial eta squared (η^2) values indicate effect sizes.

We also evaluated whether the staircase algorithm functioned as intended. A non-parametric rm aligned rank transform (ART) ANOVA on p-failure with Task-Type (Bimanual, Unimanual) and Task-Version (Gamified, Standard) as within-subject factors (Table 5) revealed no significant effects, indicating that the success rate of Stop-Change trials remained consistently around 50% across all conditions. This confirmed that our estimates of reactive inhibition (i.e., the SSRT) were reliable.

**Repeated Measures Aligned Rank Transformed ANOVA on p-failure:
Response Mode (Bimanual, Unimanual) $\times$ Task Format (Gamified, Standard)**

	Df	Residual Df	F-value	p-value
Task Format	1	60	0.0203	0.887
Response Mode	1	60	3.5797	0.063
Task Format:Response Mode	1	60	0.4446	0.507

Table 5. Results of the non-parametric repeated measures Aligned Rank Transformed analysis of variance (ART-ANOVA, Leys and Schumann, 2010) on p-failure, with Response Mode (Levels: Bimanual, Unimanual) and Task Format (Levels: Gamified, Standard) as within-subject factors. Df, degrees of freedom.

4.3.2. Response modes significantly impact all types of reaction time modalities

To assess how the response modes affected latencies across blocks (Go-Only and SCT blocks), Trial Type, and Task Format, we run a three-way rm ART ANOVA on within-subject factors Trial Type (Levels: Go-Only, No-Change, Change-success), Task Format (Gamified, Standard), and Response-Mode (Bimanual, Unimanual) as the Levene test did not confirm homogeneity of variance (Table 6).

**Repeated Measures Aligned Rank Transformed ANOVA on RTs:
Response Mode (Bimanual, Unimanual) × Task Format (Gamified, Standard)
× Trial Type (Change, Go-Only, No-Change)**

	Df	Residual Df	F-value	p-value
Trial Type	2	220	145.45	<0.001
Response Mode	1	220	97.94	<0.001
Task Format	1	220	2.56	0.111
Trial Type:Response Mode	2	220	11.20	<0.001
Trial Type:Task Format	2	220	0.97	0.379
Response Mode:Task Format	1	220	2.32	0.129
Trial Type:Response Mode:Task Format	2	220	0.38	0.686

Table 6. Repeated measures Aligned Rank Transformed ANOVA on Response Time (RT). Degrees of freedom (Df), residual degrees of freedom (Residual Df), F-values, and p-values are reported. Significant effects ($p < 0.05$) are highlighted in bold.

The rm ART ANOVA on RTs revealed significant main effects of Trial Type and Response Mode. RTs in the Unimanual condition ($M \pm SD = 482.8 \pm 88.8$ ms) were shorter than those in the Bimanual condition ($M \pm SD = 545.3 \pm 90.5$ ms), with a mean difference of -62.6 ± 89.6 ms. Post hoc tests for Trial Type showed that Go-Only trials ($M \pm SD = 453.6 \pm 45.0$ ms), Change trials ($M \pm SD = 498.4 \pm 99.3$ ms), and No-Change trials ($M \pm SD = 590.2 \pm 73.9$ ms) all differed significantly from each other (all $p < 0.001$).

These main effects were qualified by a significant Trial Type × Response Mode interaction. Table 7 summarizes the post hoc comparisons. Strategic slowing is evident in both response modes, as indicated by No-Change trials being longer than Go-Only trials. Crucially, No-Change RTs in the bimanual condition are significantly slower than in the unimanual condition, suggesting greater strategic slowing in the former. However, the finding that Go-Only trials themselves differ significantly across modes leaves open the possibility that response complexity also contributes to this slowing. Moreover, in the Bimanual condition, Change-trial RTs resembled Unimanual No-Change RTs, whereas Unimanual Change-trial RTs did not significantly differ from Go-Only trials (in either mode, see boxplots in Fig. 12).

Finally, Task Format and its interactions were not significant, suggesting that the presence or absence of a gamified or standard format did not affect proactive control, as operationalized by overall RT patterns.

Aligned Rank Transformed Contrasts (Post Hoc Tests) on RTs:
Response Mode (Bimanual, Unimanual) × Trial Type (Change, Go-Only, No-Change)

Contrast					Estimate	SE	df	t-ratio	p-value
Bimanual	Change	vs	Unimanual	Go-Only	92.6	9.0	220	10.3	<0.001
Bimanual	Change	vs	Bimanual	Go-Only	58.9	9.0	220	6.6	<0.001
Bimanual	Change	vs	Unimanual	No-Change	-16.5	9.0	220	-1.8	1.000
Bimanual	Change	vs	Bimanual	No-Change	-48.4	9.0	220	-5.4	<0.001
Unimanual	Change	vs	Bimanual	Go-Only	-25.4	9.0	220	-2.8	0.076
Unimanual	Change	vs	Unimanual	Go-Only	8.4	9.0	220	0.9	1.000
Unimanual	Change	vs	Bimanual	No-Change	-132.6	9.0	220	-14.8	<0.001
Unimanual	Change	vs	Unimanual	No-Change	-100.7	9.0	220	-11.3	<0.001
Bimanual	Change	vs	Unimanual	Change	84.2	9.0	220	9.4	<0.001
Bimanual	Go-Only	vs	Unimanual	Go-Only	33.8	9.0	220	3.8	0.003
Bimanual	No-Change	vs	Unimanual	No-Change	31.9	9.0	220	3.6	0.007
Bimanual	Go-Only	vs	Bimanual	No-Change	-107.3	9.0	220	-12.0	<0.001
Unimanual	Go-Only	vs	Unimanual	No-Change	-109.1	9.0	220	-12.2	<0.001
Bimanual	Go-Only	vs	Unimanual	No-Change	-75.4	9.0	220	-8.4	<0.001
Unimanual	Go-Only	vs	Bimanual	No-Change	-141.0	9.0	220	-15.8	<0.001

Table 7. Aligned Rank Transformed post hoc contrasts on response times (RTs). The table presents estimated differences (Estimate), standard errors (SE), degrees of freedom (df), t-ratios, and p-values for pairwise comparisons. Significant effects ($p < 0.05$) are highlighted in bold.

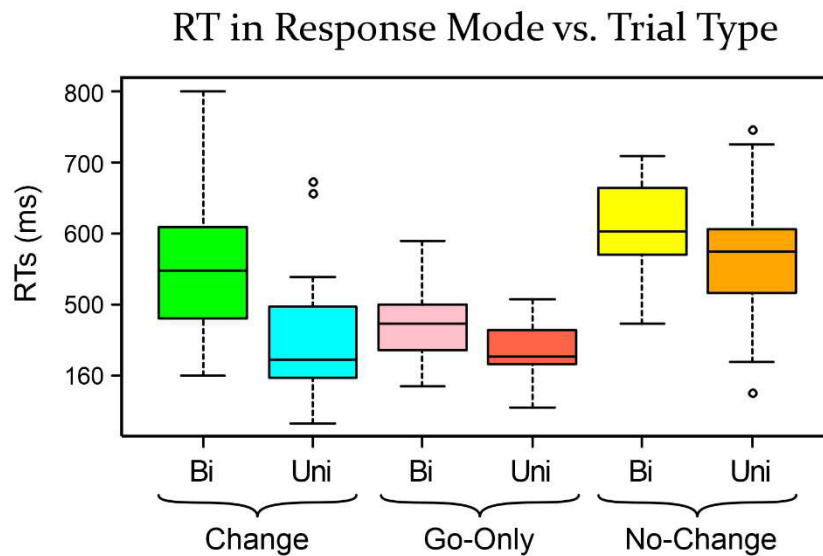


Figure 12: Reaction times (RTs) across response modes (bimanual vs. unimanual) and trial types (Change, Go-Only, and No-Change trials). Boxplots display RT means in milliseconds (ms) for each condition, with bimanual (Bi) responses shown in green, pink, and yellow, and unimanual (Uni) responses in blue, red, and orange. Change trials show the longest RTs, followed by No-Change and Go-Only trials. Bimanual responses generally exhibit longer RTs compared to unimanual responses, reflecting increased motor planning demands in more complex response conditions. For significant comparisons, see Table 7. Box plots represent the median (horizontal line within the box), the interquartile range (IQR; the height of the box), and the whiskers extend to 1.5 times the IQR or the furthest data point within that range. Outliers are represented as individual points outside the whiskers.

4.3.3. Measures of reactive inhibition: SSRT and prEMG

The two-way rm-ANOVA on SSRT (Factors: Response-Mode, Task Format) revealed a significant main effect of Response Mode ($F(1, 20) = 13.61$, $\eta^2_p = 0.405$, $p = 0.001$), as stop latencies were significantly shorter in the unimanual ($M \pm SD = 256.7 \pm 36.7$) than in the bimanual condition ($M \pm SD = 297.7 \pm 57.2$; Fig. 13A). No other significant effect was found.

With regard to prEMGs, their frequency in successful stop-change trials ($M \pm SD = 0.192 \pm 0.132$) aligned with previously reported values (Raud *et al.*, 2020a; Raud *et al.*, 2022), albeit on the lower side. Because both press and lift actions were required in our paradigm, prEMGs were detected in both the ECU and FDS muscles of the right forearm. To explore potential differences in prEMG probability, we conducted a rm ANOVA with Response Mode (bimanual vs. unimanual) and Muscle (ECU vs. FDS) as within-subject factors. This analysis revealed a significant main effect of Response Mode ($F(1, 19) = 11.38$, $\eta^2_p = 0.375$, $p = 0.003$), indicating lower prEMGs probability in the bimanual condition than in the unimanual condition. Additionally, we observed a significant Response Mode $\times$ Muscle interaction ($F(1, 19) = 5.75$, $\eta^2_p = 0.232$, $p = 0.027$), showing the highest prEMG frequency specifically in the unimanual condition when changing from press to lift (i.e., in FDS; $M \pm SD = 0.247 \pm 0.148$).

An examination of raw trial counts indicated that each participant had, on average, 62.5 correct stop-change trials per condition, yielding about 9.9 ± 5.4 prEMG trials (range: 2–20) in the bimanual condition and 13.6 ± 6.7 prEMG trials (range: 4–29) in the unimanual condition.

To assess reactive inhibition based on the timings of prEMGs, we ran paired-samples t-tests comparing onset latency, peak latency, and the SSD between response modes. The latter served as a control analysis to ensure that the conditions were comparable. All variables met normality criteria. For the full sample ($n = 20$), onset latency differed significantly between bimanual and unimanual tasks ($t(19) = 4.29$, CI [8.59, 25.00], $\text{mean}_{\text{diff}} = 16.80$, $p < 0.001$, Fig. 13B). Peak latency also showed a significant difference ($t(19) = 3.15$, CI [4.24, 21.00], $\text{mean}_{\text{diff}} = 12.62$, $p = 0.005$, Fig. 13C). In contrast, SSD did not differ significantly ($t(19) = 0.81$, CI [-17.54, 39.59], $\text{mean}_{\text{diff}} = 11.03$, $p = 0.429$).

We then repeated this analysis under a more conservative approach, excluding participants with fewer than six prEMG trials in any condition (sample $n = 14$). The results remained unchanged: onset latency differed significantly ($t(13) = 3.80$, CI [6.71, 24.36], $\text{mean}_{\text{diff}} = 15.53$, $p = 0.002$), and peak latency was also significantly different ($t(13) = 3.28$, CI [4.70, 22.89], $\text{mean}_{\text{diff}} = 13.80$, $p = 0.006$). Once again, SSD showed no significant difference ($t(13) = 1.16$, CI [-17.68, 58.40], $\text{mean}_{\text{diff}} = 20.36$, $p = 0.268$). These findings suggest a robust effect of response mode on prEMG timing indices (onset and peak), independent of the total number of prEMG trials included.

Lastly, correlation analyses revealed a strong association between SSRTs and, both, prEMG onset (Fig. 13 D, Bimanual: $r = 0.66$, $p = 0.002$; Unimanual: $r = 0.62$, $p = 0.004$) as well as peak latencies (Fig. 13 E; Bimanual: $r = 0.72$, $p < 0.001$; Unimanual: $r = 0.63$, $p = 0.003$). Also onset and peak latencies correlated strongly (Fig. 13 F; Bimanual: $r = 0.96$, $p < 0.001$; Unimanual: $r = 0.98$, $p < 0.001$). Overall, these results highlight that the timing of prEMG activity differs between bimanual and unimanual tasks, reflecting distinct reactive control demands.

Time courses of Stop-locked EMG activities for prEMG (averages over all trials) develop similarly as reported previously (Raud *et al.*, 2020a; Raud *et al.*, 2022), with a main peak around 150-160 ms (Fig. 14). However, prEMGs in the bimanual condition show a wider dispersion of burst peaks (Fig. 14D). No statistical analyses were done on prEMG time courses. Refer to Fig. 14 for qualitative comparisons of prEMGs and successful Change Trial EMG activity (Fig. 14A) or failed-Change trials (Fig. 14C). In addition, time courses of prEMG activities in individual muscles are shown for the unimanual condition (Fig. 14B) and for the bimanual condition (Fig. 14D).

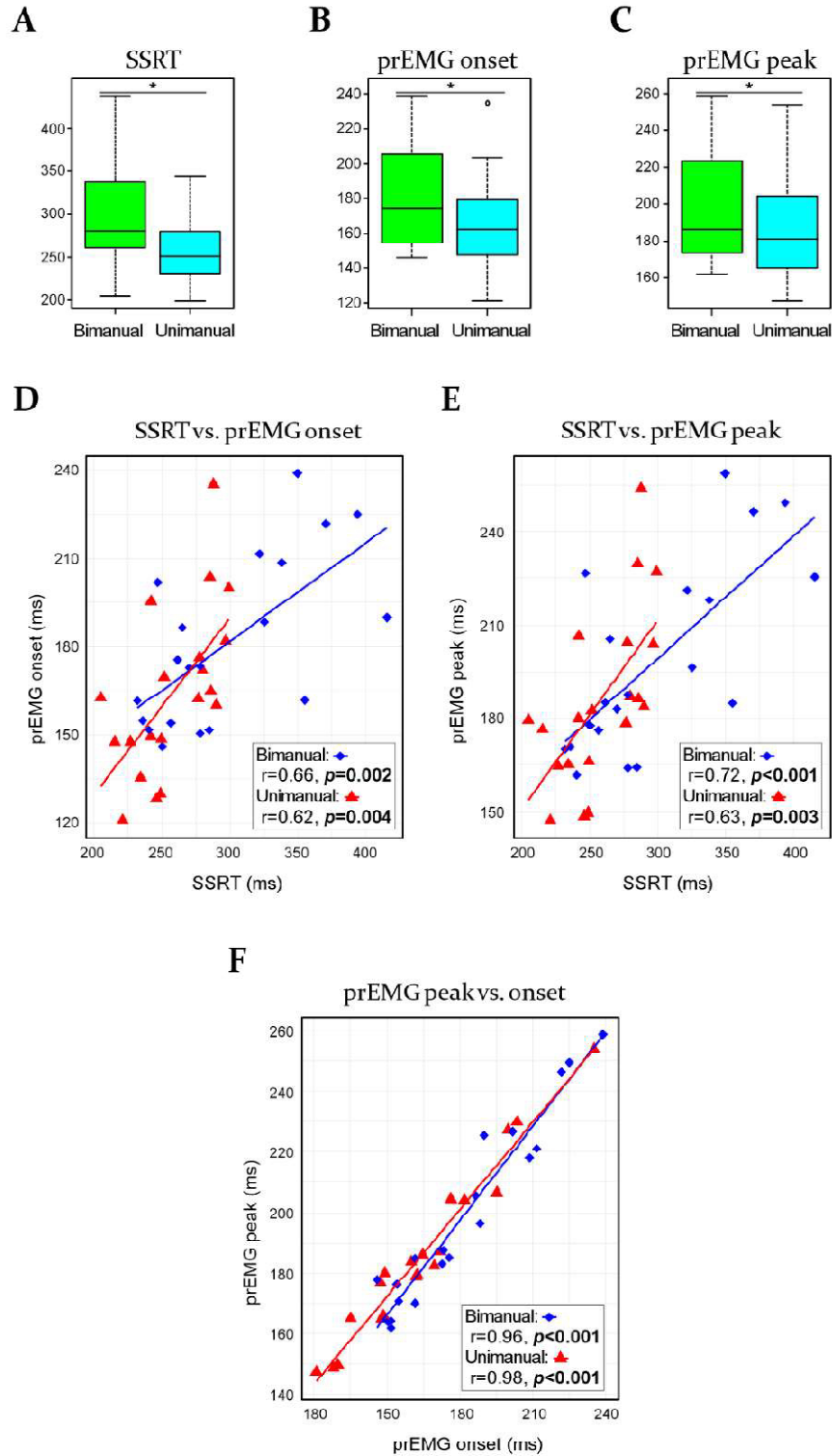


Figure 13: Comparison of Stop Signal Reaction Time (SSRT), partial response EMG (prEMG) onset, and prEMG peak across bimanual and unimanual conditions (in milliseconds, ms). Panels (A–C) show boxplots comparing SSRT (A), prEMG onset (B), and prEMG peak (C) between bimanual (green) and unimanual (blue) conditions. Panels (D–E) display correlations between SSRT and prEMG onset (D) and SSRT and prEMG peak (E), with significant positive relationships in both conditions (bimanual: blue diamonds, unimanual: red triangles). Panel (F) shows a strong correlation between prEMG peak and onset. For all panels, the box plots represent the median (horizontal line within the box), the interquartile range (IQR; the height of the box), and the whiskers extend to 1.5 times the IQR or the furthest data point within that range. Outliers are represented as individual points outside the whiskers.

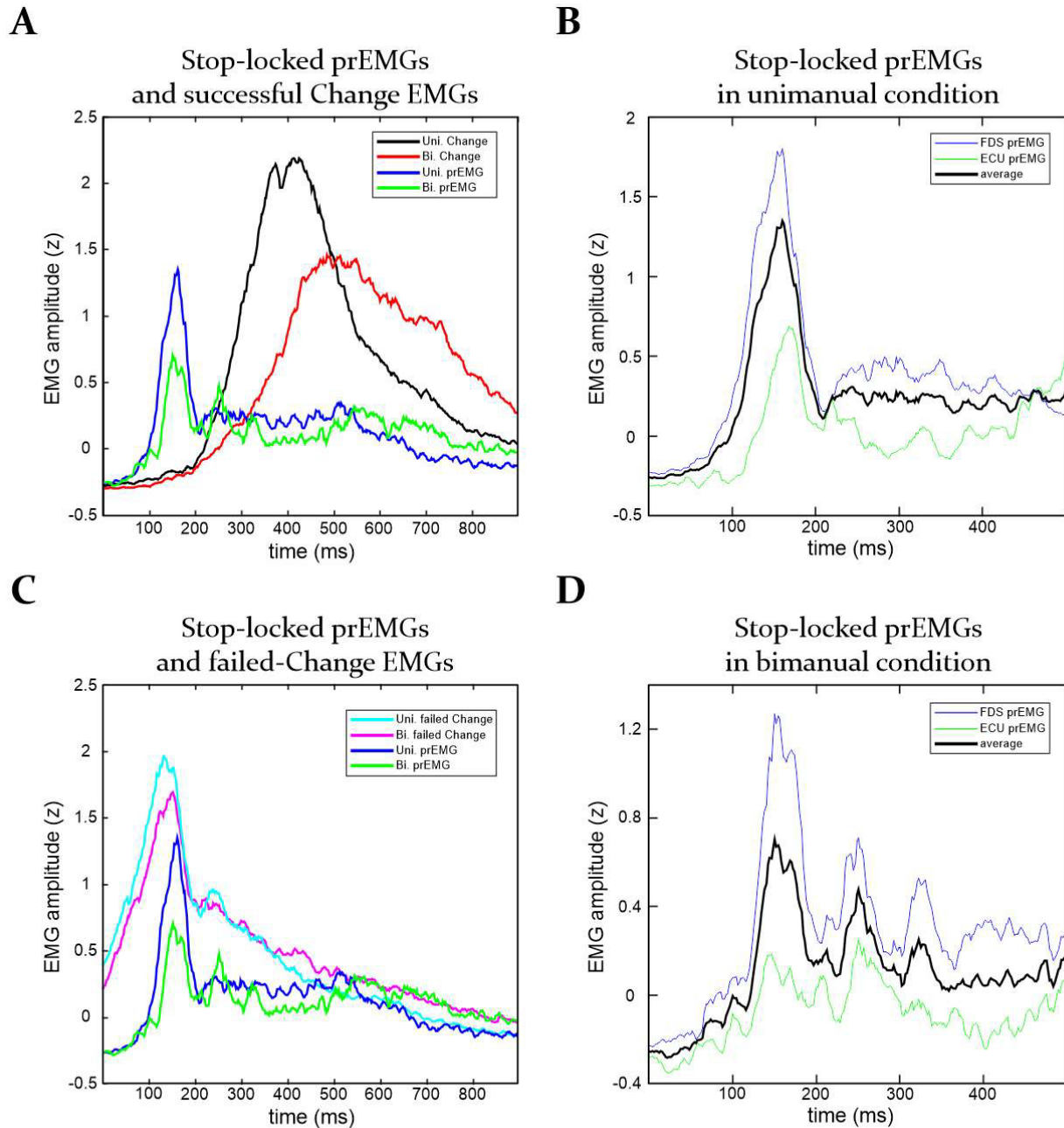


Figure 14: Time courses of Stop-locked EMG activity for partial response EMG bursts (prEMG) and for successful or failed Change activity across response modes (unimanual and bimanual). (A) Stop-locked prEMG activity and successful Change EMG signals in unimanual (Uni) and bimanual (Bi) conditions. Unimanual Change (blue) and Bimanual Change (red) EMG traces indicate successful movement execution, while prEMG activity (green for bimanual, black for unimanual) represents early movement-related activation, while the peak coincides with its inhibition. (B) Stop-locked prEMG activity in the unimanual condition, showing the separate EMG traces for the flexor digitorum superficialis (FDS) (blue) and extensor carpi ulnaris (ECU) (green), with the averaged signal (black). (C) Stop-locked prEMG activity and failed Change EMG signals. Unimanual (cyan) and bimanual (magenta) failed Change trials. (D) Stop-locked prEMG activity in the bimanual condition, showing separate FDS (blue) and ECU (green) traces, along with the averaged signal (black). Overall, prEMG signals reveal early movement preparation and inhibition processes, with evident differences between unimanual and bimanual conditions. Time in milliseconds (ms). EMG amplitudes are in z-scores, see Methods.

4.4. Discussion

Expanding on the findings of Cavallo et al. (2014) and Cardellicchio et al. (2021a), both of which indicate the behavioral and neurophysiological involvement of a slower, more selective stopping mechanism, this study takes inspiration from the established relationship between the joint Simon effect and the broader interrelation of bimanual and joint action tasks (e.g., Della Gatta et al.(2017)). By adapting methodologies from selective inhibition studies, we aimed to develop a bimanual SCT that could function as a positive control for co-representation.

Our primary hypothesis posited a greater involvement of proactive control in situations where participants are aware that an upcoming trial may demand selective stopping, while simultaneously requiring intense motor engagement and re-engagement, as is the case in the SCT. To investigate whether proactive control influences motor preparation, we compared No-Change trials against Go-Only trials. In both the bimanual and unimanual conditions, we observed pronounced differences between these two trial types, aligning with our expectations.

However, in contrast to Raud et al. (2020a), who did not detect such a divergence, we found a significant difference in No-change RTs across response modes. This finding indicates a stronger proactive control component in the bimanual condition, thereby supporting our initial hypothesis.

Furthermore, both of our reactive inhibition measures, i.e., prEMGs and SSRT, revealed longer stopping latencies in the bimanual mode. We also found that action re-engagement required more time in the bimanual condition. Notably, participants in the bimanual task tended to act in relative synchrony with both hands across all trial types, suggesting that they proactively prepared an overarching action set rather than independently controlling each effector's engagement or re-engagement.

Our findings are somewhat consistent with the initial conceptualization of selective inhibition by Aron et al. (2008), who employed a bimanual SST. In that study, one block featured informative cues, giving participants foreknowledge about which hand they might need to stop, while another block had non-informative cues. Surprisingly, when cues were informative, stopping latencies became longer, yet the stopping-interference effect (SIE) was shorter. The authors interpreted this result in terms of selective inhibition imposing less interference on the non-selected hand. Although Aron et al. (2008) did not dismiss the possibility that proactive motor preparation could account for faster SIE under foreknowledge, differently from us, they did not observe significant difference in RTs, leading them to favor a selective inhibition mechanism.

In the present study, we do not provide causal evidence that a biased proactive motor preparation directly prolongs stopping latencies during selective stopping, nor that a separate selective inhibition mechanism is involved. Crucially, however, our data reveal that the heightened motor-planning demands inherent in a bimanual SCT have a wide-ranging influence, affecting motor preparation, stopping, and re-engagement across the board. This overarching impact underscores the importance of considering how multiple concurrent actions can shape inhibitory control and action reprogramming, indicating how these demands may mirror co-representation and the challenges expected in a joint action scenario.

Moreover, the findings by Aron et al. (2008) have not been replicated consistently. Multiple studies have reported null or even opposing results regarding SSRT differences between informative and non-informative conditions (Cirillo *et al.*, 2018; Lavalée *et al.*, 2014; Raud and Huster, 2017; Smittenaar *et al.*, 2013), suggesting that the role of selective inhibition and proactive motor preparation in these tasks may be more complex than initially proposed.

Raud et al. (2020a) distinguished their design from previous work by contrasting an unimanual stop-signal task (SST) with a bimanual, selective SST, which required stopping only one component of a multi-action response. Interestingly, unlike our findings, they found no significant differences in SSRTs or strategic slowing

between the unimanual and bimanual conditions. They concluded that their results supported the recruitment of a single inhibitory stopping mechanism, with the net behavioral output depending largely on action-specific motor preparation rather than on a fundamentally distinct selective inhibition process.

The findings from Raud et al. (2020a) contribute to the ongoing debate over whether a truly selective inhibition mechanism, as originally proposed by Aron et al. (2008), genuinely exists. Consequently, it also remains uncertain whether the outcomes reported by Cavallo and Cardellicchio can be fully explained by such a selective inhibition mechanism. The same uncertainty applies to our results. Instead, alternative explanations, such as global stopping with varying degrees of action-specific motor preparation, may be equally or more plausible.

Nevertheless, our paradigm was specifically designed as a positive control for a future joint SCT rather than a direct investigation into selective inhibition. Consequently, it would be unwise to interpret our findings as explicit support for, or a refutation, of the dual-mechanism perspective (i.e., distinct global vs. selective inhibition). However, in line with Raud et al. (2020a), we also believe that what appears to be a selective inhibition effect may, in fact, reflect differences in motor preparation rather than an entirely separate inhibitory process.

We draw this conclusion because we observed direct behavioral evidence of altered motor preparation, namely, longer No-Change trial durations in the bimanual SCT, alongside longer stopping latencies. In contrast, Raud et al. (2020a) detected only neurophysiological signs of biased motor preparation in a less demanding bimanual SST, without corresponding differences in stopping latencies. Thus, it seems more likely that our results highlight how increased motor preparation can simultaneously prolong stopping latencies, rather than indicating a discrete selective inhibition mechanism.

As noted in the Introduction, this interpretation aligns with neurophysiological data suggesting that proactive control systematically biases sensorimotor and attentional systems in anticipation of a stop signal (Elchlepp *et al.*, 2016; Langford *et al.*, 2016). Although not definitive proof, our findings extend these conclusions to a Stop-Change paradigm, indicating that such biasing not only shapes motor preparation but may also modulate reactive inhibition.

This study provides promising evidence that the bimanual SCT reliably elicits longer stopping latencies and exhibits biased motor preparation, thereby offering a robust benchmark for a future joint SCT. In essence, the bimanual SCT captures what might happen if one “over”-co-represents, however not another person’s action, but two components of one’s own bimanual action. By requiring a selective stop or change in one effector (e.g., the right hand) while continuing the other, the task may probe how representing multiple action elements simultaneously shapes inhibitory control in a joint context. This design effectively magnifies the constraints that could arise in a joint action context, where an individual must inhibit only their own movement while continuing to “co-represent” a partner’s ongoing actions.

Beyond this, we also explored the potential impact of gamification on proactive and reactive control. As predicted, gamification did not fundamentally alter core inhibitory metrics, including No-Change RTs, SSRT, or prEMGs. While the gamified version may improve participant engagement or enjoyment, it did not appear to compromise or substantially enhance the inhibitory processes under investigation. This outcome is significant for future research, suggesting that task formats can be adapted to be more engaging without introducing confounds in critical inhibition measures.

In conclusion, our findings confirm that the bimanual SCT effectively manipulates and reveals changes in motor preparation when one component of multiple actions must be inhibited or reorganized in parallel. While it does not directly address joint or social contexts, the paradigm’s capacity to induce clear modifications in motor control provides a solid basis for future research that may incorporate social elements

5. STUDY II: JOINT EXPERIMENT

5.1 Background and Hypotheses

In the Positive Control Experiment, we demonstrated the validity of our Stop-Change Task (SCT) design, as all predictions were confirmed by our selective-bimanual SCT serving as a positive control paradigm. Building on these findings, we next administered the gamified unimanual version of the SCT to naïve participants under both joint and solo conditions while simultaneously recording EMG and EEG data.

Given the high yield of prEMGs observed in the flexor digitorum superficialis (FDS) during the Control Experiment (when participants switched from a press action to a lift action), we opted to simplify the SCT by assigning only go press actions (and change lift actions) to the naïve participants and likewise go lift (and change press) actions to the co-actor. This ensured a consistent subdivision of action types across the experiment between the two individuals and helped reduce overall task complexity. As in Study I, the co-actor was, in fact, a lab member who pretended to be naïve.

Our hypotheses for the Joint Experiment remain largely consistent with those of the Control Experiment. Since our data indicated that the increased motor-planning demands inherent in a bimanual SCT influenced motor preparation, stopping, and re-engagement in a transversally, we formulated our hypotheses accordingly:

- *HP1: Stronger Proactive Control in the Joint Condition*
We anticipate that participants in the joint condition will exhibit stronger proactive control than those in the solo condition. This should be reflected in longer No-Change RTs (i.e., strategic slowing), as participants preemptively adjust their response speed in anticipation of potential stop-change signals.
- *HP2: Increased Duration of Reactive Inhibition Indices*
We expect that reactive inhibition measures, specifically, SSRTs and prEMG latency, will be prolonged under the joint condition, driven by co-representation.
- *HP3: Altered Frontocentral Stop-Signal P3*
In the joint condition, we anticipate an altered pattern of the frontocentral stop-signal P3, reflecting changes in the efficiency of the inhibitory process when co-representation is involved. This electrophysiological marker is typically associated with successful inhibition, and deviations from the standard pattern would suggest a modulation of inhibitory control in the presence of a co-actor.

Taken together, these hypotheses align with the idea that biased motor preparation, this time elicited by co-representing a partner's actions rather than by selective (bimanual) stopping, can influence both proactive and reactive dimensions of inhibition.

5.2 Methods

5.2.1. Participants, sample size estimation, and exclusion criteria

To compute the sample size estimation, we used the effect size reported by Cavallo et al. (2014) in their third and final experiment (which employed TMS). It was calculated via G*Power (3.1.9.7, Faul et al., 2007) for a two-tailed paired t-test, with 90% power and a 5% significance level. Power analysis revealed a required sample size of 32 participants. A total of 33 participants with no history of neurological or psychiatric disorders

(6 males, age range 19–32 years) were enrolled after providing written informed consent, as one subject did not complete the experiment and was excluded.

As in Study II, exclusion criteria addressed potential violations of the independent race model assumption. Again, we compared each participant's mean RT on unsuccessful change trials with their mean RT on No-Change trials (including choice errors and premature responses) for joint and solo conditions, however, no participant showed numerically longer No-Change RTs. Furthermore, no participants had more than 15% omission errors in No-Change trials or exceeded the 0.75/0.25 thresholds for failed Change trials in any condition (see 4.2.1. for more details about the exclusion criteria).

The final sample comprised 32 participants (6 males, $M \pm SD = 23.5 \pm 4.1$ years). Two left-handed participants were also included in the sample, as it has been shown that handedness does not impact inhibitory control (Mancini and Mirabella, 2021). Handedness was assessed via the Edinburgh Handedness Inventory ($M \pm SD: 84.4 \pm 43.6$; Oldfield, 1971). All participants were naïve to the purpose of the study and completed the experiment in a single session lasting approximately 2.5 hours. This included about 60 minutes for informed consent procedures, EEG, and EMG setup, followed by 90 minutes for instructions, practice, testing, and short breaks between blocks. Participants received monetary reimbursement for travel expenses, if applicable. The study was approved by the Ethical Committee of the IRCCS Istituto Centro San Giovanni di Dio Fatebenefratelli (Brescia e 25/2020) and was conducted in accordance with the Declaration of Helsinki.

5.2.2. Procedure

As for Study I and II, experiments were conducted in the same electromagnetically shielded, dimly lit, and sound-attenuated room. Upon arrival, participants were informed about the experimental procedures and provided informed consent. We acquired EEG signals using 74 passive Ag/AgCl electrodes (EasyCap, BrainProducts GmbH, Munich, Germany), while surface EMG signals were recorded using disposable Ag/Cl electrodes (Delsys) all connected to a g.HIamp amplifier system (g.tec Medical Engineering GmbH, Schiedlberg, Austria), sampled at 9,600 Hz. EMG electrodes were placed in a bipolar montage over the extensor carpi ulnaris (ECU) and flexor digitorum superficialis (FDS) on the right forearm. Recordings were made without filters, and skin-electrode impedance was maintained below 5 k Ω . For visualization purposes only, a band-pass filter (10–2,500 Hz) and a notch filter were applied.

The co-actor was a member of the lab who acted as a naïve participant. A total of five lab members alternated as co-actors across experiments (all female). Participants and co-actors were seated side by side (~90 cm away), with participants on the left and co-actors on the right. Both individuals faced identical screens distanced approximately 60 cm away (eye-to-screen distance; ASUS VG248QE, 60 Hz refresh rate, 1920 $\times$ 1080 resolution, 61 cm $\times$ 34.4 cm). We used the same hand levers as in Study II (see 4.2.2.), one for each individual. Both rested comfortably on a chinrest to limit motion during EEG recordings.

Participants were instructed not to grip the lever or adopt a rigid posture, but instead to perform shovel-like motions for both hand lifts and presses. As in Study II, to reduce excessive muscle tension in the ECU and FDS muscles, the thumb and pinky finger on each hand were gently secured with a small strip of medical micropore tape (3M, Minnesota, U.S.), preventing rigid finger extension or inadvertent lever gripping. The same custom-script in MATLAB® combined with Psychophysics Toolbox 3 (Brainard and Vision, 1997; Kleiner *et al.*, 2007), with only some minor adaptations, controlled the presentation of visual stimuli and the events of the SCT.

5.2.3. Joint Stop-Change Task setup

The same gamified unimanual SCT used in the Control Experiment was administered twice in this experiment: once in a joint condition and once in a solo condition. As before, we included SC blocks (comprising Stop-Change and No-Change trials) along with a Go-Only block (consisting solely of Go-Only trials, which were identical to No-Change trials). In addition to EEG recordings, a major change from the Control Experiment was the introduction of a storytelling component that assigned distinct roles to the participant and co-actor within the gamified task, which will be described in detail later.

Another critical difference was that participants were instructed only to perform go presses and lift changes, while the co-actor always lifted on go trials and pressed on change trials. This arrangement offered several advantages, i), it simplified the task and minimized potential fatigue; ii), it replicated the opposing actions required in the bimanual positive-control; iii), it ensured a consistent subdivision of action types, reinforcing the distinct roles implied by the storytelling elements; iv), the co-actor's lift actions were silent, reducing the likelihood of auditory artifacts during the joint condition.

In fact, after a brief training phase, both players' right hands were concealed under black cardboard boxes lined with sound-absorbing foam to avoid any visual or auditory distractions. While participants believed this setup served to prevent mutual interference, the co-actor was secretly instructed not to move at all on go (lift) trials, thus eliminating any sound and further limiting potential confounds.

For each condition, participants completed two Stop-Change (SC) blocks, each consisting of pseudo-randomly intermixed No-Change trials (100 trials, 66%) and Change trials (50 trials, 33%), and one Go-Only block of 75 trials (all certain-go). The Go-Only block, which was inserted between the two SC blocks, served as a less demanding pause. In total, 600 SC and 150 Go-Only trials were administered. Conditions were counterbalanced across participants, who always completed an entire set of blocks for one condition before switching to the other.

At the start of the experiment, participants undertook a practice phase comprising 45 trials (15 Go-Only, 30 SC) to familiarize themselves with the task. This training phase employed a modified bimanual SCT (see Section 4.2.3.), where each player controlled one lever instead of both hands. Participants who needed more practice were permitted an additional training block. Altogether, counting both practice and experimental blocks, participants completed 630 SC trials and 165 Go-Only trials.

During practice, the players could see each other's hands, and the co-actor genuinely performed the task, reinforcing the belief that they were both actively engaged. Additionally, these practice trials provided detailed feedback (too slow, commission, omission, or no response) for each participant, analogous to the hand-specific feedback in the bimanual task.

In contrast, in the main experimental blocks, only the participants' actions were recorded employing the unimanual SCT version, and feedback was limited to positive or negative responses (as in the gamified version of Control Experiment). However, participants were led to believe that they were coordinating with the co-actor in the joint condition when, in reality, they performed the exact same unimanual SCT in both conditions.

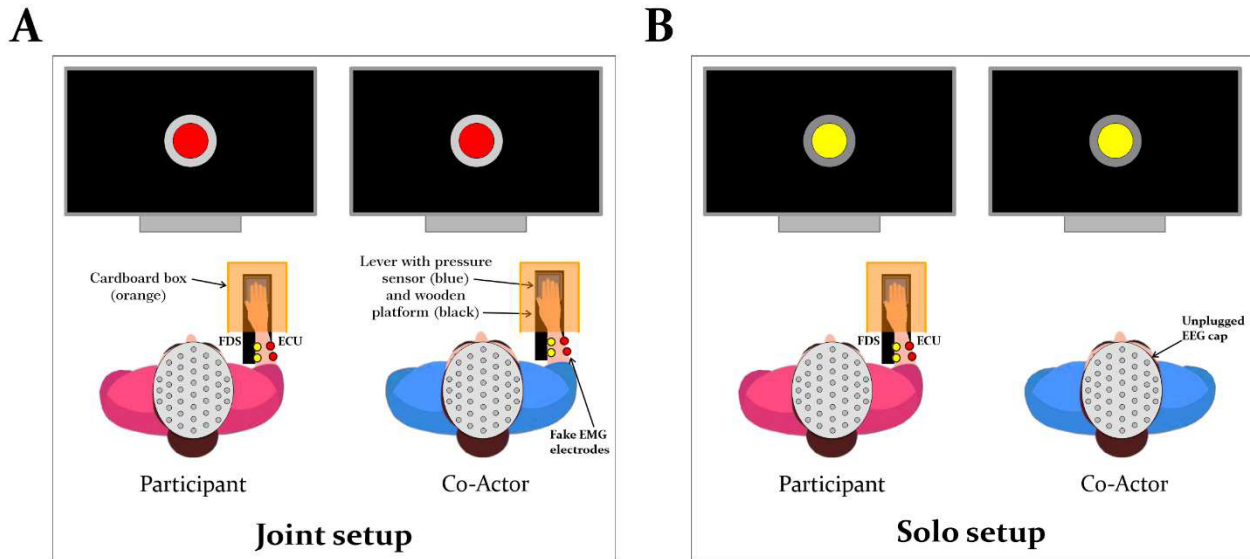


Figure 15: Experimental setup of Joint and solo conditions. (A) Joint setup (see section 4.2.5. for task mechanics). Participants were always seated on the left side, co-actors on the right side, both with chinrests. The latter pretended to be a naïve participants and wore an unplugged EEG cap, with fake EMG electrodes on the right forearm. Hands were covered by cardboard boxes with noise cancelling foam. The light gray graphical version of the gamified UFO from Control Experiment, depicted with active lights in its feedback animation (see Figure 9B, left), was used in the Joint condition. (B) In the Solo condition, the darker gray 'lights off' graphical version of the UFO was presented. Only the participant acted in this condition, while the co-actor passively observed.

5.2.4. Belief induction

The only substantial difference between the two conditions, beyond the co-actor pretending to act behind the cardboard box in the joint blocks and sitting inactive (arms crossed) in the solo blocks, was in the storytelling and belief induction components.

Upon arrival, each participant was introduced to their co-actor. They were already aware that this would be a joint EEG experiment, since during recruitment they had been informed that arriving late would inconvenience the other participant. Once introduced, both individuals were reminded that they would have been co-registered and that they would collaborate on a portion of the experiment, which was organized similarly to a simple video game with role-playing elements. Critically, the game required two distinct player roles: an astronaut and an aerospace engineer.

To assign these roles, the experimenter used a simple HTML site, ostensibly acting as a randomizer. In truth, the site always assigned the astronaut role when clicking with the left mouse button and the engineer role when clicking with the right mouse button. The two players decided freely who would click the button, but the co-actor knew to choose the right button if they were the one clicking, ensuring that they received the engineer role. In no instance did participants overtly question the authenticity of the randomizer, and the role assignment always proceeded smoothly.

After the roles were assigned, the two players were taken to separate rooms for EMG and EEG cap placement. Once the participant's setup was complete, the co-actor also wore a real EEG cap (without gel), along with inactive reference and EMG electrodes like those used by the participant. An experimenter then guided the co-actor to the recording room, where the participant was waiting. However, the experimenter only pretended to connect the co-actor's electrodes to the amplifier, in reality only the participant's EEG data were recorded.

When both individuals were ready, the experimenter began with the task instructions, which included the gamified storytelling elements. Great care was taken to ensure consistency: a total of 28 slides were used to deliver the story and task explanations uniformly across participants.

5.2.5. Storytelling and instructions

Briefly, participants were told the following story: The astronaut (the actual participant), who was exploring a distant star system in collaboration with an engineer on Earth (the co-actor), becomes stranded on an alien planet after their spaceship sustains irreparable damage. Searching for help, the astronaut discovers remnants of a now-extinct but highly advanced alien civilization, including a functional “flying saucer” (UFO). Realizing this UFO might allow a safe return to Earth, the astronaut (inside the UFO) and the engineer (remotely from Earth) must coordinate, whenever possible, to pilot this alien craft through an asteroid field.

Each experimental block was framed as a distinct game level, continuing the overarching storyline. The quality of the connection between the UFO and Earth, which determined the speed of the link, varied across levels, thereby altering how players could interact during each trial:

When the signal between the UFO and Earth is only “mediocre” (i.e., during joint SC blocks), both players must act as quickly as possible (using opposite movements) in “action” trials (No-Change trials) whenever the UFO’s canopy changes color to red (go-cue), indicating an incoming asteroid. Should the engineer act too slowly or incorrectly (signaled by a yellow change cue in Change trials), the astronaut has an opportunity to correct the engineer’s mistake by performing the lift action, thus salvaging these so-called “correction” trials.

However, when the connection between the UFO and Earth is “excellent” (i.e., during the joint Go-Only block), both players again respond as quickly as possible in “action” trials (Go-Only trials). This time, roles are switched: if the astronaut is too slow or makes a mistake, the engineer, leveraging the fast connection speed, can correct the trial with the astronaut’s action (i.e., a press). However, in practice, change signals did not actually appear in this condition unless the astronaut voluntarily omitted or mis-performed the response, making it effectively a pure Go-Only scenario.

Importantly, communication between the UFO and Earth is not guaranteed for the entire journey. In such instances, the astronaut must fly the UFO alone (solo condition). Under these circumstances, sometimes the astronaut can leverage the UFO’s built-in navigation system (solo Go-Only block), and if the astronaut fails or is too slow, the UFO itself initiates the “correction” automatically (in practice, the change signal never appeared, unless astronaut voluntarily mis-performed, as in the joint Go-Only).

At other times, however, both Earth communication and the UFO’s navigation system are unavailable (solo SC blocks). In these trials, the astronaut must respond as quickly as possible to the red UFO’s canopy (No-Change cues), but occasional random navigation errors arise (marked by the yellow canopy, i.e., change cue), prompting the astronaut to correct the action via the opposite response (press in Change trials).

Operationally, the SC blocks were identical across conditions, but the participant was led to believe that Change cues in the joint condition (when the connection with Earth was “mediocre”) were triggered by co-actor errors, giving them the ability to correct these mistakes. In this scenario, each Change cue was effectively framed as feedback about the co-actor’s performance while both players attempted to synchronize their responses to the go cues.

Conversely, in the solo condition, participants were told that the Change cues stemmed from a purely random source (which was actually true), so “salvaging” any given trial became a strictly individual sub-goal. In the joint condition, by contrast, successfully correcting a trial served a collective sub-goal within the overarching mission to return home, thereby adding a cooperative element to the same SC block mechanics.

To further differentiate between the two conditions, the light gray graphical version of the gamified UFO from the Control Experiment, depicted with active lights in its feedback animation (see Figure 9B, left), was used in the Joint condition to emphasize that a functional connection had been established between Earth and the UFO. Conversely, in the Solo condition, the darker gray 'lights off' version was presented, highlighting the absence of a connection (Fig. 9B, right).

5.2.6. ERP preprocessing

As in Study I, the preprocessing pipeline was adapted from our previous studies (Bortoletto *et al.*, 2021; Guidali *et al.*, 2023; Zazio *et al.*, 2022), and tailored specifically for ERP analysis requirements. Custom scripts were developed in MATLAB R2023a (The MathWorks, Natick, MA, USA), incorporating functions from both EEGLAB v2023.1 (Delorme and Makeig, 2004) and FieldTrip (Oostenveld *et al.*, 2011), with default parameters applied unless otherwise specified.

Continuous EEG data were high-pass filtered at 0.2 Hz using EEGLAB's windowed sinc FIR filter function (`pop_eegfiltnew`), downsampled to 600 Hz (`pop_resample`), and segmented into epochs ranging from -500 ms to 2000 ms relative to the go-cue.

We then applied automated channel rejection using the Local Outlier Factor (LOF) method (Kumaravel *et al.*, 2022a), implemented via the NEAR plugin for EEGLAB (Kumaravel *et al.*, 2022b), to identify and remove outlier channels and flatlines (LOF threshold = 1.5).

A first, lenient round of automatic artifact rejection was performed in two steps, each based on a different statistical approach. The joint probability method (`pop_jointprob`, with global and local thresholds set to 5 SD) identified epochs with extreme amplitude deviations, while the kurtosis method (thresholds set to 6 SD) detected non-Gaussian distributions indicative of atypical neural activity.

We first applied Independent Component Analysis (ICA) to remove blink-related components before running the Source-Estimate-Utilizing Noise-Discarding (SOUND) algorithm. Eye blinks are large, stereotyped artifacts that ICA can reliably isolate due to their high and globally distributed variance. ICA components associated with horizontal and vertical eye movements were automatically identified and removed using the 'ICLabel' plugin for EEGLAB. The ICA decomposition was performed with the '`pop_runica`' function (infomax algorithm), using 74 channels and extracting an equal number of components. Following ICA, the EEG data were average-referenced.

Then, we applied the SOUND algorithm (spherical 3-layer model, regularization parameter: $\lambda = 0.1$; Mutanen *et al.*, 2018) to identify and discard noise-contaminated measurements. Following the interpolation of previously rejected channels, a low-pass filter was applied at 40 Hz (4th-order IIR Butterworth filter, using the EEGLAB function `pop_basicfilter`). A second automatic artifact rejection step was then performed, using thresholds of 4.5 standard deviations (SD) for local and 3.5 SD for global detection.

The data were maintained in average reference, epoched from -200 to 1000 ms relative to the change cue, and baseline-corrected using the 200 ms to 5 ms interval preceding the change cue. The data were then averaged by experimental condition.

5.2.7. Statistical analysis of behavioral data, preMGs, and ERPs

We used RTs and SSRTs as our primary behavioral measures. Normality of each parameter's distribution was tested using the Shapiro-Wilk test, and homogeneity of variances was assessed using the Levene test. Whenever the assumptions for standard ANOVA were violated, we applied aligned rank transform analysis of

variance (ART-ANOVA, Leys and Schumann, 2010) and the aligned rank contrast for Post-Hoc testing. All Post-Hoc comparisons were corrected using the Bonferroni method.

As in the Control Experiment, to confirm that our SSRT estimates were valid, we verified the basic assumptions of the independent race model and evaluated the performance of the staircase algorithm, conducting a rm-ANOVA on RTs with Trial Type (levels: Change-Failure, No-Change) and Condition (levels: Joint, Solo) as within-subject factors. We also ran a t-test on p-failure between conditions, to verify that the staircase algorithm worked properly in both cases.

To examine how actions influenced RTs across blocks (Go-Only vs. Stop-Change) and how these interacted between conditions, we conducted a two-way rm-ANOVA with Trial Type (Go-Only, No-Change, Change-Success) and Condition (Joint, Solo) as within-subject factors. Finally, we performed t-tests on SSRT, prEMG onset, and peak. The prEMGs were preprocessed as in the Control Experiment (see 4.2.7.).

Regarding statistical analyses of ERPs, the final sample included all participants ($n = 32$). On average, 2.8 ± 1.9 channels were rejected per participant, and $13.6 \pm 3.1\%$ of stop-change trials were excluded following preprocessing. ERP comparisons were performed using cluster-based permutation tests for dependent samples, encompassing first the time window from 0 to 500 ms relative to the stop-change cue, and then focusing specifically on the 250-500 ms window, to study alteration of the fronto-central Stop P3. The analysis was conducted with FieldTrip's 'ft_timelockstatistics' function, employing a Monte Carlo approximation with 3000 permutations (Maris and Oostenveld, 2007).

5.3. Results

5.3.1. Horse race model assumptions

First, we verified the assumption of the SCT, by comparing the RTs of No-Change and Change-Failure trials (see Table 8 for an overview of all behavioral parameters). In both trial types, movements were performed in response to the (initial) go-cue. However, in Change-Failure trials, the initial action was executed because the go-process was completed before the stop-process, preventing the subsequent re-engagement of the change action. Therefore, the mean RTs of the Change-Failure trials should be shorter than those of the No-Change trials (Verbruggen *et al.*, 2019).

We conducted a non-parametric repeated-measures aligned rank transform (ART) ANOVA on RTs with Trial Type (levels: Change-Failure, No-Change) and Condition (levels: Joint, Solo) as within-subject factors (Table 9). The analysis supported the assumption by showing a significant main effect of Trial Type, with RTs in Change-Failure trials being shorter than in No-Change trials ($M_{\text{diff}} \pm SD = 85.1 \pm 54.6$). We also found a significant main effect of Condition, revealing that participants were slower in the Solo condition ($M \pm SD = 498.4 \pm 57.4$) compared to the Joint condition ($M \pm SD = 470.6 \pm 77.2$). No other significant effects were found.

	Joint	Solo
p(failure)	0.49 ± 0.02	0.49 ± 0.01
SSD	277.19 ± 70.11	315.78 ± 44.12
SSRT	225.38 ± 31.35	209.15 ± 37.96
Change RT	322.14 ± 38.91	311.34 ± 36.72
Change-Failure RT	425.53 ± 57.99	458.32 ± 42.48
No-Change RT	515.60 ± 67.51	538.38 ± 39.71
p(No-Change omission)	0.01 ± 0.01	0.01 ± 0.02
p(No-Change choice error)	0.06 ± 0.04	0.05 ± 0.04
No-Change Accuracy	0.93 ± 0.04	0.93 ± 0.04
Go-Only RT	313.10 ± 60.03	321.42 ± 50.92
p(Go-Only omission)	0.01 ± 0.01	0.01 ± 0.01
p(Go-Only choice error)	0.00 ± 0.01	0.00 ± 0.00
Go-Only Accuracy	0.99 ± 0.01	0.99 ± 0.01

Table 8. Behavioral parameters across conditions (Joint, Solo). The table presents mean values ± standard deviations for change-failure rates (p(failure)), Stop-Signal Delay (SSD), Stop-Signal Reaction Time (SSRT), successful change-action reaction times (Change RT), and Change-Failure RT. Additionally, RTs, error rates, and accuracy scores (correct trials over total trials) for No-Change and Go-Only trials are provided.

Next, we evaluated whether the staircase algorithm functioned as intended. A Wilcoxon signed-rank test with continuity correction was conducted to compare p-failure between the Joint and Solo conditions. The results indicated no significant difference between conditions ($V = 227.5$, $p = 0.187$), suggesting that the success rate of Stop-Change trials remained consistently around 50% across all conditions. This confirmed that our estimates of reactive inhibition (i.e., the SSRT) were reliable.

Repeated Measures Aligned Rank Transformed ANOVA on RTs: Trial Type (Change-Failure, No-Change) × Condition (Joint, Solo)				
	Df	Residual Df	F-value	p-value
Trial Type	1	93	188.44	<0.001
Condition	1	93	14.81	<0.001
Trial Type:Condition	1	93	0.74	0.393

Table 9. Results of the rm ART ANOVA on response times in change-failure and No-Change trials to confirm stochastic independence of the go and stop processes. Significant effects ($p < 0.05$) are highlighted in bold. Reported values include degrees of freedom (Df), residual degrees of freedom (Residual Df), F-value, and p-value for each main effect and interaction.

5.3.2. Conditions do not modulate proactive control (HP1)

To assess how the conditions affected RTs across blocks (Go-Only and SCT blocks) and Trial Types, we run a two-way rm ART ANOVA on within-subject factors Trial Type (Levels: Go-Only, No-Change, Change-success) and Condition (Joint, Solo) as the Levene test did not confirm homogeneity of variance (Table 10).

Repeated Measures Aligned Rank Transformed ANOVA on RTs: Trial Type (Change, No-Change, Go-Only) × Condition (Joint, Solo)				
	Df	Residual Df	F-value	p-value
Trial Type	2	155	240.49	< 0.001
Condition	1	155	2.02	0.157
Trial Type:Condition	2	155	2.77	0.066

Table 10. Repeated measures Aligned Rank Transformed ANOVA on Response Time (RT). Degrees of freedom (Df), residual degrees of freedom (Residual Df), F-values, and p-values are reported. Significant effects ($p < 0.05$) are highlighted in bold.

The rm ART ANOVA on RTs revealed only a significant main effect of Trial Type. Post hoc tests for Trial Type showed that Go-Only trials ($M \pm SD = 317.3 \pm 55.4$ ms) and Change trials ($M \pm SD = 316.7 \pm 37.9$ ms) were significantly different from No-Change trials ($M \pm SD = 527.0 \pm 56.1$ ms; all $p < 0.001$). However, Go-Only and Change trials were not different ($p=1$). The main effect of Condition or its interaction was not significant, suggesting no modulation of proactive control in joint actions.

5.3.3. Measures of reactive inhibition: SSRT and prEMG (HP2)

A two-tailed paired t-test was conducted to compare SSRT between the Joint and Solo conditions (HP2). The results revealed a significant difference between conditions, $t(31) = 2.82$, $p = 0.008$, indicating that SSRT was significantly longer in the Joint condition than the Solo condition ($M_{diff} \pm SD = 16.2 \pm 34.8$; 95% CI [4.48, 27.96]; Cohen's $d = 0.50$; see Table 8 and Figure 16A).

Regarding prEMGs, their frequency in successful stop-change trials was substantially higher in the current experiment (39.6%) compared to Study II (19.2%). Because only press-to-lift change actions were required, prEMGs were recorded exclusively from the FDS muscle of the right forearm. A paired t-test comparing prEMG counts between the joint and solo conditions indicated a significant difference, $t(31) = 2.25$, $p = 0.032$, with more prEMGs observed in the joint condition ($M \pm SD = 20.9 \pm 6.4$) than in the solo condition ($M \pm SD = 18.7 \pm 6.3$; $M_{diff} \pm SD = 2.3 \pm 19.8$). Only two participants produced fewer than six prEMGs in one of the conditions (two and five prEMGs, respectively). Given the larger overall sample ($n = 32$), all participants were retained for the final analyses.

As in Study II, to assess reactive inhibition based on the timings of prEMGs (HP2), we ran paired-samples t-tests comparing onset latency, peak latency, and the SSD between conditions. All variables met the normality criteria. Onset latency ($t(31) = 1.01$, CI [-3.76, 11.11], $M_{diff} = 3.67$, $p = 0.322$, Fig. 16B), as well as peak latency was not significantly different ($t(31) = 1.22$, CI [-2.56, 10.23], $M_{diff} = 3.83$, $p = 0.231$, Fig. 16C). In contrast, SSD was significantly different ($t(31) = -3.69$, CI [-70.27, -20.22], $M_{diff} = -45.24$, $p < 0.001$), as the delay was on average longer in the Solo condition, than in the Joint condition.

Correlation analyses revealed again a strong association between SSRTs and both prEMG onset (Fig. 16D; Joint: $r=0.44$, $p=0.011$; Solo: $r=0.44$, $p=0.011$) as well as peak latencies (Fig. 16E; Joint: $r=0.47$, $p=0.006$; Solo: $r=0.48$, $p=0.005$).

Regarding the time courses of Stop-locked EMG activities for prEMG (averages over all trials), they develop consistently between conditions with a main peak around 150 ms (Fig. 17). Refer to Fig. 17 for qualitative comparisons of prEMGs and successful Change Trial EMG activity (Fig. 17A) or failed-Change trials (Fig. 17B).

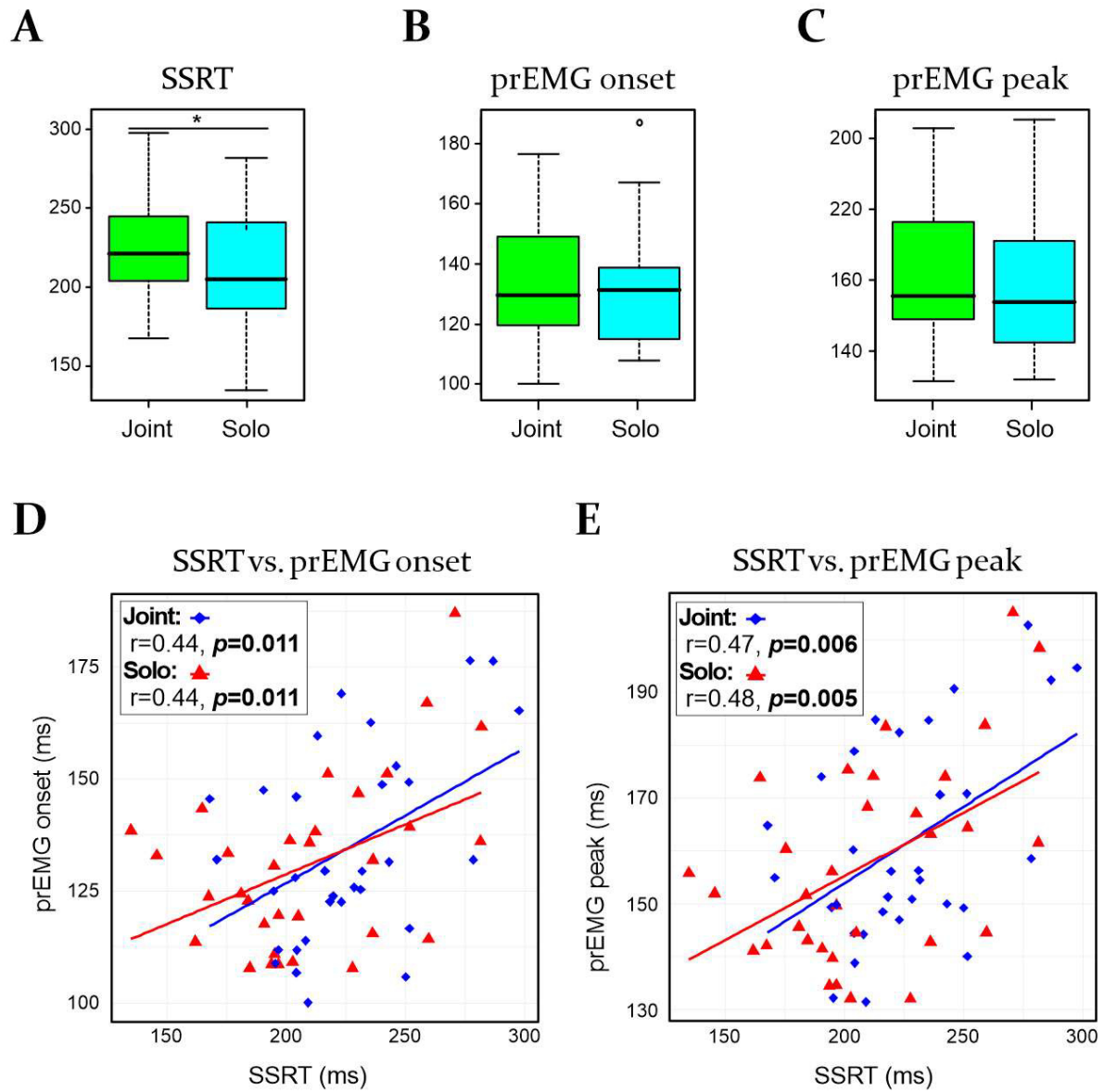


Figure 16: Comparison of Stop Signal Reaction Time (SSRT), partial response EMG (prEMG) onset, and prEMG peak across Joint and Solo conditions (in milliseconds, ms). Panels (A–C) show boxplots comparing SSRT (A), prEMG onset (B), and prEMG peak (C) between Joint (green) and Solo (blue) conditions. Panels (D–E) display correlations between SSRT and prEMG onset (D) and SSRT and prEMG peak (E), with significant positive relationships in both conditions (Joint: blue diamonds, Solo: red triangles). For all panels, the box plots represent the median (horizontal line within the box), the interquartile range (IQR; the height of the box), and the whiskers extend to 1.5 times the IQR or the furthest data point within that range. Outliers are represented as individual points outside the whiskers.

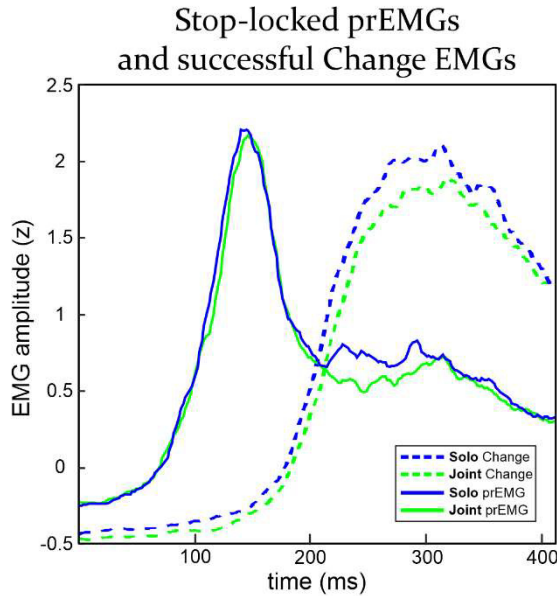
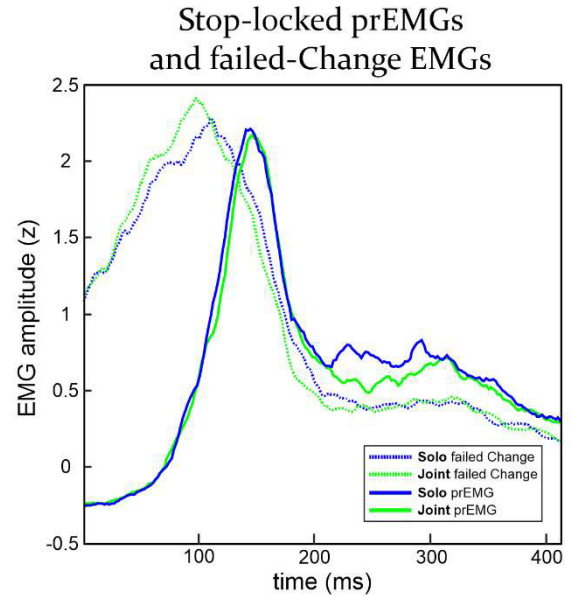
A**B**

Figure 17: Time courses of Stop-locked EMG activity for partial response EMG bursts (prEMG) and for successful or failed Change activity across conditions (Joint and Solo). (A) Stop-locked prEMG activity and successful Change EMG signals in Joint (green) and Solo (blue) conditions. Dotted EMG traces indicate successful change-movement execution, while prEMG activity (continuous line) represents early movement-related activation, while the peak coincides with its inhibition. (B) Stop-locked prEMG activity and failed Change EMG signals. The dotted lines show failed Change trials EMG activity. Overall, prEMG signals reveal early movement preparation and inhibition processes, with no evident differences between conditions. Time in milliseconds (ms). EMG amplitudes are in z-scores, see Methods.

5.3.4. Event-related potentials

As a first preliminary step, we performed a cluster-based permutation test for dependent samples across all channels and compared No-Change (Fig. 18A) and Stop-Change trials (Fig. 18D-E), starting from the go-cue/change-cue onset up to 500 ms. Consistent with expectations, given the substantial differences between the two trial types, two significant clusters (one positive, one negative; both $p < 0.001$) emerged, spanning the entire period of interest.

Next, we examined cortical response differences between Stop-Change Failure trials and Stop-Change Success trials. Comparisons were made across all channels and time points from 0 to 500 ms after the appearance of the change-cue. As expected, significant differences emerged, revealing two main clusters. A positive cluster spanned the entire period of interest (cluster-corrected $p < 0.001$; Fig. 18B), and a negative cluster was identified from 180 to 400 ms (cluster-corrected $p < 0.001$; Fig. 18C).

The first cluster captures the time-shifted cortical activity that arises because, in failed Stop-Change trials, the initial go process has already concluded, whereas in successful trials the inhibition process was still underway. The second cluster, in turn, highlights the earlier onset of the P3 in successful Stop-Change trials compared to failed ones (Hervault *et al.*, 2024).

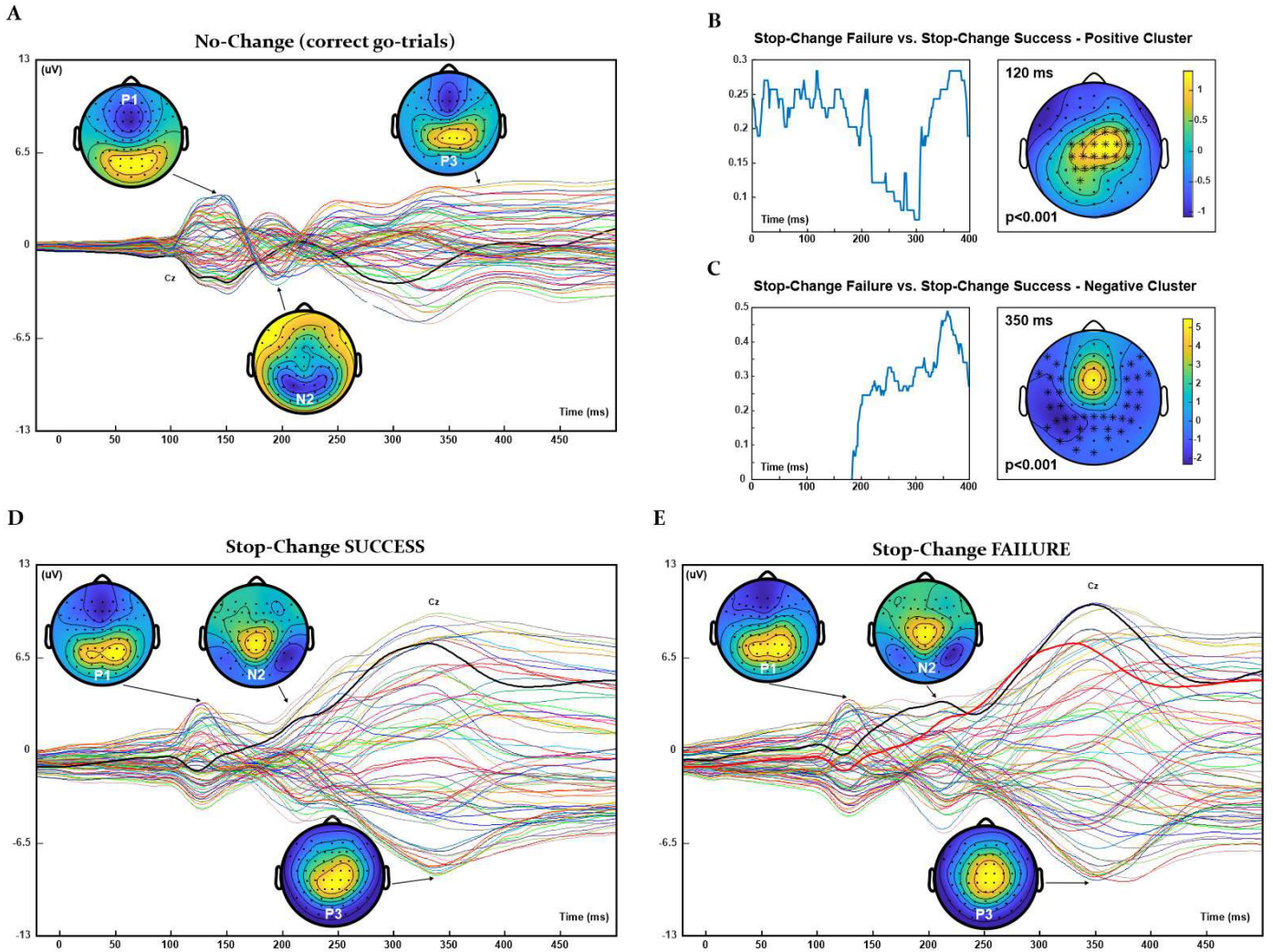


Figure 18. Grand average ERP waveforms with topographical distributions and cluster-based permutation results for Stop-Change Failure vs. Success trials. (A) ERP waveforms for No-Change trials (correct go trials in the Stop-Change blocks), with scalp maps showing the P1, N2, and P3 components. (B) Significant positive cluster ($p < 0.001$) for Stop-Change Failure vs. Stop-Change Success trials, spanning over the whole period of interest with a centro-parietal topography. (C) Significant negative cluster ($p < 0.001$) for the same contrast, peaking around 350 ms. The left panels show the time course of cluster significance, and the right panels display the topographical distribution at the cluster's peak. Black asterisks indicate significant electrodes contributing to the cluster. (D) ERP waveforms for Stop-Change Success trials, with Cz highlighted in black. (E) ERP waveforms for Stop-Change Failure trials, showing differences in amplitude and timing compared to Success trials. The Cz electrode is highlighted in black, with the corresponding trace from the Success condition overlaid in red, illustrating the earlier onset in successful inhibition.

Next, given the pronounced difference between failed and successful Stop-Change trials, we compared the Joint and Solo conditions separately for Stop-Change Failure (Fig. 19A-B) and Stop-Change Success trials. As an initial, broad-ranging approach, we conducted a cluster-based analysis spanning the 0–500 ms window after the change-cue. No significant clusters emerged for the Success trials. However, for the Failure trials, we identified a significant positive cluster between 260 and 390 ms, peaking at 280 ms (cluster-corrected $p = 0.039$; Fig. 19C), revealing an earlier onset and greater amplitude of the P3 component in the Solo condition (Fig. 19A), with respect to the Joint condition (Fig. 19B). No additional significant effects were found.

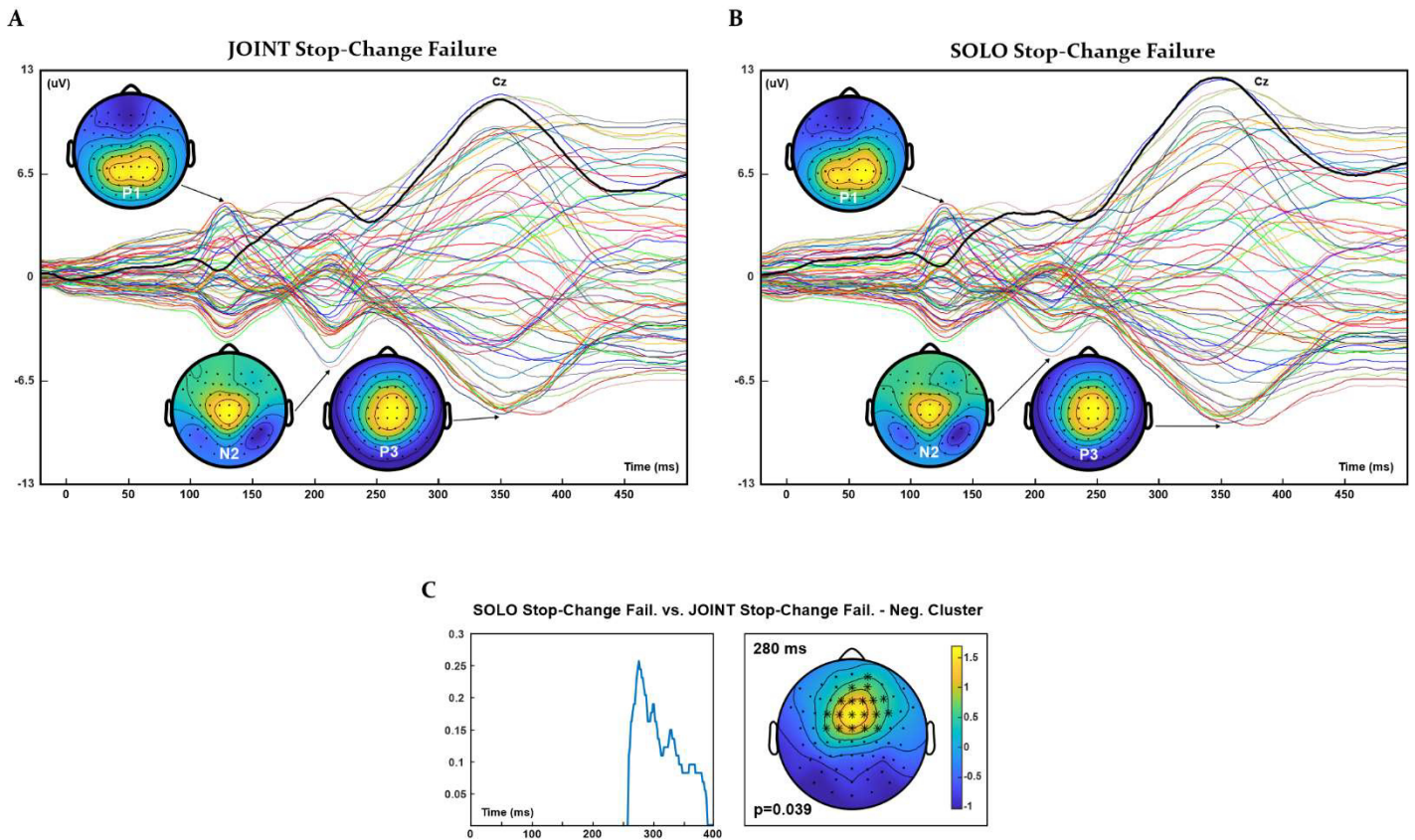


Figure 19. Grand average ERP waveforms with topographical distributions and cluster-based permutation results for Stop-Change Failure trials. (A) Stop-Change Failure trials in the Joint condition show a reduced P3 component compared to (B) Stop-Change Failure trials in the Solo condition. Each trace represents the EEG response from a single electrode, and the overlaid topographical maps illustrate ERP components at 125 ms (P1), 210 ms (N2), and 350 ms (P3). The Cz electrode is highlighted in black in both panels. (C) A significant negative cluster ($p = 0.039$) emerged for the contrast between Solo and Joint Stop-Change Failure trials, with a fronto-central scalp distribution peaking at 280 ms and spanning the interval from 260 to 390 ms, indicating an earlier onset and a greater activation in the Solo condition. The left panel shows the time course of cluster significance, while the right panel presents the topographical distribution at the cluster's peak. Black asterisks indicate electrodes contributing significantly to the cluster.

Given our specific hypothesis (HP3) that the frontocentral stop-P3 would differ between Joint and Solo conditions, we conducted a targeted cluster-based comparison in the 250–400 ms time window, which encompasses the typical peak latency of the P3. Collapsing across trial types (Stop-Change Success and Failure), we identified two significant clusters in the Joint (Fig. 20A) vs. Solo (Fig. 20B) contrast: a negative cluster ($p = 0.032$; Fig. 20C) spanning 260–355 ms, and a positive cluster ($p = 0.033$; Fig. 20D) spanning 251–356 ms. Both clusters, particularly the positive one, were driven by the earlier onset and greater amplitude of the P3 in the Solo condition compared to the Joint condition, as clearly seen in the Cz activity (Fig. 20E), a representative frontocentral site typically associated with the stop-P3.

Next, we examined each trial type separately. For Stop-Change Success trials, no significant clusters were found. However, for Stop-Change Failure trials, the previously observed cluster re-emerged (Fig. 19C) with even stronger significance ($p = 0.011$). This finding reinforces the interpretation that the stop-signal P3 is particularly sensitive to differences in reactive inhibition demands between Joint and Solo conditions, especially in the context of failed Stop-Change trials.

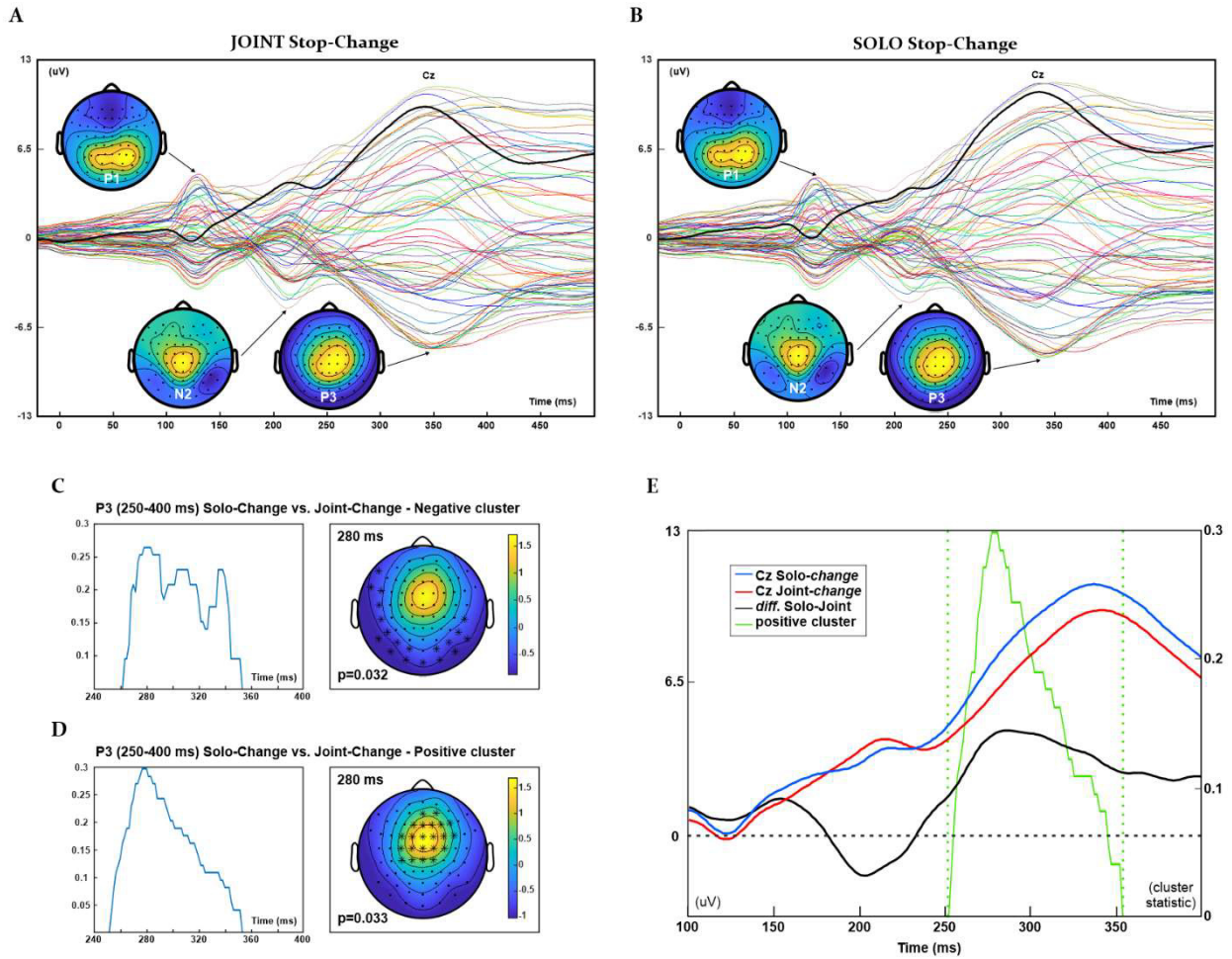


Figure 20. Grand average ERP waveforms and topographical distributions for Stop-Change trials in the Solo and Joint conditions. (A) ERP waveforms for Stop-Change trials in the Joint condition and (B) in the Solo condition, showing similar component activations (P1, N2, P3) but with notable differences in amplitude and timing. The Cz electrode is highlighted in black. (C) A significant negative cluster ($p = 0.032$) and (D) a significant positive cluster ($p = 0.033$) were identified in the P3 time window (250–400 ms) when comparing Solo vs. Joint Stop-Change trials. (E) Average activity at the Cz electrode for Solo (blue) and Joint (red) conditions. The overlaid difference wave (Solo minus Joint, in black; not to scale) highlights the amplitude divergence in the P3 window. The green line shows the cluster statistic over time, and the dotted vertical lines indicate the onset and offset of the significant positive cluster.

5.4. Discussion

To the best of our knowledge, this experiment is the first to administer a joint version of the SCT and the first to record EEG data within the broader stop-signal task family. Building on the results of our positive control experiment (Study II), we aimed to assess inhibitory control when participants performed actions either jointly or alone. We hypothesized that co-representation in joint actions would heighten proactive control, manifested as longer No-Change RTs and longer stopping latencies in the joint condition. We also predicted a later onset and reduced amplitude of the frontocentral stop-signal P3 in the joint condition, reflecting a potentially less efficient inhibitory process.

Regarding the electrophysiological data, the significant positive frontal-central cluster observed around 280 ms suggests a modulation of the P3 component that may be driven by co-representation. This electrophysiological finding is consistent with our behavioral results, which revealed significantly longer SSRTs in the joint condition compared to the solo condition. Taken together, these outcomes support the notion that engaging in a shared task may alter the efficiency of inhibitory mechanisms.

However, contrary to our findings in Study II, we did not observe significant differences in preEMG onset or latencies, indicating a dissociation between EMG-based indices of reactive inhibition and the behavioral or EEG-based measures. Furthermore, the behavioral data did not provide any clear evidence of biased motor preparation or proactive control in the joint condition, suggesting that co-representation may not uniformly affect all markers of inhibition, as seen with the bimanual SCT.

Looking ahead, additional analyses of the EEG data will be crucial for clarifying whether subtle aspects of proactive control are exerting an influence on stopping latencies that may not be captured by behavioral parameters alone. More extensive analyses, such as source localization or connectivity measures, could also shed light on the specific neural networks involved in joint action inhibitory processes.

5.4.1 Establishing collective vs. individual goals: A belief-induction approach

Joint actions inherently imply a constant, dynamic interplay between self and other (Dumas and Fairhurst, 2021), requiring individuals to continuously adapt their behaviors to effectively exchange information and coordinate with others (Vesper et al., 2016). As a result, co-actors' behaviors become interdependent, making it challenging to assess each participant's individual contributions and reactions to their partner's actions (De Vicariis et al., 2022). Our strategy for addressing this inherent behavioral interdependence was to develop a joint stop-change paradigm that leveraged gamification and belief induction, embedding the timings dictated by the staircase procedure into the belief of a coordinated interaction with the co-actor.

In practice, participants performed the identical task twice, but they were led to believe that, in the joint condition, the Change cues were triggered by the co-actor's errors, creating the impression that they were interacting with and adjusting their behavior in response to their partner's actions and feedback. In the solo condition, participants were told that the Change cues originated from a purely random source, which, by the way, was actually true. By creating this scenario, we emphasized that responding to change cues was primarily an individual sub-goal.

In the joint condition, however, successfully correcting a trial served as a collective sub-goal. Beyond the presence of the co-actor, who kept their hand either motionless under a cardboard box in the joint condition or crossed on their lap in the solo condition, all other aspects remained identical between conditions.

Our overarching strategy aimed to maximize the contrast between collective goals and individual goals. As noted in the Introduction, variables such as the relationship between co-actors, group identities and dynamics, affective valence, and the degree of cognitive empathy and familiarity all have the potential to modulate co-representation. We sought to minimize these influences by limiting direct interaction between participants and co-actors: they interacted only briefly during the role-assignment process (lasting only a few minutes) before being taken to separate rooms for EEG montage. Furthermore, when the experiment began, both individuals wore EEG caps, further reducing familiarity, conducted the task in a dimly lit room, each facing their own monitor while resting on a chinrest, and were instructed not to communicate during the experiment.

Thus, we can reasonably rule out affective valence, familiarity, or group dynamics as contributing factors to co-representation differences. Likewise, we can exclude potential effects of salience or arousal, given that the overall experimental setup remained constant across conditions.

5.4.2 Why referential coding fails to account for our results

Importantly, we can also exclude any effect of referential coding or attentional shifting. First, in contrast to previous joint SST studies (Cardellicchio *et al.*, 2021a; Cavallo *et al.*, 2014), our design did not position stimuli or movement in a horizontally organized spatial plane. Rather than using two effectors and presenting stimuli on opposing sides of the monitor (as in Cavallo *et al.* 2014), we required responses from a single effector only (right hand), moving vertically (lifting up or pressing down) while consistently presenting stimuli in the center of the screen.

The core assumption of the referential coding account is that the discrimination between two (action) events is achieved by intentionally weighting distinct action features (Memelink & Hommel, 2013; Liepelt *et al.*, 2014). This means that individuals adopt a cognitive strategy to selectively emphasize certain discriminative action features in order to distinguish more effectively between them.

In the context of the joint Simon task, referential coding entails focusing on the spatial dimension (left vs. right), such that a co-actor (or any attention-grabbing object) becomes a spatial reference point used to classify one's own actions (Dolk *et al.*, 2014). As a result, even in the absence of an actively performing social partner, a spatial compatibility effect can emerge purely from perceptual processes (Dolk *et al.*, 2011; Dolk *et al.*, 2013).

However, any sufficiently discriminative feature can serve as a reference point for coding one's own actions (Dolk *et al.*, 2014). This was demonstrated by Sellaro *et al.* (2014) using a joint Simon task in which participants responded to the geometrical shape of a centrally presented colored stimulus by pressing either a left or right button, while wearing gloves that either matched or differed in color from the stimuli. In the first experiment, the authors administered the task individually, instructing participants to respond to both stimulus shapes (pressing the right or left button). In the second experiment, participants responded to only one of the two shapes individually (solo Go/No-Go condition) or performed the same task jointly with a co-actor. The results showed that congruence between stimulus and glove color affected performance in both the two-choice and the joint tasks, but not in the individual Go/No-Go control condition, thereby empirically demonstrating a non-spatial Joint Simon Effect driven by referential coding.

On the same line of reasoning, one could argue that the go-cue color (red) and the change-cue color (yellow) provided sufficiently distinct reference features for coding one's own actions versus the co-actor's action. From the participant's perspective, because they responded consistently to the go cues, the red color might have been coded as their own action, whereas the yellow cue, believed to be triggered by the co-actor, could be associated with the co-actor's action. In fact, this reasoning aligns with the idea that, in referential coding, perceivable consequences of the other's actions shape the representation of one's own individual task share in accordance with the demands of that task share (Dolk & Prinz, 2016).

Thus, in our experiment, when change cues appeared during the joint condition, a potential conflict could arise between stimulus features ("Is it my cue or not?") and action events ("Should I move or not?"). If referential coding were driving this effect, we would expect a pattern similar to the Joint Simon paradigm, where conflicting stimulus location and stimulus identity produce a slowing of responses (joint Simon effect), assumed to reflect the inhibition of one's own responses on the other person's trials (Maier *et al.*, 2023). However, we observed no significant slowing in any type of response time (neither change RTs nor No-Change RTs). Instead of inhibiting one's responses in the allegedly "other" stop-change trials, participants showed disinhibition, as evidenced by longer stopping latencies (i.e., SSRTs).

Consequently, we consider it unlikely that referential coding explains our findings in the joint condition. Rather, we propose that the observed slowing in SSRTs stems from self-other integration and discrimination conflicts driven by co-representation. In our paradigm, the key distinction lies in the collective goal induced by our belief manipulation, which appears to modulate reactive inhibition. Thus, our results indicate that a

strong collective goal can impose a processing cost, reflected in slower stopping latencies and altered neural markers, suggesting that co-representing the other's actions indeed shapes how individuals inhibit their responses.

5.4.3 *Balancing difficulty and joint coordination: Insights from SSD and Change RT effects*

Another intriguing finding is that the solo condition yielded longer Stop-Signal Delays (SSDs) than the joint condition. Although interpreting SSD can be challenging, a longer SSD indicates a more difficult version of the Stop-Change Task (SCT) compared to one with a shorter SSD. One could argue, then, that participants expended less effort in the joint condition and more in the solo condition, but this is counterintuitive if we assume that social pressure in the joint condition would encourage greater effort. Moreover, we found no evidence of participants trying harder on the go trials in the joint condition, as reflected by the lack of significant differences in No-Change or Go-Only RTs.

A more plausible explanation involves the interplay between SSD and SSRT. In the joint condition, SSD was shorter while SSRT was longer. When these two parameters are combined, they approximate the time window in which about half of the No-Change trials are too fast to be inhibited (Verbruggen *et al.*, 2019), a point closely aligning with the mean No-Change RT, which did not differ significantly across conditions. Hence, we interpret the significant difference in SSD as an additional manifestation of the co-representation cost: with a greater burden on the motor system during joint actions, participants unintentionally “shifted” the difficulty of the SCT (i.e., used on average, a shorter SSD), resulting in similar RTs, despite longer stopping latencies that reflect the demands of coordinating with a partner.

Furthermore, another fundamental finding in the current study is that Change RTs do not significantly differ between the joint and solo conditions. This result has important implications for understanding the quality of human interactions, especially given that previous joint SST research suggested a potential compromise in inhibitory processes, leaving open questions about how such a compromise might affect collaborative tasks.

By employing a SCT, we were also able to assess Change RTs, which arguably hold greater ecological value than the simpler “freezing” of movements required in a standard Stop-Signal Task (Boecker *et al.*, 2013). In daily interpersonal interactions, joint coordination requires a constant reassessment and re-programming of actions (De Vicariis *et al.*, 2022). Our finding that Change RTs remain unaffected by co-representation suggests that while re-engaging actions may carry an additional cognitive load, this burden does not translate into slower overall movement execution. Hence, the time course of motor reprogramming and execution appears largely preserved during joint actions, aligning with the human capacity for seamless cooperation. Nonetheless, it remains plausible that certain clinical or personality disorders could impair joint action reengagement, indicating a potential avenue for future research.

5.4.4 *Significant differences in the frontocentral stop-P3*

Previous neurophysiological research has primarily examined the joint Simon task, where No-Go trials—that is, trials requiring the co-actor's response—elicit a larger P3 amplitude compared to No-Go trials in the half-task control condition (i.e., when participants act alone). This enhanced P3 is believed to reflect increased response inhibition, necessary to prevent an individual from acting during the partner's turn, and is thought to be driven by co-representation (Ruissen and de Bruijn, 2015; Sebanz *et al.*, 2006b; Tsai *et al.*, 2006). The significant role of inhibition in this paradigm is further supported by behavioral findings, which show how participants adjust their responses on a trial-to-trial basis following the co-actor's responses (Maier *et al.*, 2023).

However, the No-Go P3 observed in the joint Simon paradigm differs substantially from the stop-signal P3 in SSTs or SCTs. In the joint Simon task, which essentially operates as a turn-based Go/No-Go paradigm, participants must inhibit their own response when it is the partner's turn. In contrast, our paradigm led participants to believe they needed to act in synchrony with a co-actor, occasionally changing their action in response to the co-actor's alleged mistake. Thus, whereas the joint Simon paradigm presents a timing-discrimination challenge—deciding whose turn it is—our Stop-Change task involves a behavioral adjustment challenge in response to perceived errors.

It is therefore unsurprising that our findings show an opposite P3 pattern with respect to the No-go P3 in the Joint Simon: when participants must adjust their action in response to the co-actor's mistake, their stop P3 is significantly delayed and reduced in amplitude (i.e., diminished inhibitory engagement) compared to conditions in which they respond to a random event (acting alone).

Taken together, these results suggest that co-representation imposes greater inhibitory control when it is the partner's turn (as in the joint Simon), yet attenuates action cancellation during joint action re-adjustments in our paradigm. In other words, co-representation appears to facilitate self–other differentiation, preventing one from acting during the other's turn, while at the same time disrupting action cancellation once the action process has already begun.

Furthermore, our results suggest that differences between the Joint and Solo conditions arise through two mechanisms. First, earlier onset of the P3 in the Solo condition indicates a faster initiation of the inhibition process (Diesburg et al., 2024; Hervault *et al.*, 2024), aligning with the observed shorter SSRT in that condition. Second, smaller P3 amplitude in the Joint condition reflects lowered or less efficient performance monitoring (Barcelo and Cooper, 2018; Huster *et al.*, 2020; Murphy et al., 2015).

Notably, when distinguishing between Stop-Change Failure and Success trials, we observe significant differences only in Failure trials. In other words, most of the detected effects occur when inhibition fails rather than when it is successfully implemented. This suggests that the overall engagement of the inhibition process may not be the sole factor driving the differences, rather, the performance-monitoring component of the P3 appears pivotal. In practical terms, failing to stop in the Joint condition elicits a weaker error-monitoring response compared to Solo, implying that co-representation, may also alter error-related processes.

5.4.5 Integrating our results with previous joint SST literature

As observed in earlier studies (Cardellicchio *et al.*, 2021a; Cavallo *et al.*, 2014), we recorded longer SSRTs in the Joint condition, accompanied by a later onset and smaller amplitudes of the stop P3. The latter finding points to a weaker performance monitoring process under joint actions. These outcomes suggest that co-representation contributes to slower or less efficient reactive inhibition. However, we did not observe any difference in preEMG latencies, our secondary index of reactive inhibition, nor did we find evidence of distinct proactive control.

Relating our results to prior joint SST studies, we question the idea that an alternative, slower yet more selective inhibition mechanism (as proposed by Aron & Verbruggen, 2008) fully explains these observations (Cirillo *et al.*, 2018; Lavalley *et al.*, 2014; Raud and Huster, 2017; Smittenaar *et al.*, 2013). In fact, single-process accounts that posit a mutually exclusive and context-dependent choice between selective or global stopping have come under increased scrutiny, as emerging evidence shows that these long-standing models often fail to capture all experimental outcomes (Tatz et al., 2024).

Instead, two-process frameworks, such as the “pause-then-cancel” (PTC) model, appear to better capture observed data (Diesburg and Wessel, 2021; Diesburg *et al.*, 2024; Guan and Wessel, 2022; Schmidt and Berke,

2017; Tatz *et al.*, 2024; Tatz *et al.*, 2021; Waller *et al.*, 2021). Briefly, PTC models posit that action stopping involves two distinct processes. First, a fast and global “Pause process” (Pp) quickly suppresses the motor system in response to detecting a salient stimulus. Second, a slower but more selective “Cancel process” (Cp) specifically determines which action is ultimately suppressed.

Notably, prEMG, reduced corticospinal excitability (CSE) of task-unrelated effectors, and short-interval intracortical inhibition (SICI), reflecting rapid, GABA_A-mediated inhibition, appear to index the Pp, whereas SSRT and the cortical silent period (CSP), which reflect slower, GABA_B-mediated inhibition, align with the Cp (Tatz *et al.*, 2024). Indeed, SSRT, which represents the total time required to implement stopping (Diesburg and Wessel, 2021), is positively correlated with CSP length (Paci *et al.*, 2021) but negatively correlated with SICI (Chowdhury *et al.*, 2018). From a PTC perspective, this makes sense: if the Pp contributes less to stopping, the (slower) Cp must compensate, resulting in an overall longer stopping duration.

The PTC model also appears compatible with current findings in joint action. In a previous study that employed a comparable reaching task (but without stop trials), Cardellicchio *et al.* (2020) observed reduced SICI and prolonged CSP in the joint condition during the reaching phase. More recently, the same group replicated these results and further demonstrated that CSP modulation emerged only after action onset, irrespective of prior information (Vescovo *et al.*, 2024). One interpretation of these findings is that joint action execution entails a divergent modulation of the PTC processes, wherein the Pp is attenuated (lower SICI), and the Cp is delayed (longer CSP), ultimately leading to an overall prolongation of motor inhibition (i.e., slower SSRTs).

Furthermore, the stop-signal frontocentral P3 is proposed as a signature of the Cp, as it peaks at around 300 ms after a stop signal and shows an earlier onset in successful compared to failed stop trials (Kok *et al.*, 2004; Wessel and Aron, 2015a). Notably, blind source separation techniques such as ICA can be used to isolate neural activities from distinct cortical sources, thereby significantly enhancing the single-trial signal-to-noise ratio of ERPs (Huster *et al.*, 2020; Wessel, 2018; Wessel & Ullsperger, 2011). Recent work leveraging this approach indicates that the stop-signal P3 arises from thalamocortical inputs that arrive later during failed stop trials than in successful ones. Aligned with the idea of Cp as a top-down process, these inputs are not weaker in failed stops, rather, they are simply too late to avert the response (Diesburg *et al.*, 2024; Logan *et al.*, 1984). Additionally, the amplitude of the P3 is larger when participants explicitly attempt to stop versus when they ignore the stimulus (Dutra *et al.*, 2018; Tatz *et al.*, 2021; Waller *et al.*, 2021), reinforcing its role as an index of inhibitory engagement of the Cp.

This PTC model aligns well with our findings. We observed a dissociation between earlier stages of reactive inhibition (i.e., prEMG peak latencies), which reflect the fast and global Pp, and later, more targeted inhibitory stages (i.e., SSRTs and stop-P3), linked to the Cp. This pattern echoes the results of Cavallo *et al.* (2014), who assessed corticospinal excitability in non-effector muscles during a joint SST condition and found greater involvement of a later-acting cancellation mechanism, coupled with a diminished role for quick, global inhibition. Interpreted within the PTC framework, the longer time required by the Cp in the Joint condition reduces the likelihood of detecting reduced corticospinal excitability in task-unrelated effectors, an indicator of the Pp (Tatz *et al.*, 2024). Collectively, these data suggest that the Joint condition predominantly relies on the slower, more selective Cp, whereas the Solo condition is driven mainly by the faster Pp, aligning with previous neurophysiological findings of SICI and CSP (Cardellicchio *et al.*, 2020; Vescovo *et al.*, 2024).

If our reasoning holds, it dovetails nicely with Cardellicchio *et al.* who demonstrated that lateral premotor cortex (IPMd) modulates joint action stopping performance using cTBS. Their findings suggest that IPMd is involved in co-representation and helps shape the balance between the Pause (Pp) and Cancel (Cp) processes. Seminal work by Cisek and Kalaska (2005) showed that, in the premotor cortex, multiple potential reaching actions can coexist during periods of uncertainty, and once an unambiguous cue appears, the selected motor plan is strengthened while alternative plans are inhibited. Applying this principle to joint actions, the

uncertainty may not arise from multiple competing self-generated motor plans but rather from the coexistence of one's own plan with the co-actor's representation, i.e., co-representation. Possibly, under joint conditions, the strengthening of the selected motor plan in response to an unambiguous cue may require greater reliance on the slower, targeted Cp mechanism with respect to solo conditions.

Subsequent studies on premotor regions indicate that selective weighting—or, more precisely, competition—of representations can be biased by attentional processes (Cisek and Kalaska, 2010; Klaes *et al.*, 2011). However, our findings do not suggest the involvement of attentional biases or proactive biasing. This makes sense if co-representation of another person's actions does not inherently entail competition, unlike situations in which multiple action plans coexist in uncertain contexts. It may also account for why we observed a broad impairment of inhibition markers, including proactive control, in our bimanual Positive Control Experiment, whereas only a specific extension of the Cancel process (Cp) emerged in our Joint Experiment. As noted in Study II's shared background, disrupting PMd activity during joint actions (as in Cardellicchio *et al.*, 2021a), could interfere with the competition among motor plans, but alternatively, and in a simpler sense, it may also directly disrupt co-representation. The authors proposed that the PMd “segregates observed (other) and self-motor outputs via a selective inhibition mechanism.” Building on previous research, and based also on our own findings, however, we suggest that PMd may instead enable the coexistence of self-generated motor plans and co-represented actions without requiring an additional, independent selective inhibition mechanism. Functionally, this coexistence mirrors maintaining multiple potential actions under uncertainty, so that once an unambiguous cue appears (in our case, the initial go cue), the Cp must engage longer to implement action cancellation in joint contexts. Nonetheless, we currently lack evidence of a direct causal link by which PMd activity specifically triggers the Cp, highlighting the need for further research to clarify these relationships.

5.4.6. Conclusions

By implementing the first known joint version of the SCT, we advanced the understanding of action cancellation in shared-action contexts. Our carefully gamified paradigm was designed to control for potential confounds while highlighting the contrast between collective and individual goals, and we expanded it to incorporate prEMG and EEG measures. Consistent with prior research, our behavioral findings suggest that co-representation significantly influences reactive inhibition. However, this influence did not manifest as slower Change RTs, indicating that action reprogramming remains relatively efficient even under joint conditions. In other words, while shared task goals may increase cognitive load, they do not necessarily compromise the speed or execution of re-engaging one's actions.

A key observation is the apparent mismatch between early inhibition markers (prEMG onset and latencies) and later behavioral (SSRT) and neurophysiological indices (stop P3). Although our EEG analysis is still at its beginning, these initial results imply that co-representation may specifically target later inhibitory processes. Recent two-process frameworks, particularly the PTC model, offer a compelling perspective on how different phases of inhibition may be distinctly affected in joint contexts.

6. FINAL CONCLUSIONS

Planned and goal-directed joint actions, which lie at the heart of this PhD thesis, are as intricate to investigate as they are to perform. They involve a delicate interplay of complex action planning, cognitively demanding engagement and re-engagement, and taxing co-representation and self–other integration processes. While many species coordinate tasks, the human capacity to do so rapidly, flexibly, and often automatically is unique. Crucially, communication is not always necessary for effective joint coordination. Instead, the presence of a collective or shared goal, a mutual vision or agreed-upon sequence of actions, proves essential for cooperation.

Another major challenge in this research is the frequent conflation of goal-oriented joint coordination with spontaneous, or emergent, interpersonal coordination (Ayache et al., 2021), making it difficult to tease apart the impact of joint goals from unconscious mutual attunement, like, for example, referential coding. Across both studies presented here, every effort was made to reduce this risk, even though the projects themselves addressed markedly different facets of joint action.

While Study I was a preliminary exploration of motor-level representations of collective goals via TMS–EEG co-registration, and Study II investigated how inhibitory control differs between joint and solo contexts, these projects share a pivotal overarching link: co-representation and collective goals. In particular, the intriguing and not yet fully explored question is how these two factors are related and how they might interact in shaping motor control. In Study I, we hypothesized that MEPs would be modulated according to the confederate’s intended action, thereby reflecting a hypothesized motor representation of collective goals. Contrary to this prediction, we observed no such modulation. Instead, significant changes emerged in the Solo condition. Moreover, TEP recordings from both the SMA and M1 offered no clear support for a motoric representation of shared goals, as the results in these regions were inconclusive.

In Study II, we confirmed that joint action stopping is less effective than stopping alone. These results align well with the pause-then-cancel (PTC) framework, indicating that prolonged stopping latencies primarily arise from a lengthened Cancel process (Cp) rather than alterations to the Pause process (Pp). In light of previous joint SST findings, this extended Cp appears closely linked to co-representation, as corroborated by previous work (Cavallo *et al.*, 2014). Additionally, it seems that co-representation’s influence can be attenuated by cTBS applied to the IPMd (as in Cardellicchio *et al.*, 2021a), further suggesting a pivotal role for premotor circuits in shaping these processes.

6.1. Do Premotor Circuits Encode the Motoric Representation of Collective Goals?

If co-representation is tightly linked to collective goal representations, as it may be plausible to assume, it could be argued that the motoric representation of collective goals, as investigated in Study I, might be localized in premotor areas rather than in M1, as previously hypothesized (Barchiesi *et al.*, 2022). However, the inhibitory mechanisms assessed in Study II likely represent just one component within a continuously updating motor plan, which encompasses both facilitatory and inhibitory influences (Raud *et al.*, 2020a). Moreover, these dynamics may depend on the broader sensorimotor control system, potentially involving motor, premotor, and dorsal attentional regions (Cisek and Kalaska, 2010; Mirabella, 2014). In such a model, a key function of cortical inhibition could be to adjust the gain of motor representations, as proposed by Greenhouse *et al.* (2015), so that inhibitory strength adapts in response to uncertainty about available actions or the requirements of proactive control. While this framework aligns well with our findings on joint action stopping, given the complexities of the involved mechanisms, directly linking collective goal representations to premotor regions remains a challenging endeavor.

Further evidence of the complexity of collective goal representations lies in the role of predictions. In a seminal fMRI study, Ramnani and Miall (2004), introduced an associative joint stimulus–response task in which visual cues signaled upcoming actions for co-actors located in adjacent rooms. Participants thus formed predictions about the co-actor’s actions, drawing on their own task representation and action anticipation processes. In this paradigm, the color of an instruction cue determined the acting agent (the scanned participant, the co-actor, or a non-agent computer), while the shape of the cue specified the finger movement. Certain cues also required the agent to withhold a response until a trigger, effectively preventing early motor planning. Critically, the resulting neural activity patterns differed according to whether participants were preparing their own action or anticipating the co-actor’s. While preparing self-directed movements selectively engaged PMd, anticipating the co-actor’s actions activated the paracingulate cortex, superior temporal cortex, and interconnected premotor areas (Ramnani and Miall, 2004). These findings indicate that distinct subsystems within the human motor control network manage self-generated actions versus the prediction or simulation of someone else’s actions. Notably, these “other-oriented” regions lie outside the classical mirror system and have also been implicated in mental state attribution (Frith and Frith, 1999; Gallagher and Frith, 2003).

The Ramnani and Miall (2004) results thus underscore how premotor regions may differentially process self-oriented and other-oriented tasks. However, whether these areas specifically encode collective goals, or merely facilitate a broader simulation and prediction of another person’s actions, remains an open question for future research.

6.2. Final remarks

Overall, this thesis illustrates the multifaceted interplay among motor preparation, inhibitory control, and collective goal representations when individuals act in concert. Although we have yet to definitively pinpoint the neural underpinnings of shared goals, our findings underscore the critical role that co-representation, and the flexible engagement of inhibitory mechanisms, play in human social coordination.

Crucially, future research should more fully integrate predictive processes into the study of joint actions, as they appear central to collaborative success yet remain underexplored. By employing advanced neuroimaging techniques and refined behavioral paradigms, such investigations can shed new light on how the brain orchestrates rapid, flexible, and goal-directed cooperation and how these abilities may be compromised in neurological and psychiatric disorders.

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