

RESEARCH REPORT

Excitatory/inhibitory motor balance reflects individual differences during joint action coordination

Enrico Vescovo^{1,2}  | Pasquale Cardellicchio^{2,3} | Alice Tomassini¹ |
Luciano Fadiga^{1,2} | Alessandro D'Ausilio^{1,2}

¹Center for Translational Neurophysiology of Speech and Communication, Istituto Italiano di Tecnologia, Ferrara, Italy

²Department of Neuroscience and Rehabilitation, Section of Physiology, University of Ferrara, Ferrara, Italy

³Physical Medicine and Rehabilitation Unit, IRCCS Istituto Giannina Gaslini, Genoa, Italy

Correspondence

Enrico Vescovo, Center for Translational Neurophysiology of Speech and Communication, Istituto Italiano di Tecnologia, Ferrara, Italy; Department of Neuroscience and Rehabilitation, Section of Physiology, University of Ferrara, Ferrara, Italy.
Email: vscnrc@unife.it

Funding information

EU project PRIMI, Grant/Award Number: HORIZON-CL4-2022-DIGITAL-EMERGING-02-101120727; EU project EnTimeMent, Grant/Award Number: H2020-FETPROACT-824160; Ministero della Salute, Grant/Award Number: GR-2018-12366027; Ministero dell'Università e della Ricerca, Grant/Award Numbers: 20208RB4N9, P2022J8AXY

Edited by: Francisco Alvarez

Abstract

Joint action (JA) is a continuous process of motor co-regulation based on the integration of contextual (top-down) and kinematic (bottom-up) cues from partners. The fine equilibrium between excitation and inhibition in sensorimotor circuits is, thus, central to such a dynamic process of action selection and execution. In a bimanual task adapted to become a unimanual JA task, the participant held a bottle (JA), while a confederate had to reach and unscrew either that bottle or another stabilized by a mechanical clamp (No_JA). Prior knowledge was manipulated in each trial such that the participant knew (K) or not (No_K) the target bottle in advance. Online transcranial magnetic stimulation (TMS) was administered at action-relevant landmarks to explore corticospinal excitability (CSE) and inhibition (cortical silent period [cSP]). CSE was modulated early on before the action started if prior information was available. In contrast, cSP modulation emerged later during the reaching action, regardless of prior information. These two indexes could thus reflect the concurrent elaboration of contextual priors (top-down) and the online sampling of partner's kinematic cues (bottom-up). Furthermore, participants selected either one of two possible behavioural strategies, preferring early or late force exertion on the bottle. One translates into a reduced risk of motor coordination failure and the other into reduced metabolic expenditure. Each strategy was characterised by a specific excitatory/inhibitory profile. In conclusion, the study of excitatory/inhibitory balance paves the way for the neurophysiological determination of individual differences in the combination of top-down and bottom-up processing during JA coordination.

KEYWORDS

joint action, motor control, motor inhibition, sensorimotor communication, TMS

Abbreviations: aMT, active motor threshold; ANOVA, analysis of variance; CSE, corticospinal excitability; cSP, cortical silent period; EHI, Edinburgh Handedness Inventory; EMG, electromyography; FDI, first dorsal interosseous; FDR, false discovery rate; GABA, gamma-aminobutyric acid; IMS, individual motor signature; JA, joint action; MCD, mean consecutive difference; MEP, motor-evoked potential; MT, movement time; OP, opponens pollicis; OSP, optimal scalp position; RMS, root mean square; RP, readiness potential; RT, reaction time; SD, standard deviation; SEM, standard error of the mean; TMS, transcranial magnetic stimulation.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Authors. *European Journal of Neuroscience* published by Federation of European Neuroscience Societies and John Wiley & Sons Ltd.

1 | INTRODUCTION

Multi-agent coordination is an essential component of animal behaviour (Couzin et al., 2005; Frith, 2008; Nagy et al., 2010; Rands et al., 2003) that might have fundamental implications for cognitive and social development in humans (Cirelli, 2018; Feldman, 2007; Murray & Trevarthen, 1986; Rauchbauer & Grosbras, 2020). It covers a spectrum of activities ranging from the spontaneous synchronization of clapping (Néda et al., 2000) to the most complex and intentional forms of human coordination, such as dancing or playing together with other elements of an orchestra (D'Ausilio et al., 2015; Keller et al., 2014; Pezzulo et al., 2019). The ability of two or more agents to mutually adapt their motor outputs to achieve a shared outcome, referred to as joint action (JA), often requires refined coordination in both space and time (Sebanz et al., 2006; Tomassini et al., 2022).

Based on the hierarchical organization of brain functions, one's motor plans are necessarily based on the integration of information on different scales, such as discrete changes of context (i.e. task instructions or contextual priors) and the continuous flow of information reaching our senses, such as body configuration and its changes (Wolpert et al., 2003). During JA coordination, bottom-up processes are believed to also extract relevant kinematic cues from partner's movements which are used—depending on the context—to plan and adapt the appropriate behaviour to achieve the shared goal (e.g. in Torricelli et al., 2023). When the task forces a contextual information asymmetry (i.e. some prior information is not available to both partners), one of the partners should compensate for the missing bits by devoting more effort to the bottom-up extraction of the partner's kinematic information in order to properly coordinate (Pezzulo et al., 2019; Sacheli et al., 2013). Summing up, mutual coordination is based on the fine balance between the online analysis of kinematic cues that specify partners' action and the simultaneous integration with available contextual information (Aglioti et al., 2008; Amoruso et al., 2018; Amoruso & Urgesi, 2016; Avenanti et al., 2013). Consequently, understanding multi-agent coordination concerns how bottom-up and top-down processes come together to select and generate appropriate actions with appropriate timing.

The behavioural co-regulation emerging during JA can thus be reduced to a continuous, dynamic process of action selection, which is known to be sculpted—from a neurophysiological perspective—through the regulation of the excitation/inhibition balance in the sensorimotor circuits (Bestmann & Duque, 2016; Derosiere & Duque, 2020). Previous studies, employing

transcranial magnetic stimulation (TMS), have mostly explored excitatory mechanisms during interactive behaviour, demonstrating an increase in corticospinal excitability (CSE) compared with a non-interactive scenario (Novembre et al., 2012; Sartori et al., 2011). More recently, JA coordination was also associated with specific modulations of motor inhibition (Cardellicchio, Dolfini, Fadiga, & D'Ausilio, 2020). Although several studies have highlighted the importance of the integration of top-down and bottom-up processes during JA (Sacheli et al., 2013, 2022; Sacheli et al., 2018), fundamental evidence concerning the neurophysiological regulation of the excitation/inhibition balance underlying this integration during JA is lacking.

Here we used a typical bimanual task—reaching/grasping for a bottle and unscrewing its cap—which has been adapted to be an interactive unimanual task (Cardellicchio et al., 2021). The participant is asked to hold a bottle (JA) while the other member of the dyad (the confederate) has to reach either for the JA bottle or for another bottle stabilized by a mechanical clamp (No_JA; Figure 1). It is important to note that in the JA condition, participants must decide when and with what force to squeeze the bottle to stabilize it in anticipation of the haptic exchange with the confederate. This simple fact forces a refined degree of motor coordination to achieve a goal that would otherwise be unattainable by each partner separately.

In addition, we designed a manipulation to dissociate the relative contribution of top-down and bottom-up processing. In fact, participants were either informed or uninformed about whether it would be a JA or No-JA trial (i.e. whether the confederate would reach their bottle or the other). In informed trials (Knowledge—K), bottom-up processing of partner's movement cues is not strictly essential to action coordination, except for its fine-tuning over time. In uninformed trials (No Knowledge—No_K), action coordination relies solely on bottom-up information.

We used TMS to investigate CSE and cortical silent period (cSP) length in this interactive scenario. CSE reflects the convergence of several inputs to the primary motor cortex (M1) and provides an instantaneous readout not only of the net excitation directed to the target muscles (Ridding & Rothwell, 1997; Spampinato et al., 2023) but also of the functional state of sensorimotor circuits during action control (Derosiere et al., 2020; Klein-Flügge & Bestmann, 2012). On the other hand, cSP length is a gamma-aminobutyric acid B (GABA_B)-mediated neurophysiological index of inhibition (Ziemann, 2004) that is considered as a marker of slow corticospinal inhibition required for response selection

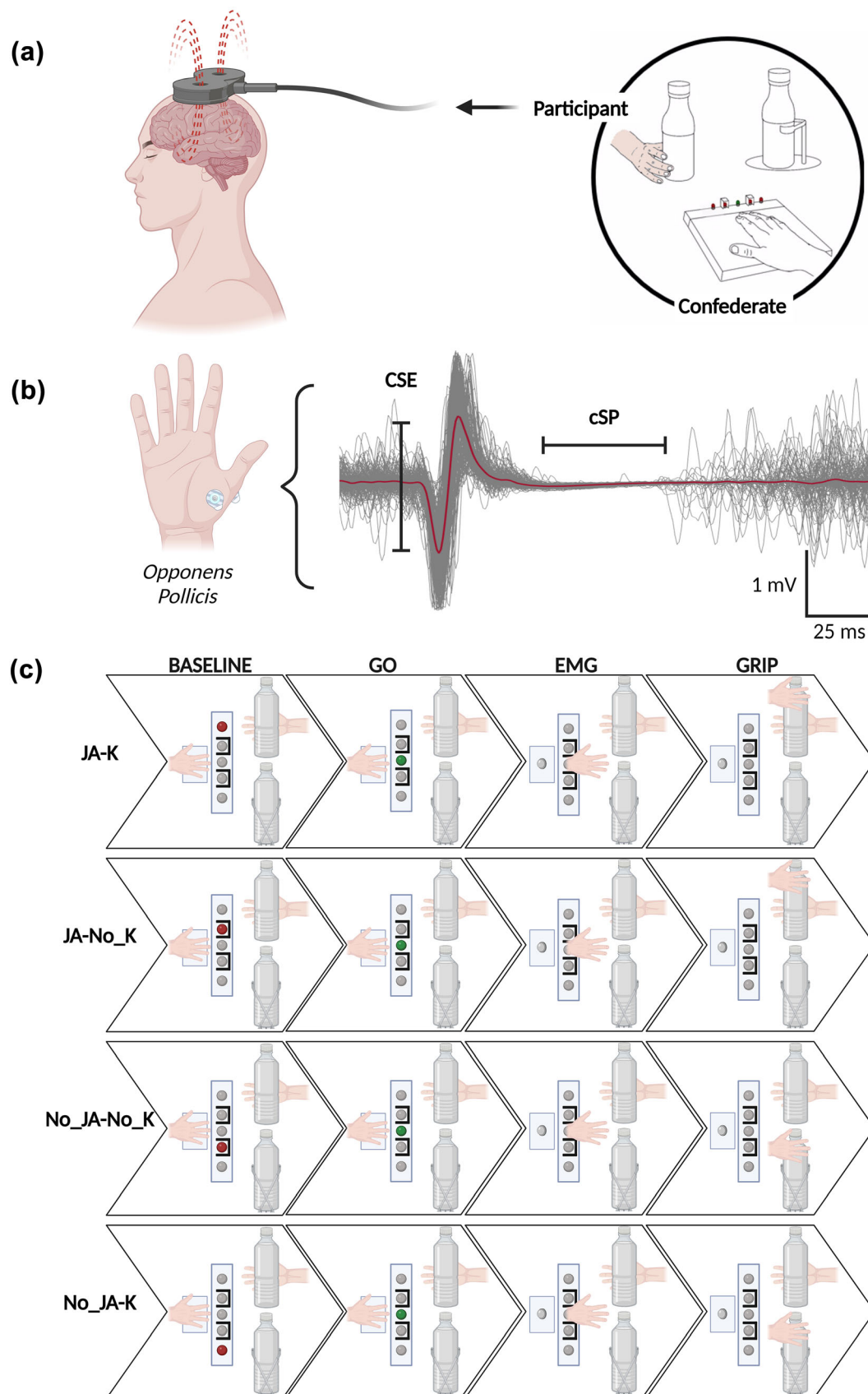


FIGURE 1 Legend on next page.

FIGURE 1 Behavioural task and conditions. (a) Graphic representation of the experimental setup. In the starting position, confederate's right hand is resting on a button box in front of the red directional LEDs and the green Go LED. The two innermost red LEDs are visible only from confederate's perspective. The two bottles—representing the target of the action—are equally distant from the starting position. One was held by a mechanical clamp (no joint action [No_JA]) and the other by the participant (joint action [JA]). (b) Neurophysiological indexes measured in all participants. Corticospinal excitability (CSE) is measured as the peak-to-peak amplitude value (mV) of the motor-evoked potential (MEP). Cortical silent period (cSP) is measured as the period (ms) which starts at the isoelectric state that follows the MEP offset and ends with the resuming of voluntary muscular activity; (c) illustration of the four experimental conditions (from top to bottom: JA-K; JA-No_K; No_JA-No_K; No_JA-K). Each timeline represents one hypothetical trial. Each trial starts with the switching on of one of the red directional LEDs, followed by the switching on of the green Go LED. Single transcranial magnetic stimulation (TMS) pulses were delivered at one of four timings: Baseline (switching on of the red LED); Go (confederate's movement onset); electromyography (EMG; confederate's EMG, as described below); Grip (touch of the bottle).

(Davranche et al., 2007; Klein et al., 2014; Tandonnet et al., 2012). We sampled participants' neurophysiological indexes of excitation/inhibition time-locked to action-relevant landmarks calculated online based on the confederate's movement. Namely, before the presentation of any cue and, thus, before motor preparation (baseline); at the onset of the confederate's reaching movement (Go); during the confederate's reaching phase (electromyography [EMG]); during the active exchange of forces between partners (Grip).

We demonstrated that excitatory and inhibitory indexes have different temporal modulations, depending on their differential dependence on prior information. Furthermore, we characterized participants in conformity to their (naturally) selected coordination strategy and described neurophysiological individual differences related to their behavioural styles. In the present work, we provide evidence that differential excitatory and inhibitory modulations reflect the neurophysiological unfolding of two complementary processes, bottom-up and top-down, whose combination contributes to the optimization of social motor interaction while explaining individual idiosyncrasies.

2 | MATERIALS AND METHODS

2.1 | Participants

A total of 22 naïve volunteers took part in the study (12 females; age: 22.9 ± 1.8 ; mean $\pm$ standard deviation [SD]). All participants were right-handed, as assessed by the Edinburgh Handedness Inventory (EHI; Oldfield, 1971; to be enrolled in the study, participants had to obtain an EHI score ≥ 40 ; EHI: 92.5 ± 31 ; mean $\pm$ SD). Sample size estimation was based on previous studies that investigated the same theoretical framework (i.e. dyadic JA) using similar task designs and measuring similar neurophysiological indexes (Cardellicchio et al., 2021; Cardellicchio, Dolfini, Fadiga, &

D'Ausilio, 2020). No a priori effect size was chosen: embracing Meehl's (1978) 'situation-taxonomy problem' (i.e. the number of different settings and stimuli that researchers can use for testing hypotheses is restricted only by their imagination; Meehl, 1978), 'there is no objective basis for expecting an observed effect size found on a particular outcome scale in one setting with one set of stimuli to be exactly or even roughly equal to the size of the same effect expressed on a different outcome scale in another setting with different stimuli' (Broers, 2021, p. 702). Here, we are interested in gaining an understanding of the way in which determinants of behaviour operate behind the scenes, and because it is this understanding that we wish to generalize, to increase support for its 'verisimilitude' or truthlikeness, we chose to perform post-hoc and sensitivity analyses (Table S1; Mook, 1983; Broers, 2021). None of the participants reported neurological, psychiatric or other contraindications to TMS (Rossi et al., 2021). Participants were informed about the experimental procedure and gave their written consent according to the Declaration of Helsinki of 1975, as revised in 2013. The study was conducted in accordance with the guidelines of the local ethics committee ('Comitato Etico di Area Vasta Emilia Centro', ref: EM255-2020_UniFe/170592) and the participants were paid 30€ for their participation.

2.2 | Experimental setup and task

The task consisted of coordinating with a confederate to perform a goal-directed action, namely, unscrewing a bottle cap (similar to Cardellicchio et al., 2021). In practice, we asked participants to perform a two-person (joint) version of a usual solo action (opening a bottle): the inherent bimanual nature of this action was therefore designed to be distributed between two actors. In this way, the haptic exchange of forces between the participant and the confederate is essential to perform the task. Thus, the coordinative essence of the task is clearly

expressed by the fact that the participant anticipatorily squeezes the bottle to stabilize it before the partner has yet to touch the cap.

The confederate (one of the authors) was seated in a comfortable armchair with his forearm pronated and the right hand resting on a button box (Cedrus RB-840 response Box) placed on a table in front of him (length = 160 cm; width = 80 cm). Two identical deformable plastic bottles (height: 25 cm, cap diameter: 5 cm, texture: rough plastic) were placed on the table 15 cm apart and at the same distance from the starting position of the confederate's hand (40 cm, about 2/3 of his arm length). One of the bottles was held by a mechanical clamp, while the other one was held with the right hand by the participant sitting on the opposite side of the table from the confederate (Figure 1). The caps of both bottles were equipped with a capacitive sensor to measure the confederate's hand touch; the bottle held by the participant was also equipped with a pressure sensor to measure the participant's hand squeezing force. In each trial, the confederate had to reach and unscrew one of the two bottles. To achieve this goal, the mechanical clamp and the participant were required to stabilize the respective bottle. To consider the trial valid, the participant had to continuously hold the grasped bottle with the hand and maintain the same posture until the action was completed.

In the present study, we introduced a new manipulation to dissociate the relative contribution of top-down and bottom-up processing. Five equally spaced LED lights were placed in the centre of the table between the confederate and the participant. Three LEDs, one central green and two outermost red ones, were visible to both the confederate and the participant, while the two innermost red LEDs were visible only to the confederate (Figure 1). Each trial began by turning on one of the four red LEDs that served as a spatial cue to the bottle (left/right) the confederate had to reach and unscrew. The confederate was always presented with the cue (which instructed the target bottle), while the participant could be shown (outermost red LEDs) or not shown (innermost red LEDs) the same cue (which informed on the target bottle of the confederate's action), depending on the experimental condition (see below). The cue was followed by the lighting of the green LED representing the go signal for the confederate to begin the action (Figure 1). The time interval between the presentation of the cue (red LED) and the go signal (green LED) was chosen randomly from a uniform distribution ranging from 500 to 1500 ms. Each trial ended when the confederate returned to the starting position.

In summary, the confederate could reach the bottle either held by the participant (joint action—JA) or the

mechanical clamp (no joint action—no_JA), and the participant could either know (knowledge—K) or not know (no knowledge—no_K) the target bottle in advance (cue provided by the outermost or innermost red LEDs, respectively), resulting in a total of four different experimental conditions (JA-K, JA-no_K, no_JA-K, no_JA-no_K; Figure 1). In no_K trials, the participant could only use the kinematic cues provided by the confederate's action to decode which bottle he was pointing toward and, therefore, whether it was a JA or a no_JA trial. In K trials, by contrast, this information was provided explicitly by the cue (i.e. left/right red LED).

The experiment was conducted in separate blocks (6) consisting of 96 trials each for a total of 576 trials. The four experimental conditions were randomized and distributed equally within each block (i.e. 24 trials for each condition; 144 trials per condition in total). The position (left/right) of the two bottles (held by the participant/mechanical clamp) was randomized across blocks and the initial position was counterbalanced across participants. The experiment was run in a single session lasting ≈ 90 min.

2.3 | TMS and EMG

For each experimental condition (JA-K, no_JA-K, JA-no_K, no_JA-no_K), a single pulse TMS protocol was used to assess CSE and the duration of the cSP. These indexes were measured on the participant holding the bottle (whereas in Cardellicchio et al., 2021, TMS was delivered to the participant reaching and unscrewing the cap). TMS was delivered through a figure-of-eight coil (70 mm) connected to a Magstim BiStim stimulator (Magstim, Whitland, UK) to the opponens pollicis (OP) primary motor representation (M1). The OP optimal scalp position (OSP) was established by moving the coil in 0.5-cm steps around the left M1 hand area and using a slightly suprathreshold stimulus. The TMS coil was held tangentially to the scalp with the handle pointing backward and laterally to form a 45° angle with the midline. The OSP was marked on a cap, and the active motor threshold (aMT) was established as the lowest stimulus intensity eliciting motor-evoked potentials (MEPs; >0.1 mV) in at least 5 trials out of 10 (Rossini et al., 2015) while participants maintained a slight contraction of the right OP (measured as the 10% of the mean of the rectified EMG signal recorded in a 3 s window of maximum voluntary contraction). The target muscle was chosen because it plays a central role in power grasp (i.e. holding the bottle). EMG was recorded from the participants' OP with a wireless EMG system (WavePlus EMG, Cometa, Italy) using pairs of Ag/AgCl surface adhesive electrodes

(5 mm in diameter) placed with a tendon-belly montage. The same wireless system was also used to measure the confederate's EMG of the first dorsal interosseous (FDI; chosen as it plays a central role in precision grip actions and more specifically in unscrewing the cap) and reaching kinematics. In fact, the Zerowire EMG system has also an analogue 3-axis accelerometer (sampling rate: 100 Hz) embedded in the same low-weight wearable unit. EMG data were digitized (sampling rate: 2 kHz; LP and HP filters: 1st order, 6 dB/octave; bandwidth: 10–500 Hz) and acquired by a CED Power 1401-3A board (Signal 6.05 software; Cambridge Electronic Device, UK). The mean ($\pm$ SD) aMT across participants was $39.4 \pm 4.1\%$ of the maximum stimulator output. During the task, TMS was delivered at 120% of aMT and, after assessing the threshold, the experimenter verified that no saturation of the EMG signal was present at this stimulation intensity. The mean ($\pm$ SD) TMS stimulus intensity across participants was 47.5 ± 4.8 of the maximum stimulator output.

The TMS pulse was delivered with four different timings: (1) 'Baseline', at the same time as the cue presentation (red LED), (2) 'Go', at the onset of the confederate's movement (i.e. the release of the button), (3) 'EMG', during the confederate's movement, and triggered according to the confederate's electromyographic activity (see below) and (4) 'Grip', at the same time as the confederate touched the bottle cap (Figure 1). In the 'EMG' timing, TMS was delivered depending on the activation of the confederate's FDI. More specifically, the EMG activity for the FDI was processed online (rectified and averaged within nonoverlapping windows of 50 ms during the unfolding of the confederate's movement); the TMS pulse was triggered as soon as the EMG exceeded the baseline value (mean rectified activity within the 100-ms window immediately preceding movement onset) by a threshold value (estimated upon the grand mean of 10 training reach-to-grasp EMGs performed by the confederate before every experimental session; similar to Cardellicchio et al., 2021). In this way, we were able to time-lock the TMS pulse to the action-dependent activation of the muscle of interest without relying on an a priori decided spatial or temporal landmark. The 'EMG' timing occurred approximately in the middle of the reaching movement, namely, between the release of the button and the touch of the bottle cap ($40 \pm 20\%$ of the total movement time [MT]; mean $\pm$ SD). TMS was administered in 50% of the trials (i.e. 288 trials), and its timing was randomized and distributed equally across conditions, resulting in 18 trials for each combination of experimental conditions (JA-K, JA-no_K, no_JA-K, no_JA-no_K) and timing ('Baseline', 'Go', 'EMG' and 'Grip').

2.4 | Data analysis

Two participants were excluded from the analyses of both CSE and cSP because of artefactual contamination of the electromyographic signal and technical problems related to the triggering of the TMS in the 'EMG' timing condition. One additional participant was excluded only from the cSP analysis because of the absence of a clearly detectable silent period (CSE analysis $n = 20$; cSP analysis $n = 19$; see Table S2). Data processing and analysis were performed with Matlab (The MathWorks, Inc., Natick, MA, 2020), using built-in functions and custom-made code to extract the following indexes:

1. CSE: peak-to-peak amplitude value (mV) of the MEP identified in the 100 ms window following the TMS pulse;
2. cSP: the period (ms) which starts at the isoelectric state that follows the MEP offset and ends with the resuming of voluntary muscular activity (using the mean consecutive difference [MCD] method; Garvey et al., 2001);
3. Kinetic parameters of the participant: onset and offset of the squeezing force applied to the bottle;
4. Kinematic parameters of the confederate: the three components (x, y, z) of acceleration values (g) and the resulting acceleration vector across time.

CSE and cSP normality of data distribution was visually checked and further analysed by means of a one-sample Kolmogorov–Smirnov test. Values that were $>$ or $<$ than their respective mean values ± 2 SD were excluded from the analysis (see Table S2). To account for individual and trial-by-trial variability in muscle activity, MEPs and cSPs were normalized trial-by-trial to the root mean square (RMS) of EMG activity calculated in the 150 ms window immediately preceding the TMS pulse (i.e. $CSE = \frac{MEP}{RMS}$; $cSP = \frac{cSP}{RMS}$). In addition, the mean values of CSE and cSP for each relevant timing (Go, EMG, Grip) were further normalized to their respective mean value of the Baseline timing, separately for each condition (JA-K, JA-No_K, No_JA-K, No_JA-No_K; e.g. for JA-K: $CSE_{GO} = CSE_{GO}/CSE_{BASELINE}$; $CSE_{EMG} = CSE_{EMG}/CSE_{BASELINE}$; $CSE_{GRIP} = CSE_{GRIP}/CSE_{BASELINE}$). To examine participants' behaviour, we analysed no-TMS trials (50% of the total), thus avoiding the interference on motor output imposed by the suprathreshold TMS. We estimated the onset (P_{onset}) and offset (P_{offset}) of the participants' bottle squeezing in the JA conditions (JA-K and JA-no_K). More specifically, we first low-pass filtered the output of the pressure sensor (double-pass Butterworth, cutoff frequency: 5 Hz, order: 2) and then applied the MCD

method to estimate P_{onset} and P_{offset} (similarly to what was described for the cSP estimation).

In principle, participants could start dosing their force to stabilize the bottle before or after the onset of the confederate's reaching action (i.e. the release of the button, $\text{Mov}_{\text{onset}}$). This led us to explore whether this was the case by investigating the time interval (namely, Delay) between the onset of the participants' squeezing action (P_{onset}) and $\text{Mov}_{\text{onset}}$ (Equation 1: $\text{Delay} = P_{\text{onset}} - \text{Mov}_{\text{onset}}$). Specifically, we calculated the average value of Delay for the whole experimental session in each participant. This parameter, with regard to Equation 1, could take either positive (Delay+) or negative (Delay-) values, where a positive Delay value represents that the participant started squeezing the bottle—on average—after confederate's movement onset, and a negative value that the participant started squeezing the bottle—on average—before confederate's movement onset.

This exploratory analysis of Delay revealed that this parameter eventually took negative values only in the JA-K condition (Table S3; see Section 3), and thus we calculated the percentage of Delay+ and Delay- (count of total Delay+ and Delay- out of the 72 relevant unstimulated trials) and their mean values in each participant for the whole experimental session (Figure 3). The evaluation of one's (average) Delay enabled the qualification of one's (predominant) individual motor strategy in JA-K, revealing the presence of two discrete behavioural groups: the Late group which comprises participants who exhibited mean Delay+ (i.e. the participant started squeezing the bottle after confederate's action onset), and the Early group which includes participants who showed mean Delay- (i.e. the participant started squeezing the bottle before confederate's action onset; Figure 3, red line). Lastly, to evaluate the stability of the adopted strategy over time, we calculated mean Delay as well as the percentage of Delay+ and Delay- in the six experimental blocks for each participant (see Figure S1 and Table S4). We then explored whether CSE and cSP were modulated differently in the two groups.

Finally, we tested if differences between the Early/Late groups were due to differences in the confederate's behaviour. For each participant in every no-TMS trial (i.e. the same trials in which we measured Delay), we calculated the confederate's mean reaction time (RT_{led} ; the time between go signal and $\text{Mov}_{\text{onset}}$) and mean MT (the time between $\text{Mov}_{\text{onset}}$ and $\text{Mov}_{\text{offset}}$). We also analysed the confederate's hand acceleration profile. First, we low-pass filtered the three acceleration time series [x,y,z] (double-pass Butterworth, cutoff frequency: 5 Hz, order: 2), normalized each filtered time series to a baseline (mean acceleration in the initial 500 ms window after trial onset) and computed the resulting acceleration

vector (Acc_{VEC}). Acc_{VEC} was then rescaled on a trial-by-trial basis to the total duration of the movement (time-scale linear normalization). Statistical tests were confined to the initial 60% of the movement acceleration profile (from $\text{Mov}_{\text{onset}}$ to 60%*MT) which is known to contain the most relevant kinematic cues used by observers (here, the participants) to decode the actions of others (here, the confederate) and effectively coordinate with them (Torricelli et al., 2023).

2.5 | Statistical analysis

Statistical analyses were conducted using STATISTICA 12 (StatSoft, Inc.; analysis of variance [ANOVA]) and Matlab (nonparametric permutation test, false discovery rate [FDR] correction).

2.5.1 | CSE and cSP modulation by task conditions and TMS timing

The MEP and cSP normalized values were entered in two separate $2 \times 2 \times 3$ ANOVAs for repeated measures, with TASK (JA, no_JA), KNOWLEDGE (K, no_K) and TIMING (Go, EMG, Grip) as within-subject factors. Significant interactions were further explored with Newman-Keuls post-hoc tests.

2.5.2 | CSE and cSP modulation by coordination strategy

To test whether the modulation of CSE and cSP by task condition (K vs. No_K) and TMS timing (Go, EMG, Grip) depended on the individual motor strategy (Group: Early vs. Late), we performed within and between groups nonparametric permutation tests (number of permutations = 5000, alpha level = 0.05) and controlled the FDR according to the Benjamini and Hochberg procedure (Benjamini & Hochberg, 1995). Permutation tests were chosen for these exploratory analyses because they are more robust and thus preferable for small sample sizes (Ludbrook & Dudley, 1998).

Within groups comparison: we evaluated by means of a nonparametric permutation test whether, within each group, there were statistically significant differences between task conditions (K vs. No_K) across TMS timings. Statistical analyses were performed for both CSE and cSP.

Between groups comparison: we evaluated by means of a nonparametric permutation test whether, within the relevant condition (i.e. JA_K), there were statistically significant differences between groups (Early vs. Late)

across TMS timings. Statistical analyses were performed for both CSE and cSP.

2.5.3 | Control analyses on the confederate's kinematics

To evaluate whether confederate's kinematics might have biased participants toward the adoption of either one of the two strategies, we performed a nonparametric permutation test on RT_{led} and MT. We computed the mean absolute difference of the confederate RT_{led} and MT between the Early and Late groups ($\Delta_{original}$). We then calculated the same difference after randomly permuting (5000 iterations) the confederate data between the Early and Late groups ($\Delta_{surrogate}$). The p -values were obtained by computing the proportion of permutations for which $\Delta_{surrogate}$ was greater than $\Delta_{original}$.

We also compared the acceleration profile of the confederate's hand between the Early and Late groups. We first calculated the mean acceleration profile (ACC_M) for each condition and participant. We then statistically evaluated the difference in the confederate acceleration between the Early and Late groups by means of a nonparametric permutation test. For each time point (on the normalized time scale from 0% to 60% of MT), we calculated the mean absolute difference in the confederate acceleration between the Early and Late groups ($\Delta_{original}$). We then calculated the same difference after randomly permuting (5000 iterations) the confederate data between the Early and Late groups ($\Delta_{surrogate}$). The p -values were obtained by computing the proportion of permutations for which $\Delta_{surrogate}$ was greater than $\Delta_{original}$ (for each time point). The confederate data for one participant (belonging to the Early group) was excluded from the analysis because they were corrupted.

3 | RESULTS

3.1 | CSE and cSP reflect dissociable time- and information-dependent JA processes

For both CSE and cSP, the ANOVA yielded a significant interaction between TASK, KNOWLEDGE and TIMING (CSE: $F(2,38) = 4.13$, $p = 0.023$, observed power = 0.69, partial eta-squared = 0.17; cSP: $F(2,36) = 4.04$, $p = 0.026$, observed power = 0.68, partial eta-squared = 0.18; see Table 1). Further Newman-Keuls post-hoc tests showed that, in the Go timing only, CSE for JA-K (mean $\pm$ SD, 1.26 ± 0.36) was greater than for all other conditions (mean $\pm$ SD, JA-No_K = 0.98 ± 0.15 , $p = 0.0008$; No_JA-

TABLE 1 Repeated measures analysis of variance (ANOVA) table of effects for CSE and cSP.

	CSE			cSP		
J	$F(1,19) = 16.4$	$p = 0.0006$	Obs. power = 0.96	Part. eta-squared = 0.46	$F(1,18) = 8.1$	$p = 0.01$
K	$F(1,19) = 4.5$	$p = 0.04$	Obs. power = 0.52	Part. eta-squared = 0.19	$F(1,18) = 11.6$	$p = 0.003$
Timing	$F(2,38) = 11.2$	$p = 0.0001$	Obs. power = 0.98	Part. eta-squared = 0.37	$F(2,36) = 16.2$	$p = 0.00001$
J*K	$F(1,19) = 1.7$	$p = 0.2$	Obs. power = 0.24	Part. eta-squared = 0.08	$F(1,18) = 3.9$	$p = 0.06$
J*Timing	$F(2,38) = 14.4$	$p = 0.00002$	Obs. power = 0.99	Part. eta-squared = 0.43	$F(2,36) = 9$	$p = 0.0006$
K*Timing	$F(2,38) = 0.65$	$p = 0.5$	Obs. power = 0.15	Part. eta-squared = 0.03	$F(2,36) = 2.7$	$p = 0.07$
J*K*Timing	$F(2,38) = 4.1$	$p = 0.02$	Obs. power = 0.69	Part. eta-squared = 0.17	$F(2,36) = 4$	$p = 0.02$

Abbreviations: CSE, corticospinal excitability; cSP, cortical silent period; J, JA vs. no_JA; JA, joint action; K, K vs. no_K; Obs. power, observed power; Part. eta-squared, partial eta-squared; timing, TMS timings; TMS, transcranial magnetic stimulation.

$K = 1.03 \pm 0.16$, $p = 0.004$; No_JA-No_K = 1.06 ± 0.2 , $p = 0.004$; see Table S6 for the full table of effects). For the EMG and Grip timings, a statistically significant difference was found between JA and No_JA, while there was no difference on CSE between K and No_K (mean $\pm$ SD, EMG: JA-K = 1.41 ± 0.28 vs. JA-No_K = 1.34 ± 0.39 , $p = 0.26$; No_JA-K = 1.06 ± 0.19 , $p = 0.0001$; No_JA-No_K = 0.97 ± 0.13 , $p = 0.0001$; GRIP: JA-K = 1.44 ± 0.45 vs. JA-No_K = 1.34 ± 0.31 , $p = 0.28$; No_JA-K = 1.07 ± 0.19 , $p = 0.0001$; No_JA-No_K = 1 ± 0.11 , $p = 0.0001$; Figure 2a). In contrast, post-hoc Newman-Keuls analysis for cSP showed no significant differences in the Go timing, but a significant difference emerged for the EMG and subsequent Grip timing. Specifically, in the EMG timing, JA-K (mean $\pm$ SD, 1.53 ± 0.63) produced longer cSP which differed from all the other experimental conditions (mean $\pm$ SD, JA-No_K = 1 ± 0.41 , $p = 0.0001$; No_JA-K = 1 ± 0.17 , $p = 0.0001$; No_JA-No_K = 0.95 ± 0.16 , $p = 0.0001$), and this effect was conserved also in the later Grip timing (mean $\pm$ SD, JA-K = 1.61 ± 0.74 vs. JA-No_K = 1.36 ± 0.69 , $p = 0.007$; No_JA-K = 1.04 ± 0.21 , $p = 0.0001$; No_JA-No_K = 0.99 ± 0.17 , $p = 0.0001$; Figure 2b). Furthermore, in the Grip timing also JA-No_K (mean $\pm$ SD, 1.36 ± 0.69) was different from the two No_JA conditions (mean $\pm$ SD, No_JA-K = 1.04 ± 0.21 , $p = 0.0005$; No_JA-No_K = 0.99 ± 0.17 , $p = 0.0004$; Figure 2b; see Table S7 for the full table of effects).

Taken together, our results show that JA generally produces larger CSE and longer cSPs. At the same time, the two neurophysiological indexes seem to reflect two temporally dissociable processes. CSE was modulated early on before the action started but only for JA-K, not for JA-No_K (Go). Instead, the cSP modulation emerged during the reaching action for JA-K (EMG) and only later at the time of haptic interaction for JA-No_K (Grip). At Go, prior information is available, but no kinematic cues are yet present. In this case, only the CSE is modulated and only for JA-K trials, thus supporting the conclusion that the CSE reflects the processing of prior information. At EMG, early kinematic cues begin to emerge and, in fact, the CSE is modulated for JA-No_K as well. However, if we look at the cSPs, we observe a gradual modulation, such that JA-K is differentiated already at EMG, while later it develops into a differentiation between JA and No_JA, at Grip timing. These two indexes could thus reflect the concurrent, and partially overlapping, elaboration of contextual priors (i.e. CSE) and the online sampling of kinematic cues (i.e. cSP).

3.2 | JA coordination strategies

In principle, participants could start dosing their force to stabilize the bottle early during the trial (i.e. as soon as prior information became available in JA-K trials) or wait

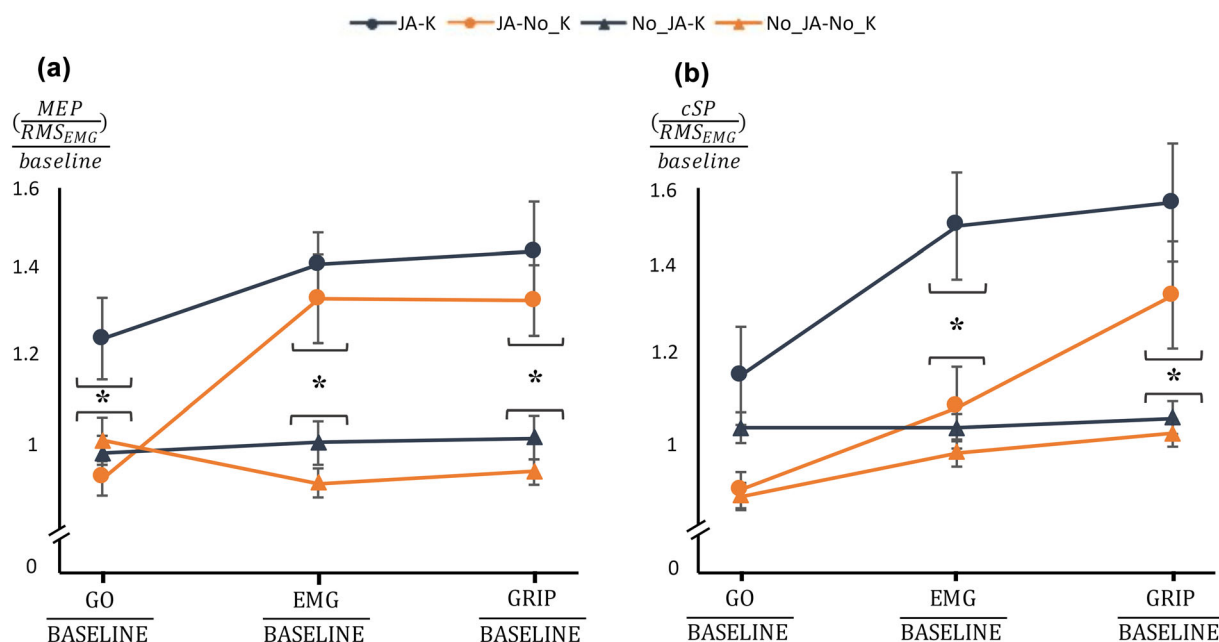


FIGURE 2 Modulation of neurophysiological excitation and inhibition. (a) Corticospinal excitability (CSE) results in all participants. (b) Cortical silent period (cSP) results in all participants. Parentheses and asterisks show statistically significant results according to Newman-Keuls post-hoc test, error bars represent standard error of the mean (SEM).

until much later (i.e. when prior information was complemented by confederate's movement cues) and thus squeeze the bottle right before the haptic force exchange was about to happen with the confederate. The former strategy is safer (i.e. carries less risk of motor coordination failure) but also more expensive.

Exploratory analyses of Delay's values across participants revealed that this parameter could take negative values only in JA-K (see Table S3), enabling the further characterization of two behavioural groups precisely on the basis of the sign of average Delay (i.e. positive or negative value). That is, participants who showed mean Delay+ in JA-K were included in the Late group, whereas participants who showed mean Delay- were included in the Early group (Figure 3, red line). We then

checked for individual consistency in the selected strategy by evaluating the count of Delay+ and Delay- in each participant (Figure 3, histogram bars). The mean $\pm$ SD count of Delay+ in the Late group was 67.85 (± 3.95), whereas for Delay-, this value was 4.08 (± 4.03). On the other hand, in the Early group, the mean $\pm$ SD count was, respectively, 11.77 (9.48) and 60.22 (± 9.48) for Delay+ and Delay-. The grand average $\pm$ SD of Delay+ and Delay- was, respectively, 322 ms (± 93 ms) and -127 ms (± 152 ms) for the Late group, and 251.5 ms (± 108 ms) and -751 ms (± 361 ms) for the Early group.

When prior information was missing, as in JA-No_K, the vast majority of trials had a positive delay (i.e. Delay+; participants could not anticipate their squeezing; see Table S3). There were no Delay- in the Late group, while

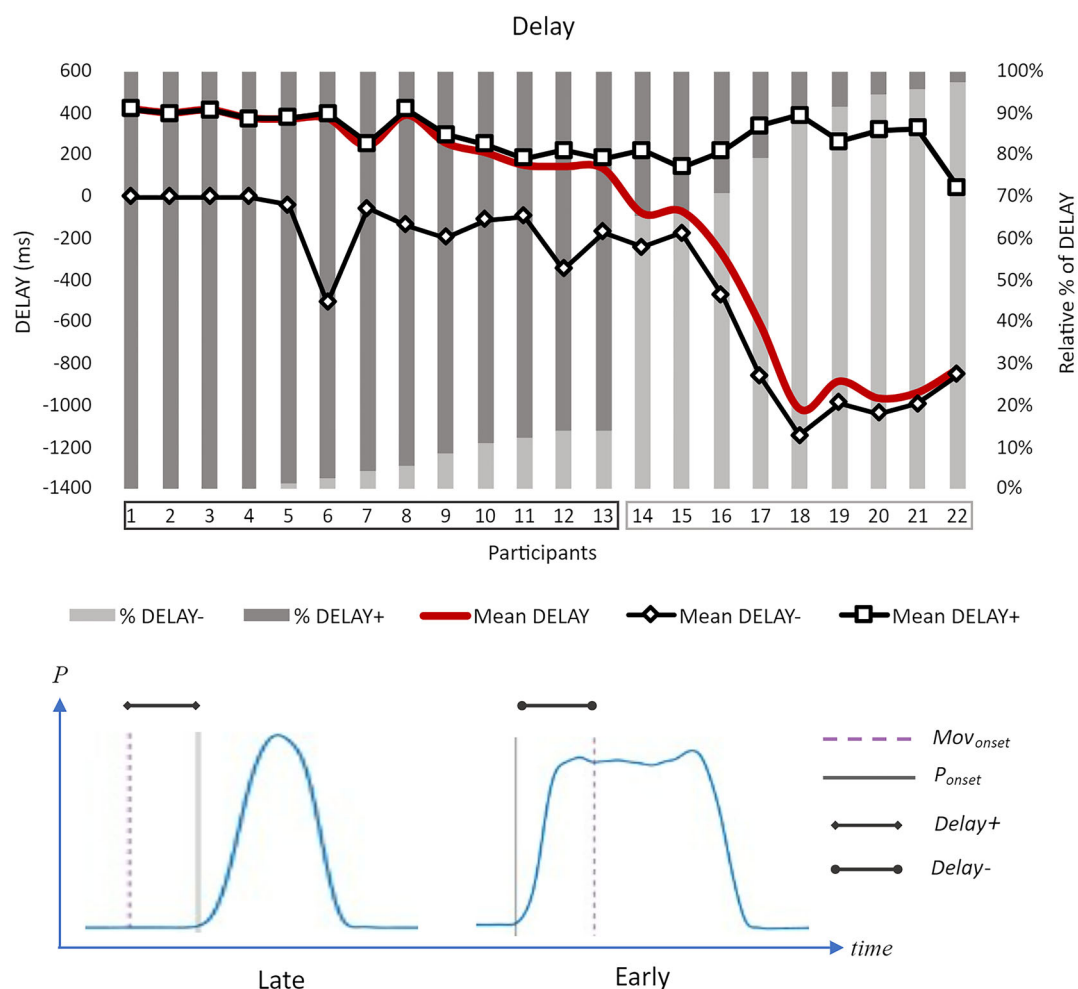


FIGURE 3 Behavioural determination of joint action (JA) coordination strategy. (a) Relative percentage of DELAY and mean DELAY values for each participant. Participants were included in Late group if mean DELAY was positive (red line; $n = 13$, dark grey box) or in Early group if mean DELAY was negative ($n = 9$, light grey box). The coherence between mean DELAY (red line) and the % positive/negative DELAY (black lines) reflects how much a selected strategy is represented within a participant (histogram bars). These data reveal the individual robustness of one's selected strategy. (b) Distinct profiles of the pressure curves obtained from the characteristic squeezing of the bottle by participants belonging to the two groups. Mov_{onset} = onset of confederate's movement; P_{onset} = onset of pressure squeezing; Delay+ = Delay positive; Delay- = Delay negative.

in the Early group, anticipatory squeezing was observed in only a few trials (mean count 0.44 ± 0.72 and 71.55 ± 0.72 for Delay– and Delay+, respectively). The grand average of Delay+ was 968.52 ms (± 233.56 ms) and 771.22 ms (± 193.68 ms) for the Late and Early groups, respectively.

Furthermore, we examined whether the coordination strategy (i.e. squeezing behaviour) evolved over time by measuring and counting Delay+ and Delay– across blocks. Each participant from both groups adopted his/her preferred strategy and maintained it throughout the experiment (see Figure S1 and Table S4).

Overall, when prior information was available (JA_K), participants in the Late group consistently stabilized (i.e. squeezed) the bottle after the confederate movement had already begun. The other participants, belonging to the Early group, began to apply their force before the confederate's movement and thus well before it was actually needed to stabilize the bottle (Figure 3b). When no prior information was available, the two groups practically adopted the same strategy, waiting until they could more reliably infer whether the confederate would target their bottle (JA) or the other bottle (No-JA).

3.3 | JA strategies are reflected in different neurophysiological modulations

We then examined whether neurophysiological indexes underwent different modulations in the Early and Late groups, that is, depending on the coordination strategy adopted. We specifically targeted modulations induced by task knowledge (K vs. No_K) on JA coordination. Indeed, prior knowledge allows participants to anticipate their squeezing behaviour, whereas No_K trials simply do not offer this possibility (see Table S3). To test whether the modulation of CSE and cSP by task condition and TMS timing depended on coordination strategy, we performed within and between groups nonparametric permutation tests with FDR correction (reported *p*-values are FDR corrected).

Both CSE and cSP showed different modulations in the two groups. Notably, CSE did not undergo any significant change between task conditions in the Late group (i.e. no significant differences between K and No_K across the three TMS timings; Figure 4a), while larger modulation during JA-K (mean $\pm$ SD, 1.56 ± 0.36) in the Go timing was present for the Early group (mean $\pm$ SD, JA-No_K = 1.05 ± 0.19 , $p = 0.008$; Figure 4b). Between groups analyses further revealed that at the Go timing the Early group exhibits a significantly higher CSE than the Late group in JA-K (Early = 1.56 ± 0.36 ; Late = 1.02 ± 0.18 ; $p = 0.001$). Participants anticipating their squeeze when prior information is available, presented an early

modulation of CSE, further confirming it reflects top-down processing. The late group, based on behavioural data, seems rather insensitive to prior information and does not show any CSE modulation.

Interestingly, a different pattern of results was found for cSP: within groups results show that in the Late group, larger inhibition for JA-K (mean $\pm$ SD, 1.29 ± 0.44) is present only in the EMG timing (mean $\pm$ SD, JA-No_K = 0.86 ± 0.24 , $p = 0.02$; Figure 4c), whereas the Early group showed effects in the same direction but with premature onset, beginning from the Go timing (mean $\pm$ SD, GO: JA-K = 1.70 ± 0.69 , JA-No_K = 0.95 ± 0.21 , $p = 0.04$; EMG: JA-K = 2.05 ± 0.80 , JA-No_K = 1.24 ± 0.62 , $p = 0.04$; Figure 4d). Further between groups comparisons revealed that in JA-K the magnitude of (temporal unspecific) inhibition in the Early group is significantly higher than in the Late group before haptic interaction (mean $\pm$ SD, GO: Early = 1.70 ± 0.69 ; Late = 0.78 ± 0.19 ; $p = 0.002$; EMG: Early = 2.05 ± 0.80 , Late = 1.29 ± 0.44 , $p = 0.02$). Here, cSP is modulated in both groups but with a very different degree of temporal specificity and amplitude between coordination strategies. Participants anticipating their squeeze show a (tonic) higher level of inhibition before the haptic exchange of forces, compared with participants not anticipating their squeeze, possibly indicating an intensive focus on sampling kinematic cues from a single motor hypothesis (see Section 4). The Late group, instead, shows a temporally selective change in cSP, precisely when kinematic information starts to become available (EMG).

3.4 | Confederate's behaviour did not influence coordination strategy

Finally, we performed some control analyses to rule out that differences between the Early/Late groups were due to differences in the confederate's behaviour. For each participant in every no-TMS trial (i.e. the same trials in which we measured Delay), we calculated the confederate's mean RT (RT_{led} ; the time between go signal and Mov_{onset}) and mean MT (the time between Mov_{onset} and Mov_{offset}). We also analysed the confederate's hand acceleration profile (see Section 2 for analyses).

The confederate showed comparable RT_{led} (Early: 515.03 ± 17.35 ms; Late: 520.95 ± 45.41 ms; $p = 0.67$) and MT (Early: 920.8 ± 59.73 ms; Late: 881.5 ± 65.02 ms; $p = 0.16$) during interaction with participants from both groups (mean RT_{led} and MT are reported for all participants in Table S5).

Similarly, no difference was observed in the acceleration profile (at any time point) of the confederate's movements between the Early and Late groups

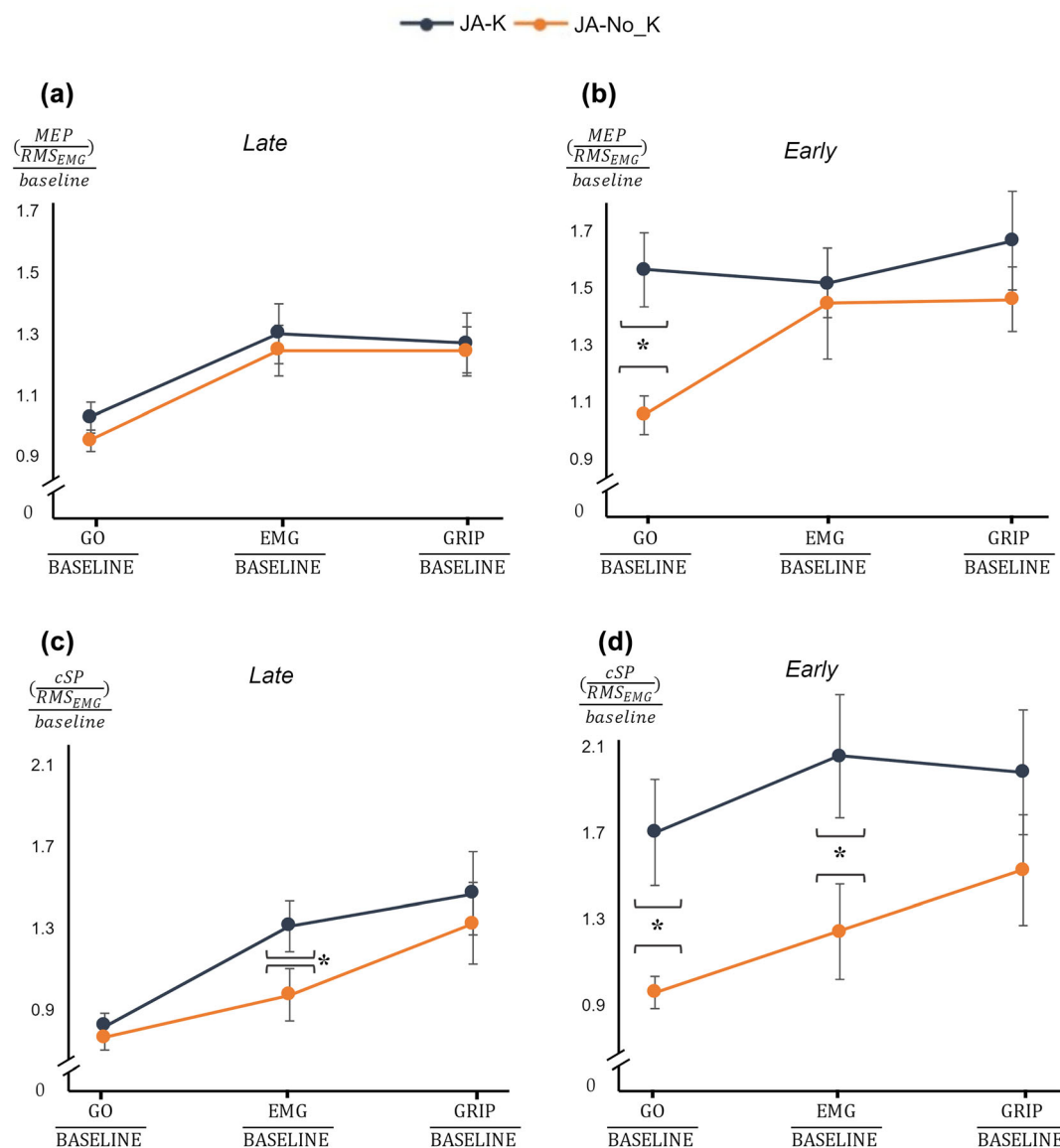


FIGURE 4 Neurophysiological modulations depending on joint action (JA) coordination strategy. (a) Corticospinal excitability (CSE) results in Late group. (b) CSE results in Early group. (c) Cortical silent period (cSP) results in Late group. (d) cSP results in Early group. Parentheses and asterisks show statistically significant results according to permutation tests with false discovery rate (FDR) correction. Please note that *between groups* significant results are not reported for graphical purposes. Error bars represent standard error of the mean (SEM).

(all p -values > 0.05, permutation test). For illustration purposes, the grand average of the mean acceleration profile of each participant (ACC_M) in both groups for each condition (JA-K, JA-No_K, No_JA-k, No_JA-No_K) is plotted in Figures S2–S5. Overall, we can rule out that the adoption of a particular strategy was driven by the confederate's behaviour.

4 | DISCUSSION

A significant amount of empirical research has investigated the cognitive processes contributing to JA

(Konvalinka et al., 2010; Pezzulo et al., 2019; Sacheli et al., 2022; Vesper et al., 2013, 2016) and, in particular, the psychosocial factors modulating social coordination (Bieńkiewicz et al., 2021; D'Ausilio et al., 2012). However, much less has been reported in relation to the neurophysiological substrates of low-level sensorimotor coordination (Cardellicchio et al., 2021; Cardellicchio, Dolfini, Fadiga, & D'Ausilio, 2020), although it is becoming increasingly evident that it may provide the scaffolding on which higher-order cognitive processes are built during development (Brownell, 2011; Carpenter, 2009).

Here, participants had to focus on a shared goal that could only be achieved via the spatio-temporal alignment

of complementary actions. In fact, we transformed a naturally bimanual task into an interactive unimanual task (Cardellicchio et al., 2021). In agreement with earlier studies, we find larger CSE and longer cSPs (more inhibition) in JA than no_JA (Cardellicchio, Dolfini, Fadiga, & D'Ausilio, 2020). At the same time, we show that the two neurophysiological indexes reflect two temporally dissociable processes. CSE was modulated earlier, before the action started, if prior information on the upcoming action was provided. Modulation of cSP emerged during the reaching phase when partner's kinematic cues were available. These two indexes could thus reflect the concurrent processing of contextual priors (top-down) and the online sampling of partner's kinematic cues (bottom-up), respectively.

Moreover, the availability of prior knowledge revealed the emergence of two opposite coordination strategies (Late vs. Early). The two strategies seem to trade energy expense with safety by timing the force production early during the trial or later on, just before the haptic exchange (Figure 3b). Importantly, individual strategies emerged from the earliest trials, proved stable across the whole experiment and were not informed by the partner's behaviour, thus suggesting they may constitute an individual motor signature (IMS; Hilt et al., 2020; Słowiński et al., 2016). The neurophysiological modulations in the two groups appear to reflect fundamental differences in how JA is planned and controlled. Namely, the two coordinative strategies might imply a different weighting of top-down and bottom-up inferential processes. The Early group modulated CSE when prior information was available and maintained a tonic (temporally non-specific) lengthening of cSP throughout the trial. Thus, the Early group could complement top-down processes with extended and potentially less efficient sampling of kinematic cues. The Late group, on the other hand, did not show the CSE modulation driven by prior information and rather seemed to generate a phasic modulation of cSP just when key kinematic information was available. As a consequence, the Early group may have weighed much more heavily on prior information than the Late group, who instead relied almost exclusively on temporally selective tuning of bottom-up processing.

4.1 | CSE modulation reflects the processing of contextual information

CSE reflects the combined readout of local and distal inputs projecting to the descending motor neurons together with the excitability of their spinal targets (Ridding & Rothwell, 1997; Spampinato et al., 2023). The

activity sampled via single-pulse TMS, however, is related not only to the generation of motor commands but is also involved in the processing of higher-order signals for motor planning and undergoes dynamic changes during the choice of an action (Klein et al., 2014; Hannah et al., 2018; Derosiere et al., 2022; for a full review, see Bestmann & Duque, 2016). Importantly, prior to movement onset in RT tasks, a progressive increase in MEP amplitude can be observed in the effectors selected for the forthcoming action (Chen et al., 1998; Leocani et al., 2000; Soto et al., 2010; Tandonnet et al., 2012). In general, CSE provides a highly temporally selective description of the functional state of the motor system—as a whole—during action *transformations* (i.e. the dynamic process of converting extrinsic coordinates, like target locations in the environment, into intrinsic coordinates in terms of EMG activity), while also taking into account the history of motor outputs (Julkunen et al., 2012; Pellicciari et al., 2016).

CSE is modulated even in the absence of explicit action preparation, as in the case of action observation (Fadiga et al., 1995). In this case, modulation of CSE possibly reflects the reactivation of motor circuits in a sort of simulative mode (D'Ausilio, Bartoli, & Maffongelli, 2015; Fadiga et al., 1995; Flanagan & Johansson, 2003; Naish et al., 2014). At the same time, it is now clear that these modulations do not necessarily map low-level features of the observed actions, but may also reflect higher-order, even symbolic, contextual information during action observation tasks (Amoruso et al., 2018; Amoruso & Urgesi, 2016; Avenanti et al., 2013). Overall, these results converge toward the idea that CSE is highly prone to top-down modulation (Amoruso et al., 2018; Barchiesi & Cattaneo, 2013; Liuzza et al., 2015; Ubaldi et al., 2015).

In line with this, Kilner et al. (2004) have shown that readiness potential (RP)—an electrophysiological marker of motor preparation—is present not only when observing someone else's action, but also prior to it, if the nature and onset of the action are predictable. Taken together, knowledge of an upcoming event (e.g. someone else's action) is sufficient to excite one's own motor system. Hence, modulation of CSE could reflect the processing of higher-order contextual cues and inform us about the individual propensity to make use of these cues in shaping JA motor coordination. Therefore, our data support the claim that CSE during action observation/execution encodes far more than the low-level motor details of actions (Amoruso et al., 2018; Hilt et al., 2020; Sartori et al., 2011). Indeed, we find modulation before the onset of movement (observed and executed), based on cues that anticipate whether interpersonal haptic coordination will occur.

4.2 | cSP modulation reflects the monitoring of kinematic features

cSP length provides a measure of slow metabotropic postsynaptic GABA_B-mediated inhibition (Hallett, 2007; Werhahn et al., 1999). The specific attribute of GABA_B-mediated inhibition is that it requires associative neuronal firing to generate enough GABA pooling (Brown et al., 2007; Cash et al., 2010; Nicoll, 2004; Poncer et al., 2000; Scanziani, 2000), thus revealing its role in the coordination of neuronal ensembles (Brown et al., 2007; Cash et al., 2010; Mann & Paulsen, 2007; Nicoll, 2004; Scanziani, 2000). Corticospinal inhibition has been associated with response selection (Davranche et al., 2007; Tandonnet et al., 2012) as well as suppression of voluntary motor drive (Klein et al., 2014). In fact, suppression of activity in the motor system is central during action control to momentarily drive neural activity away from the triggering threshold and give time for sensory information to accumulate to do the 'right thing' (Alamia et al., 2019; Aron et al., 2016; Derosiere & Duque, 2020).

Interestingly, the direction of cSP modulation may be particularly informative in a socio-motor coordination context. Indeed, cSP is reduced when the observed action does not match a concurrently executed action (Cardellicchio, Dolfini, Hilt, et al., 2020) and is increased during JA motor coordination (Cardellicchio, Dolfini, Fadiga, & D'Ausilio, 2020). Along these lines, cSP lengthening could reflect goal sharing in JA, while its shortening could indicate goal misalignment between partners (Cardellicchio, Dolfini, Fadiga, & D'Ausilio, 2020). According to the active inference framework (Donnarumma et al., 2017; Friston, 2010; Friston et al., 2009), action perception is seen as an active process of sensory hypothesis testing. The active sampling of information that is used to update predictions and the probability of competing hypotheses could explain our cSP results. In our experiment, there was no significant modulation of cSP at the beginning of the trial, regardless of the availability of information to unambiguously predict the upcoming action. Instead, modulations of cSP emerged later, when the partner's movement progressively disclosed kinematic cues of the ongoing action. Monitoring and proactive use of these cues could be accounted for by cSP fluctuations.

Furthermore, our cSP results—regarding the availability of priors (i.e. JA_K vs JA_noK)—suggest an important feature of this bottom-up inferential process. Indeed, if we are provided with reliable contextual cues, the sampling function monitors kinematic cues to test a specific motor hypothesis (i.e. in JA_K, participants track information to confirm a cued outcome). On the other hand, the absence of prior information necessarily leads

to sensory sampling that must disambiguate among multiple motor hypotheses. Our data clearly show that in the former case, cSP modulation emerged earlier (i.e. EMG) than in the latter (i.e. Grip), thus confirming that less evidence needs to be accumulated to verify a specific hypothesis, whereas disambiguating between two requires accumulating more evidence.

4.3 | Individual motor signatures of JA coordination

In our experiment, participants naturally settled for either one of two opposite strategies. Interestingly, the two coordination strategies did not emerge during the task but were chosen very early and then maintained throughout the experiment. This is highly suggestive of the fact that participants implicitly evaluated the trade-off between energy expenditure (i.e. muscular activity) and safety (i.e. engagement of the bottle well before the initiation of the partner's movement and minimisation of the risk of motor co-ordination failure) according to individual idiosyncrasies. In fact, the absence of any behavioural change or drift suggests that each participant identified his or her own strategy as acceptable and advantageous to properly carry out the task.

This is not surprising if we consider that human ecological movement is only partially constrained by intrinsic (body-centred) and extrinsic (target-related) factors that reduce the very large redundancy of control. Yet, in most cases, participants still have to select one motor solution among several potential ones (Hilt et al., 2016). In contrast to classical laboratory tasks in which exogenous and normative values largely constrain the specific coordination strategy to be adopted (Camerer et al., 2005; Levy & Glimcher, 2012; O'Brien & Ahmed, 2013), our task belongs to a group of paradigms in which the goal is specified, but a set of subjective sensorimotor and homeostatic values are left free to vary. In principle, although there was a well-defined and clear goal (i.e. stabilize the bottle *before* the partner touches the cap), there were also fundamental degrees of freedom by which individual decision-making processes could emerge (i.e. *how long before* engaging the bottle to stabilize it). As a result, the flexibility designed in our task made participants free to shape their behaviour according to their motor-related idiosyncrasies or IMS (Słowiński et al., 2016; Hilt et al., 2020).

Prior neurophysiological evidence shows that CSE is modulated during action observation depending on participants' sensorimotor strategies or IMSs (Hilt et al., 2020; Torricelli et al., 2023). The present study extends these results to the domain of JA, showing that

each JA strategy is reflected in a specific modulation of CSE and cSP. As described above, the Early group showed a premature modulation of CSE not present in the Late group. Furthermore, the Early group is associated with a higher degree of inhibition compared with the Late group, which possibly represents the difference in the cost of the sampling function which either monitors a single kinematic hypothesis (i.e. Early group) or keeps track of multiple hypotheses (i.e. Late group). All in all, given that different coordinative strategies imply different weighting and temporal mixing of top-down and bottom-up processes, we suggest that the combination of both indexes has the potential to highlight individual neurobehavioural fingerprints during JA tasks.

4.4 | Conclusions

We show that motor inhibition and excitation could reflect robust individual differences in how top-down and bottom-up inferential processes are naturally mixed during JA motor coordination. Goal-directed behaviour is built upon the proper selection of the motor programme and eventual switching between different possible motor options. However, several conditions are characterized by the disruption of interactive (JA) motor behaviour, either due to generally accepted factors (e.g. Parkinson's disease) or to less understood mechanisms (e.g. schizophrenia). Nonetheless, neuropsychiatric conditions dominated by disorganized social behaviour are principally described in their phenomenological aspect. Therefore, although more research is necessary to further understand normal and abnormal (JA) motor behaviour, we believe that our results bear implications to advance the neurobehavioural characterization of conditions associated with impaired (social) motor behaviour.

In fact, a significant interest is emerging in the quantitative subtyping of neuropsychiatric conditions affecting the sensorimotor functions beside the more eloquent socio-communicative dimension (Clementz et al., 2022; Qi et al., 2023). Moreover, since its introduction more than three decades ago, TMS has been a valid tool not only to shape new treatment frontiers but also to investigate the nature and aetiology of these conditions (Frantseva et al., 2014; Haraldsson et al., 2004; Howes et al., 2017; Rossi et al., 2021; Rossini et al., 2015). Indeed, an increasing body of evidence is accumulating in favour of new methodologies to 'biotype' psychiatric conditions and move from clinical phenomenological diagnosis to a more biomarker-based perspective (Clementz et al., 2022). All in all, neurobiological and physiological stratification, also based on the non-invasive assessment of excitation and

inhibition, could facilitate the search for specific aetiology and improve treatment targeting.

AUTHOR CONTRIBUTIONS

Conceptualization: Enrico Vescovo, Pasquale Cardellicchio and Alessandro D'Ausilio. *Investigation:* Enrico Vescovo and Pasquale Cardellicchio. *Methodology:* Enrico Vescovo, Pasquale Cardellicchio, Alice Tomassini and Alessandro D'Ausilio. *Software:* Enrico Vescovo and Pasquale Cardellicchio. *Formal analysis:* Enrico Vescovo. *Writing—original draft:* Enrico Vescovo. *Writing—review and editing:* Enrico Vescovo, Pasquale Cardellicchio, Alice Tomassini, Luciano Fadiga and Alessandro D'Ausilio. *Supervision:* Alessandro D'Ausilio. *Project administration:* Luciano Fadiga and Alessandro D'Ausilio. *Funding acquisition:* Luciano Fadiga and Alessandro D'Ausilio.

ACKNOWLEDGEMENTS

This work was supported by Ministero della Salute, Ricerca Finalizzata 2018 – Giovani Ricercatori (GR-2018-12366027) to AD; Ministero dell'Università e della Ricerca, PRIN 2020 (20208RB4N9) to LF and PRIN-PNRR 2022 (P2022J8AXY) to AD; EU project EnTimeMent (H2020-FETPROACT-824160) to L.F. and EU project PRIMIS (HORIZON-CL4-2022-DIGITAL-EMERGING-02-101120727) to LF and AD.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ejn.16365>.

DATA AVAILABILITY STATEMENT

All data reported in this paper are published and available to the public at the following repository: DOI: [10.17632/xmh9xmw39g.1](https://doi.org/10.17632/xmh9xmw39g.1).

ORCID

Enrico Vescovo  <https://orcid.org/0009-0003-9219-696X>

REFERENCES

- Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience*, 11(9), 1109–1116. <https://doi.org/10.1038/nn.2182>
- Alamia, A., Zénon, A., VanRullen, R., Duque, J., & Derosiere, G. (2019). Implicit visual cues tune oscillatory motor activity during decision-making. *NeuroImage*, 186, 424–436. <https://doi.org/10.1016/j.neuroimage.2018.11.027>
- Amoruso, L., Finisguerra, A., & Urgesi, C. (2018). Contextualizing action observation in the predictive brain: Causal

- contributions of prefrontal and middle temporal areas. *NeuroImage*, 177, 68–78. <https://doi.org/10.1016/j.neuroimage.2018.05.020>
- Amoruso, L., & Urgesi, C. (2016). Contextual modulation of motor resonance during the observation of everyday actions. *NeuroImage*, 134, 74–84. <https://doi.org/10.1016/j.neuroimage.2016.03.060>
- Aron, A. R., Herz, D. M., Brown, P., Forstmann, B. U., & Zaghoul, K. (2016). Frontosubthalamic circuits for control of action and cognition. *Journal of Neuroscience*, 36, 11489–11495. <https://doi.org/10.1523/JNEUROSCI.2348-16.2016>
- Avenanti, A., Candidi, M., & Urgesi, C. (2013). Vicarious motor activation during action perception: Beyond correlational evidence. *Frontiers in Human Neuroscience*, 7, 185. <https://doi.org/10.3389/fnhum.2013.00185>
- Barchiesi, G., & Cattaneo, L. (2013). Early and late motor responses to action observation. *Social Cognitive and Affective Neuroscience*, 8(6), 711–719. <https://doi.org/10.1093/scan/nss049>
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, 57, 289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>
- Bestmann, S., & Duque, J. (2016). Transcranial magnetic stimulation: Decomposing the processes underlying action preparation. *The Neuroscientist*, 22(4), 392–405. <https://doi.org/10.1177/1073858415592594>
- Bieńkiewicz, M. M. N., Smykovskyi, A. P., Olugbade, T., Janaqi, S., Camurri, A., Bianchi-Berthouze, N., Björkman, M., & Bardy, B. G. (2021). Bridging the gap between emotion and joint action. *Neuroscience and Biobehavioral Reviews*, 131, 806–833. <https://doi.org/10.1016/j.neubiorev.2021.08.014>
- Broers, N. J. (2021). When the numbers do not add up: The practical limits of stochastical models for soft psychology. *Perspectives on Psychological Science*, 16(4), 698–706. <https://doi.org/10.1177/1745691620970557>
- Brown, J. T., Davies, C. H., & Randall, A. D. (2007). Synaptic activation of GABA_B receptors regulates neuronal network activity and entrainment. *European Journal of Neuroscience*, 25(10), 2982–2990. <https://doi.org/10.1111/j.1460-9568.2007.05544.x>
- Brownell, C. A. (2011). Early developments in joint action. *Review of Philosophy and Psychology*, 2, 193–211. <https://doi.org/10.1007/s13164-011-0056-1>
- Camerer, C., Loewenstein, G., & Prelec, D. (2005). Neuroeconomics: How neuroscience can inform economics. *Journal of Economic Literature*, 43, 9–64. <https://doi.org/10.1257/0022051053737843>
- Cardellicchio, P., Dolfini, E., & D'Ausilio, A. (2021). The role of dorsal premotor cortex in joint action stopping. *iScience*, 24(11), 103330. <https://doi.org/10.1016/j.isci.2021.103330>
- Cardellicchio, P., Dolfini, E., Fadiga, L., & D'Ausilio, A. (2020). Parallel fast and slow motor inhibition processes in Joint Action coordination. *Cortex*, 133, 346–357. <https://doi.org/10.1016/j.cortex.2020.09.029>
- Cardellicchio, P., Dolfini, E., Hilt, P. M., Fadiga, L., & D'Ausilio, A. (2020). Motor cortical inhibition during concurrent action execution and action observation. *NeuroImage*, 208, 116445. <https://doi.org/10.1016/j.neuroimage.2019.116445>
- Carpenter, M. (2009). Just how joint is joint action in infancy? *Topics in Cognitive Science*, 1(2), 380–392. <https://doi.org/10.1111/j.1756-8765.2009.01026.x>
- Cash, R. F. H., Ziemann, U., Murray, K., & Thickbroom, G. W. (2010). Late cortical disinhibition in human motor cortex: A triple-pulse transcranial magnetic stimulation study. *Journal of Neurophysiology*, 103(1), 511–518. <https://doi.org/10.1152/jn.00782.2009>
- Chen, R., Yaseen, Z., Cohen, L. G., & Hallett, M. (1998). Time course of corticospinal excitability in reaction time and self-paced movements. *Annals of Neurology*, 44(3), 317–325. <https://doi.org/10.1002/ana.410440306>
- Cirelli, L. K. (2018). How interpersonal synchrony facilitates early prosocial behavior. *Current Opinion in Psychology*, 20, 35–39. <https://doi.org/10.1016/j.copsyc.2017.08.009>
- Clementz, B. A., Parker, D. A., Trotti, R. L., McDowell, J. E., Keedy, S. K., Keshavan, M. S., Pearlson, G. D., Gershon, E. S., Ivleva, E. I., Huang, L. Y., Hill, S. K., Sweeney, J. A., Thomas, O., Hudgens-Haney, M., Gibbons, R. D., & Tamminga, C. A. (2022). Psychosis biotypes: Replication and validation from the B-SNIP Consortium. *Schizophrenia Bulletin*, 48(1), 56–68. <https://doi.org/10.1093/schbul/sbab090>
- Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, 433(7025), 513–516. <https://doi.org/10.1038/nature03236>
- D'Ausilio, A., Badino, L., Li, Y., Tokay, S., Craighero, L., Canto, R., Aloimonos, Y., & Fadiga, L. (2012). Leadership in orchestra emerges from the causal relationships of movement kinematics. *PLoS ONE*, 7(5), e35757. <https://doi.org/10.1371/journal.pone.0035757>
- D'Ausilio, A., Bartoli, E., & Maffongelli, L. (2015). Grasping synergies: A motor-control approach to the mirror neuron mechanism. *Physics of Life Reviews*, 12, 91–103. <https://doi.org/10.1016/j.plrev.2014.11.002>
- D'Ausilio, A., et al. (2015). What can music tell us about social interaction? *Trends in Cognitive Sciences*, 19(3), 111–114. <https://doi.org/10.1016/j.tics.2015.01.005>
- Davranche, K., Tandonnet, C., Burle, B., Meynier, C., Vidal, F., & Hasbroucq, T. (2007). The dual nature of time preparation: Neural activation and suppression revealed by transcranial magnetic stimulation of the motor cortex. *European Journal of Neuroscience*, 25(12), 3766–3774. <https://doi.org/10.1111/j.1460-9568.2007.05588.x>
- Derosiere, G., & Duque, J. (2020). Tuning the corticospinal system: How distributed brain circuits shape human actions. *The Neuroscientist*, 26(4), 359–379. <https://doi.org/10.1177/1073858419896751>
- Derosiere, G., Thura, D., Cisek, P., & Duque, J. (2022). Hasty sensorimotor decisions rely on an overlap of broad and selective changes in motor activity. *PLoS Biology*, 20(4), e3001598. <https://doi.org/10.1371/journal.pbio.3001598>
- Derosiere, G., Vassiliadis, P., & Duque, J. (2020). Advanced TMS approaches to probe corticospinal excitability during action preparation. *NeuroImage*, 213, 116746. <https://doi.org/10.1016/j.neuroimage.2020.116746>
- Donnarumma, F., Costantini, M., Ambrosini, E., Friston, K., & Pezzulo, G. (2017). Action perception as hypothesis testing. *Cortex*, 89, 45–60. <https://doi.org/10.1016/j.cortex.2017.01.016>

- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, 73(6), 2608–2611. <https://doi.org/10.1152/jn.1995.73.6.2608>
- Faul, F., Erdfelder, E., Lang, A. G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, 39(2), 175–191. <https://doi.org/10.3758/BF03193146>
- Feldman, R. (2007). Parent–infant synchrony: Biological foundations and developmental outcomes. *Current Directions in Psychological Science*, 16(6), 340–345. <https://doi.org/10.1111/j.1467-8721.2007.00532.x>
- Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Nature*, 424(6950), 769–771. <https://doi.org/10.1038/nature01861>
- Frantseva, M., Cui, J., Farzan, F., Chinta, L. V., Perez Velazquez, J. L., & Daskalakis, Z. J. (2014). Disrupted cortical conductivity in schizophrenia: TMS-EEG study. *Cerebral Cortex*, 24(1), 211–221. <https://doi.org/10.1093/cercor/bhs304>
- Friston, K. (2010). The free-energy principle: A unified brain theory? *Nature Reviews Neuroscience*, 11, 127–138. <https://doi.org/10.1038/nrn2787>
- Friston, K. J., Daunizeau, J., & Kiebel, S. J. (2009). Reinforcement learning or active inference? *PLoS ONE*, 4(7), e6421. <https://doi.org/10.1371/journal.pone.0006421>
- Frith, C. D. (2008). Social cognition. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 363(1499), 2033–2039. <https://doi.org/10.1098/rstb.2008.0005>
- Garvey, M. A., Ziemann, U., Becker, D. A., Barker, C. A., & Bartko, J. J. (2001). New graphical method to measure silent periods evoked by transcranial magnetic stimulation. *Clinical Neurophysiology*, 112(8), 1451–1460. [https://doi.org/10.1016/S1388-2457\(01\)00581-8](https://doi.org/10.1016/S1388-2457(01)00581-8)
- Hallett, M. (2007). Transcranial magnetic stimulation: A primer. *Neuron*, 55, 187–199. <https://doi.org/10.1016/j.neuron.2007.06.026>
- Hannah, R., Cavanagh, S. E., Tremblay, S., Simeoni, S., & Rothwell, J. C. (2018). Selective suppression of local interneuron circuits in human motor cortex contributes to movement preparation. *Journal of Neuroscience*, 38(5), 1264–1276. <https://doi.org/10.1523/JNEUROSCI.2869-17.2017>
- Haraldsson, H. M., et al. (2004). Transcranial magnetic stimulation in the investigation and treatment of schizophrenia: A review. *Schizophrenia Research*, 71(1), 1–16. <https://doi.org/10.1016/j.schres.2003.10.006>
- Hilt, P. M., Berret, B., Papaxanthis, C., Stapley, P. J., & Pozzo, T. (2016). Evidence for subjective values guiding posture and movement coordination in a free-endpoint whole-body reaching task. *Scientific Reports*, 6, 23868. <https://doi.org/10.1038/srep23868>
- Hilt, P. M., Cardellicchio, P., Dolfini, E., Pozzo, T., Fadiga, L., & D'Ausilio, A. (2020). Motor recruitment during action observation: Effect of interindividual differences in action strategy. *Cerebral Cortex*, 30(7), 3910–3920. <https://doi.org/10.1093/cercor/bhaa006>
- Howes, O. D., McCutcheon, R., Agid, O., de Bartolomeis, A., van Beveren, N. J. M., Birnbaum, M. L., Bloomfield, M. A. P., Bressan, R. A., Buchanan, R. W., Carpenter, W. T., Castle, D. J., Citrome, L., Daskalakis, Z. J., Davidson, M., Drake, R. J., Dursun, S., Ebdrup, B. H., Elkis, H., Falkai, P., ... Correll, C. U. (2017). Treatment-resistant schizophrenia: Treatment response and resistance in psychosis (TRIP) working group consensus guidelines on diagnosis and terminology. *American Journal of Psychiatry*, 174(3), 216–229. <https://doi.org/10.1176/appi.ajp.2016.16050503>
- Julkunen, P., Säisänen, L., Hukkanen, T., Danner, N., & Könönen, M. (2012). Does second-scale intertrial interval affect motor evoked potentials induced by single-pulse transcranial magnetic stimulation? *Brain Stimulation*, 5(4), 526–532. <https://doi.org/10.1016/j.brs.2011.07.006>
- Keller, P. E., Novembre, G. and Hove, M. J. (2014) 'Rhythm in joint action: Psychological and neurophysiological mechanisms for real-time interpersonal coordination', *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 369, 20130394. <https://doi.org/10.1098/rstb.2013.0394>
- Kilner, J. M., Vargas, C., Duval, S., Blakemore, S. J., & Sirigu, A. (2004). Motor activation prior to observation of a predicted movement. *Nature Neuroscience*, 7(12), 1299–1301. <https://doi.org/10.1038/nn1355>
- Klein, P. A., Petitjean, C., Olivier, E., & Duque, J. (2014). Top-down suppression of incompatible motor activations during response selection under conflict. *NeuroImage*, 86, 138–149. <https://doi.org/10.1016/j.neuroimage.2013.08.005>
- Klein-Flügge, M. C., & Bestmann, S. (2012). Time-dependent changes in human corticospinal excitability reveal value-based competition for action during decision processing. *Journal of Neuroscience*, 32(24), 8373–8382. <https://doi.org/10.1523/JNEUROSCI.0270-12.2012>
- Konvalinka, I., Vuust, P., Roepstorff, A., & Frith, C. D. (2010). Follow you, follow me: Continuous mutual prediction and adaptation in joint tapping. *Quarterly Journal of Experimental Psychology*, 63(11), 2220–2230. <https://doi.org/10.1080/17470218.2010.497843>
- Leocani, L., Cohen, L. G., Wassermann, E. M., Ikoma, K., & Hallett, M. (2000). Human corticospinal excitability evaluated with transcranial magnetic stimulation during different reaction time paradigms. *Brain*, 123(6), 1161–1173. <https://doi.org/10.1093/brain/123.6.1161>
- Levy, D. J., & Glimcher, P. W. (2012). The root of all value: A neural common currency for choice. *Current Opinion in Neurobiology*. Elsevier Ltd, 22, 1027–1038. <https://doi.org/10.1016/j.conb.2012.06.001>
- Liuzza, M. T., Candidi, M., Sforza, A. L., & Aglioti, S. M. (2015). Harm avoiders suppress motor resonance to observed immoral actions. *Social Cognitive and Affective Neuroscience*, 10(1), 1–6. <https://doi.org/10.1093/scan/nsu025>
- Ludbrook, J., & Dudley, H. (1998). Why permutation tests are superior to t and F tests in biomedical research. *The American Statistician*, 52(2), 127–132. <https://doi.org/10.1080/00031305.1998.10480551>
- Mann, E. O., & Paulsen, O. (2007). Role of GABAergic inhibition in hippocampal network oscillations. *Trends in Neurosciences*, 30, 343–349. <https://doi.org/10.1016/j.tins.2007.05.003>
- Meehl, P. E. (1978). Theoretical risks and tabular asterisks: Sir Karl, Sir Ronald, and the slow progress of soft psychology. *Journal of Consulting and Clinical Psychology*, 46(4), 806–834. <https://doi.org/10.1037/0022-006X.46.4.806>

- Mook, D. G. (1983). In defense of external invalidity. *American Psychologist*, 38(4), 379–387. <https://doi.org/10.1037/0003-066X.38.4.379>
- Murray, L., & Trevarthen, C. (1986). The infant's role in mother-infant communications. *Journal of Child Language*, 13(1), 15–29. <https://doi.org/10.1017/S0305000900000271>
- Nagy, M., Ákos, Z., Biro, D., & Vicsek, T. (2010). Hierarchical group dynamics in pigeon flocks. *Nature*, 464(7290), 890–893. <https://doi.org/10.1038/nature08891>
- Naish, K. R., Houston-Price, C., Bremner, A. J., & Holmes, N. P. (2014). Effects of action observation on corticospinal excitability: Muscle specificity, direction, and timing of the mirror response. *Neuropsychologia*, 64, 331–348. <https://doi.org/10.1016/j.neuropsychologia.2014.09.034>
- Néda, Z., Ravasz, E., Brechet, Y., Vicsek, T., & Barabási, A. L. (2000). The sound of many hands clapping. *Nature*, 403(6772), 849–850. <https://doi.org/10.1038/35002660>
- Nicoll, R. A. (2004). My close encounter with GABA_B receptors. *Biochemical Pharmacology*, 68(8), 1667–1674. <https://doi.org/10.1016/j.bcp.2004.07.024>
- Novembre, G., Ticini, L. F., Schutz-Bosbach, S., & Keller, P. E. (2012). Distinguishing self and other in joint action. Evidence from a musical paradigm. *Cerebral Cortex*, 22(12), 2894–2903. <https://doi.org/10.1093/cercor/bhr364>
- O'Brien, M. K., & Ahmed, A. A. (2013). Does risk-sensitivity transfer across movements? *Journal of Neurophysiology*, 109(7), 1866–1875. <https://doi.org/10.1152/jn.00826.2012.-An>
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113. [https://doi.org/10.1016/0028-3932\(71\)90067-4](https://doi.org/10.1016/0028-3932(71)90067-4)
- Pellicciari, M. C., Miniussi, C., Ferrari, C., Koch, G., & Bortoletto, M. (2016). Ongoing cumulative effects of single TMS pulses on corticospinal excitability: An intra- and inter-block investigation. *Clinical Neurophysiology*, 127(1), 621–628. <https://doi.org/10.1016/j.clinph.2015.03.002>
- Pezzulo, G., Donnarumma, F., Dindo, H., D'Ausilio, A., Konvalinka, I., & Castelfranchi, C. (2019). The body talks: Sensorimotor communication and its brain and kinematic signatures. *Physics of Life Reviews*. Elsevier B.V., 28, 1–21. <https://doi.org/10.1016/j.plrev.2018.06.014>
- Poncer, J. C., McKinney, R. A., Gähwiler, B. H., & Thompson, S. M. (2000). Differential control of GABA release at synapses from distinct interneurons in rat hippocampus. *Journal of Physiology*, 528(1), 123–130. <https://doi.org/10.1111/j.1469-7793.2000.00123.x>
- Qi, T., Mandelli, M. L., Pereira, C. L. W., Wellman, E., Bogley, R., Licata, A. E., Chang, E. F., Oganian, Y., & Gorno-Tempini, M. L. (2023). *Anatomical and behavioral correlates of auditory perception in developmental dyslexia*. Cold Spring Harbor Laboratory. Available at: <https://doi.org/10.1101/2023.05.09.539936>
- Rands, S. A., Cowlshaw, G., Pettifor, R. A., Rowcliffe, J. M., & Johnstone, R. A. (2003). Spontaneous emergence of leaders and followers in foraging pairs. *Nature*, 423(6938), 432–434. <https://doi.org/10.1038/nature01630>
- Rauchbauer, B. and Grosbras, M.H. (2020) 'Developmental trajectory of interpersonal motor alignment: Positive social effects and link to social cognition', *Neuroscience and Biobehavioral Reviews*, 118, 411–425. <https://doi.org/10.1016/j.neubiorev.2020.07.032>
- Ridding, M. C., & Rothwell, J. C. (1997). Stimulus/response curves as a method of measuring motor cortical excitability in man. *Electroencephalography and Clinical Neurophysiology/Electromyography and Motor Control*, 105(5), 340–344. [https://doi.org/10.1016/S0924-980X\(97\)00041-6](https://doi.org/10.1016/S0924-980X(97)00041-6)
- Rossi, S., Antal, A., Bestmann, S., Bikson, M., Brewer, C., Brockmüller, J., Carpenter, L. L., Cincotta, M., Chen, R., Daskalakis, J. D., di Lazzaro, V., Fox, M. D., George, M. S., Gilbert, D., Kimiskidis, V. K., Koch, G., Ilmoniemi, R. J., Lefaucheur, J. P., Leocani, L., ... Hallett, M. (2021). *Safety and recommendations for TMS use in healthy subjects and patient populations, with updates on training, ethical and regulatory issues: Expert guidelines* (Vol. 132, pp. 269–306). Elsevier Ireland Ltd. <https://doi.org/10.1016/j.clinph.2020.10.003>
- Rossini, P. M., Burke, D., Chen, R., Cohen, L. G., Daskalakis, Z., di Iorio, R., di Lazzaro, V., Ferreri, F., Fitzgerald, P. B., George, M. S., Hallett, M., Lefaucheur, J. P., Langguth, B., Matsumoto, H., Miniussi, C., Nitsche, M. A., Pascual-Leone, A., Paulus, W., Rossi, S., ... Ziemann, U. (2015). Non-invasive electrical and magnetic stimulation of the brain, spinal cord, roots and peripheral nerves: Basic principles and procedures for routine clinical and research application: An updated report from an I.F.C.N Committee. *Clinical Neurophysiology*, 126(6), 1071–1107. <https://doi.org/10.1016/j.clinph.2015.02.001>
- Sacheli, L. M., Arcangeli, E., & Paulesu, E. (2018). Evidence for a dyadic motor plan in joint action. *Scientific Reports*, 8(1), 5027. <https://doi.org/10.1038/s41598-018-23275-9>
- Sacheli, L. M., Musco, M. A., Zazzera, E., Banfi, G., & Paulesu, E. (2022). How shared goals shape action monitoring. *Cerebral Cortex*, 32(21), 4934–4951. <https://doi.org/10.1093/cercor/bhac019>
- Sacheli, L. M., Tidoni, E., Pavone, E. F., Aglioti, S. M., & Candidi, M. (2013). Kinematics fingerprints of leader and follower role-taking during cooperative joint actions. *Experimental Brain Research*, 226(4), 473–486. <https://doi.org/10.1007/s00221-013-3459-7>
- Sartori, L., Cavallo, A., Buccioni, G., & Castiello, U. (2011). Corticospinal excitability is specifically modulated by the social dimension of observed actions. *Experimental Brain Research*, 211(3–4), 557–568. <https://doi.org/10.1007/s00221-011-2650-y>
- Scanziani, M. (2000). GABA spillover activates postsynaptic GABA_B receptors to control rhythmic hippocampal activity. *Neuron*, 25(3), 673–681. [https://doi.org/10.1016/S0896-6273\(00\)81069-7](https://doi.org/10.1016/S0896-6273(00)81069-7)
- Sebanz, N., Bekkering, H., & Knoblich, G. (2006). Joint action: Bodies and minds moving together. *Trends in Cognitive Sciences*, 10(2), 70–76. <https://doi.org/10.1016/j.tics.2005.12.009>
- Słowiński, P., Zhai, C., Alderisio, F., Salesse, R., Gueugnon, M., Marin, L., Bardy, B. G., di Bernardo, M., & Tsaneva-Atanasova, K. (2016). Dynamic similarity promotes interpersonal coordination in joint action. *Journal of the Royal Society Interface*, 13(116), 20151093. <https://doi.org/10.1098/rsif.2015.1093>
- Soto, O., Valls-Solé, J., & Kumru, H. (2010). Paired-pulse transcranial magnetic stimulation during preparation for simple and choice reaction time tasks. *Journal of Neurophysiology*, 104(3), 1392–1400. <https://doi.org/10.1152/jn.00620.2009>
- Spampinato, D. A., Ibanez, J., Rocchi, L., & Rothwell, J. (2023). Motor potentials evoked by transcranial magnetic stimulation: Interpreting a simple measure of a complex system. *The*

- Journal of Physiology*, 601, 1–25. <https://doi.org/10.1113/JP281885#support-information-section>
- Tandonnet, C., Davranche, K., Meynier, C., Burle, B., Vidal, F., & Hasbroucq, T. (2012). How does temporal preparation speed up response implementation in choice tasks? Evidence for an early cortical activation. *Psychophysiology*, 49(2), 252–260. <https://doi.org/10.1111/j.1469-8986.2011.01301.x>
- Tomassini, A., Laroche, J., Emanuele, M., Nazzaro, G., Petrone, N., Fadiga, L., & D'Ausilio, A. (2022). Interpersonal synchronization of movement intermittency. *iScience*, 25(4), 104096. <https://doi.org/10.1016/j.isci.2022.104096>
- Torricelli, F., Tomassini, A., Pezzulo, G., Pozzo, T., Fadiga, L., D'Ausilio, A. (2023) 'Motor invariants in action execution and perception', *Physics of Life Reviews*, 44, 13–47. <https://doi.org/10.1016/j.plrev.2022.11.003>,
- Ubaldi, S., Barchiesi, G., & Cattaneo, L. (2015). Bottom-up and top-down visuomotor responses to action observation. *Cerebral Cortex*, 25(4), 1032–1041. <https://doi.org/10.1093/cercor/bht295>
- Vesper, C., Schmitz, L., Safra, L., Sebanz, N., & Knoblich, G. (2016). The role of shared visual information for joint action coordination. *Cognition*, 153, 118–123. <https://doi.org/10.1016/j.cognition.2016.05.002>
- Vesper, C., van der Wel, R. P. R. D., Knoblich, G., & Sebanz, N. (2013). Are you ready to jump? Predictive mechanisms in interpersonal coordination. *Journal of Experimental Psychology: Human Perception and Performance*, 39(1), 48–61. <https://doi.org/10.1037/a0028066>

- Werhahn, K. J., Kunesch, E., Noachtar, S., Benecke, R., & Classen, J. (1999). Differential effects on motorcortical inhibition induced by blockade of GABA uptake in humans. *Journal of Physiology*, 517(2), 591–597. <https://doi.org/10.1111/j.1469-7793.1999.0591t.x>
- Wolpert, D.M., Doya, K. and Kawato, M. (2003) 'A unifying computational framework for motor control and social interaction', *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 358, 593–602. <https://doi.org/10.1098/rstb.2002.1238>
- Ziemann, U. (2004). TMS and drugs. *Clinical Neurophysiology*, 115, 1717–1729. <https://doi.org/10.1016/j.clinph.2004.03.006>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Vescovo, E., Cardellicchio, P., Tomassini, A., Fadiga, L., & D'Ausilio, A. (2024). Excitatory/inhibitory motor balance reflects individual differences during joint action coordination. *European Journal of Neuroscience*, 59(12), 3403–3421. <https://doi.org/10.1111/ejn.16365>