

Title: *Excitatory/inhibitory motor balance reflects individual differences during joint action coordination.*

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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.

Key words: Motor Control, Joint Action, Motor Inhibition, TMS, Sensorimotor Communication.

INTRODUCTION

Multi-agent coordination is an essential component of animal behaviour (Rands *et al.*, 2003; Couzin *et al.*, 2005; Frith, 2008; Nagy *et al.*, 2010) that might have fundamental implications for cognitive and social development in humans (Murray and Trevarthen, 1986; Feldman, 2007; Cirelli, 2018; Rauchbauer and 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 (Keller, Novembre and Hove, 2014; D'Ausilio *et al.*, 2015; 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, Bekkering and Knoblich, 2006; Tomassini *et al.*, 2022). Indeed, mutual coordination is based on online analysis of kinematic cues that specify partners' action and simultaneous integration with available contextual information (Aglioti *et al.*, 2008; Avenanti, Candidi and Urgesi, 2013; Amoruso and Urgesi, 2016; Amoruso, Finisguerra and Urgesi, 2018). 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 and Duque, 2016; Derosiere and Duque, 2020). Although recent works have started to explore both excitatory and inhibitory mechanisms during interactive behaviour (Cardellicchio, Dolfini, Fadiga, *et al.*, 2020; Cardellicchio, Dolfini, Hilt, *et al.*, 2020; Cardellicchio, Dolfini and D'Ausilio, 2021), their relative contribution to the simultaneous unfolding of top-down and bottom-up processes is far from being fully elucidated in JA scenarios.

Here we used a typical bimanual task – reaching/grasping for a bottle and unscrew its cap – which has been adapted to be an interactive unimanual task (Cardellicchio, Dolfini and D'Ausilio, 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; Fig.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 transcranial magnetic stimulation (TMS) to investigate corticospinal excitability (CSE) and cortical silent period length (cSP) 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 and Rothwell, 1997; Spampinato *et al.*, 2023), but also of the functional state of sensorimotor circuits during action control (Klein-Flügge and Bestmann, 2012; Derosiere, Vassiliadis and Duque, 2020). On the other hand, cSP length is a GABA_B-mediated neurophysiological index of inhibition (Ziemann, 2004) that is considered as a marker of slow corticospinal inhibition required for response selection (Davranche *et al.*, 2007; Tandonnet *et al.*, 2012; Klein *et al.*, 2014). 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 (EMG); during the active exchange of forces between partners (Grip).

We demonstrated a temporal dissociation in the modulation of excitatory and inhibitory indexes and a differential dependence on prior information. Specifically, CSE modulation is subject to the presence of prior information, while cSP modulation depends on online sampling of bottom-up information (i.e., confederate's movement kinematics).

Interestingly, when both prior information and bottom-up cues were available (i.e., JA-K condition), participants naturally selected a specific coordination strategy. They either squeezed the bottle as soon as prior information became available, or later when that information was complemented by bottom-up movement-related cues. The adoption of each strategy remained constant throughout the experiment and is associated with consistent differences in neurophysiological modulations, suggesting that they may correspond to stable individual coordination styles.

These results 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.

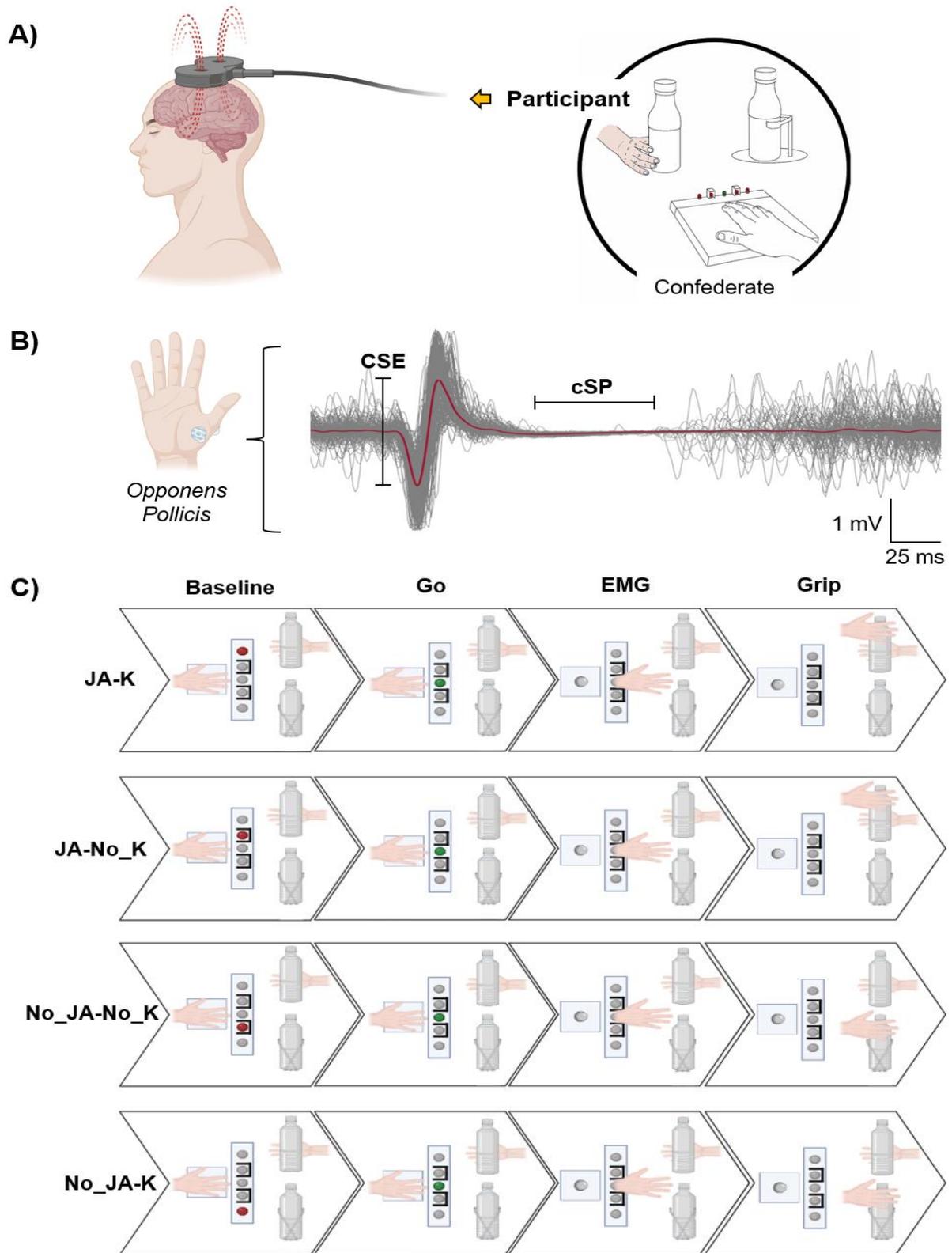


Figure 1. Behavioural task and conditions. (A) Graphic representation of the experimental setup. In the starting position, confederate's right hand is resting on a button box in front of the red directional LEDs and the green Go LED. The two innermost red LEDs are visible only from confederate's perspective. The two bottles – representing the target of the action – are equally distant from the starting position. One was held by a mechanical clamp (No_JA) and the other by

the participant (JA). **(B)** Neurophysiological indexes measured in all participants. CSE is measured as the peak-to-peak amplitude value (mV) of the motor-evoked potential (MEP). 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 TMS pulses were delivered at one of four timings: Baseline (switching on of the red LED); Go (confederate's movement onset); EMG (confederate's electromyography, as described below); Grip (touch of the bottle).

MATERIALS AND METHODS

Participants

A total of 22 naïve volunteers took part in the study (12 females; age: 22.9 ± 1.8 ; MEAN \pm SD). All participants were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; to be enrolled in the study, participants had to obtain an EHI score ≥ 40 ; EHI: 92.5 ± 31 ; MEAN \pm SD). The sample size was established on the basis of prior studies that investigated similar physiological indexes and used similar tasks (Cardellicchio, Dolfini, Fadiga, *et al.*, 2020; Cardellicchio, Dolfini and D'Ausilio, 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.

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 usually 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 = 160cm; width = 80cm). Two identical deformable plastic bottles (height: 25cm, cap diameter: 5cm, 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 (40cm, 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 (Fig.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 center of the table between the confederate and the participant. Three LEDs, 1 central green and 2 outermost red ones, were visible to both the confederate and the participant, while the two innermost red LEDs were visible only to the confederate (Fig.1). Each trial began by turning on one of the 4 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 (Fig.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 1500ms. 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 4 different experimental conditions (JA-K, JA-no_K, no_JA-K, no_JA-no_K; Fig.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 4 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.

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 Corticospinal Excitability (CSE) and the duration of the Cortical Silent Period (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 Opponens Pollicis (OP) ($\approx 10\%$ of the maximum voluntary contraction). The target muscle was chosen because it plays a central role in power grasp (i.e., holding the bottle). Electromyography 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 analog 3-axis accelerometer (sampling rate: 100Hz) embedded in the same low-weight wearable unit. EMG data were digitized (2 kHz) 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., 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 (Fig.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 ten 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; 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 condition (JA-K, JA-no_K, no_JA-K, no_JA-no_K) and timing ("Baseline", "Go", "EMG", and "Grip").

Data Analysis

Two participants were excluded from the analyses of both CSE and cSP due to 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 due to absence of a clearly detectable silent period (CSE analysis $n=20$; cSP analysis $n=19$). Data processing and analysis was performed with Matlab (The MathWorks, Inc., Natick, MA, 2020), using built-in functions and custom-made code to extract the following indexes:

- A. CSE: peak-to-peak amplitude value (mV) of the MEP;
- B. 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 method, MCD; (Garvey *et al.*, 2001));
- C. Kinetic parameters of the participant: onset and offset of the squeezing force applied to the bottle;
- D. 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 values that were $>$ or $<$ than their respective mean values ± 2 SD were excluded from the analysis (5% and 8% for CSE and cSP values, respectively). To account for individual and trial-by-trial variability in muscle activity, MEPs and cSPs were normalized to the root mean square (RMS) of EMG activity calculated in the 150 ms window immediately preceding the TMS pulse. In addition, separately for each condition (JA-K, JA-no_K, no_JA-K, no_JA-no_K), the CSE and cSP values for the "Go", "EMG", and "Grip" timings were normalized to the respective values obtained for the "Baseline" timing.

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 described for the cSP estimation). To estimate individual motor strategies, we calculated the time interval (Delay) between the onset of the participants' squeezing action (P_{onset}) and the onset of the confederate's reaching action (i.e., release of the button, Mov_{onset} ; $\text{Delay} = P_{\text{onset}} - Mov_{\text{onset}}$). After labelling 'Delay+' positive values of Delay, and 'Delay-' negative values of Delay, we measured in each participant the average value of both Delay+ and Delay- for the whole experimental session. Since Delay took negative values only in the JA-K condition (Table S2; see Results), 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 (Fig.3). Participants were then categorized in two groups depending on their predominant squeezing behaviour in JA_K, namely whether they tended to start squeezing the bottle before (Early group) or after (Late group) the onset of the confederate's action, thus yielding, on average, negative (Delay-) or positive (Delay+) values, respectively. 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 6 experimental blocks for each participant (see Figure S1 and Table S1). We then explored whether CSE and cSP were modulated differently in the two groups.

Finally, we tested if differences between the Early/Late group 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} ; time between go signal and Mov_{onset}) and mean movement time (MT; time between Mov_{onset} and Mov_{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 Mov_{onset} to $60\% \cdot MT$) 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).

Statistical Analysis

Statistical analyses were conducted using STATISTICA 12 (StatSoft, Inc.; ANOVA) and Matlab (nonparametric permutation test).

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.

CSE and cSP modulation by coordination strategy

To test whether the modulation of CSE and cSP by task condition and TMS timing depended on coordination strategy, we performed two separate $2 \times 3 \times 2$ mixed-effects model ANOVAs with KNOWLEDGE (K, no_K) and TIMING (Go, EMG, Grip) as within-subject factors, and STRATEGY (Early, Late) as a between-subject factor. Significant interactions were further explored with Newman-Keuls post-hoc tests.

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 group. 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 group ($\Delta_{surrogate}$). 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.

RESULTS

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 (see Table S4 for the full table of effects). Further Newman-Keuls post-hoc tests showed that, in the Go timing only, CSE for JA_K was greater than for all other conditions (see Table S5 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 (Fig.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 produced longer cSP which differed from all the other experimental conditions, whereas in the later Grip timing there was a significant difference between JA and No_JA but not between K and No_K (Fig.2B; see Table S6 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 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).

—●— JA-K —○— JA-No_K —▲— No_JA-K —▲— No_JA-No_K

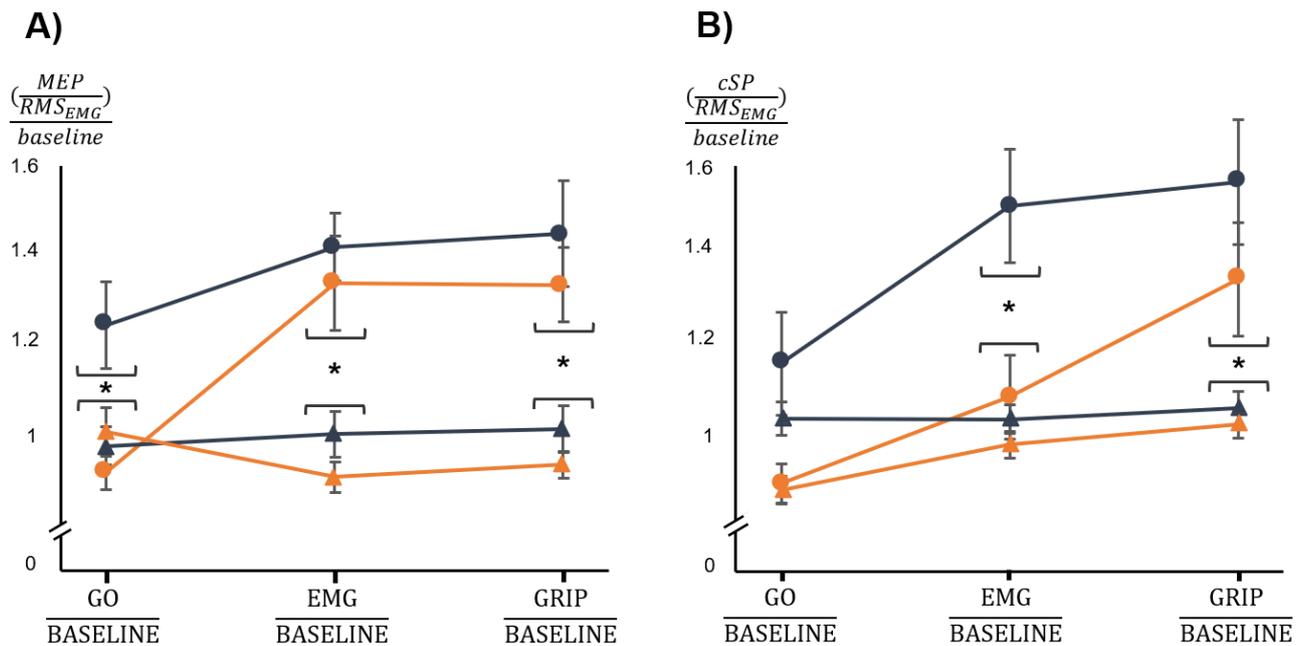


Figure 2. Modulation of neurophysiological excitation and inhibition. (A) CSE results in all participants. **(B)** cSP results in all participants. Parentheses and asterisks show statistically significant results according to Newman-Keuls post-hoc test.

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 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.

We were able to divide the participants into two groups based precisely on the average value of Delay. That is, participants which showed mean Delay+ in the whole experimental session were included in the Late group, whereas participants which showed mean Delay- were included in the Early group (Fig.3, red line). We then checked for individual consistency in the selected strategy by evaluating the count of Delay+ and Delay- in each participant (Fig.3, histogram bars). The mean \pm SD count of Delay+ in the Late group was 67.85 (\pm 3.95) whereas for Delay- this value was 4.08 (\pm 4.03). On the other hand, in the Early group the mean \pm SD count was respectively 11.77 (9.48) and 60.22 (\pm 9.48) for and Delay+ and Delay-. The grand average \pm SD of Delay+ and Delay- was respectively 322ms (\pm 93ms) and -127ms (\pm 152ms) for the Late group, and 251.5ms (\pm 108ms) and -751ms (\pm 361ms) 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 S2). There were no Delay- in the Late group, while in the Early group anticipatory squeezing was observed in only a few trials (mean count 0.44 \pm 0.72 and 71.55 \pm 0.72 for Delay- and Delay+, respectively). The grand average of Delay+ was 968.52ms (\pm 233.56ms) and 771.22ms (\pm 193.68ms) for the Late and Early group, 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 S1).

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).

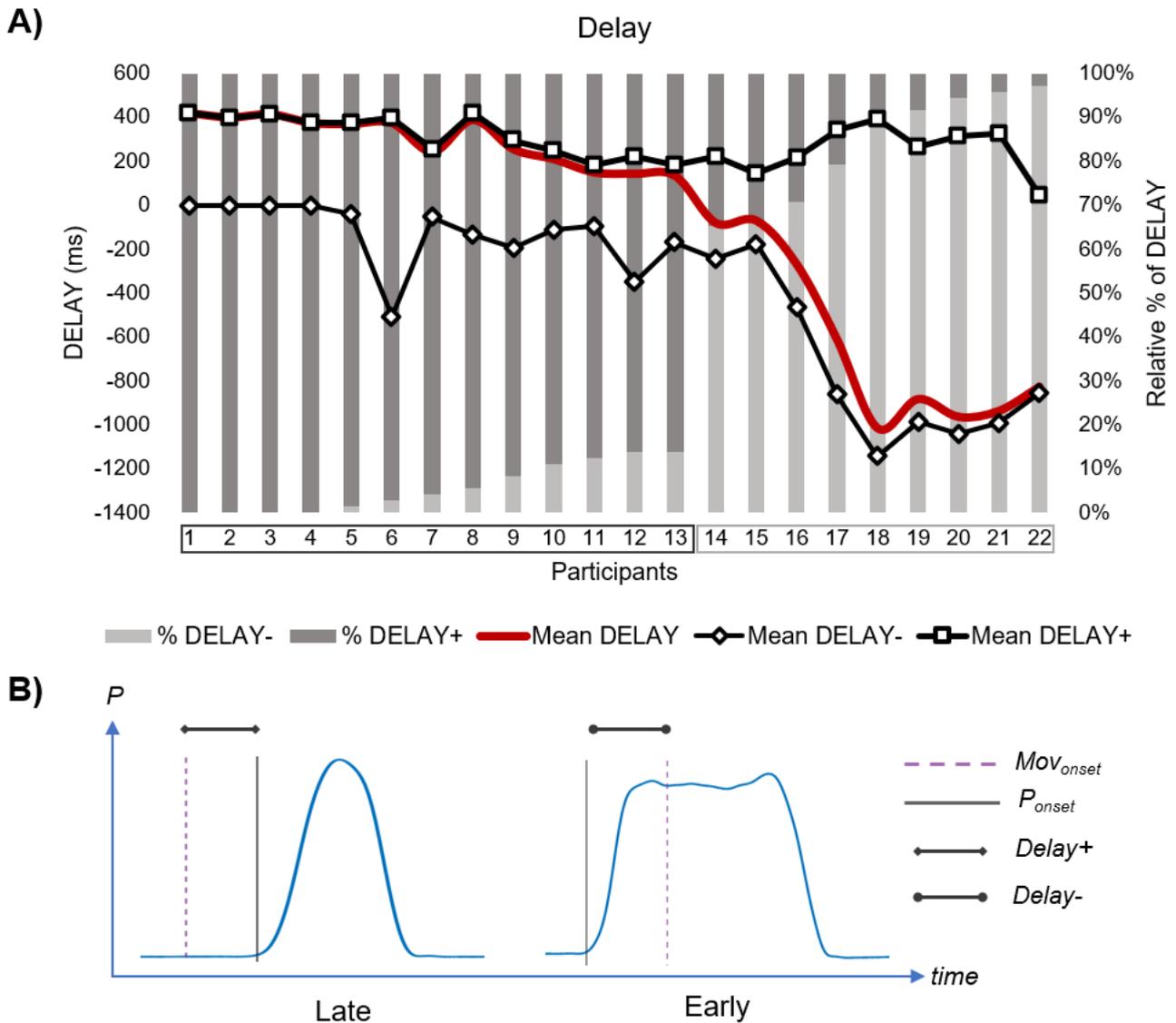


Figure 3. Behavioural determination of JA coordination strategy. (A) Relative percentage of DELAY and mean DELAY values for each participant. Participants were included in Late group if mean DELAY was positive (red line; $n=13$, dark grey box) or in Early group if mean DELAY was negative ($n=9$, light 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.

JA strategies are reflected in different neurophysiological modulations

We then examined whether neurophysiological indexes underwent different modulations in the Early and Late group, 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 S2). To test whether the modulation of CSE and cSP by task condition and TMS timing depended on coordination strategy, we performed two separate $2 \times 3 \times 2$ mixed-effects model ANOVAs with KNOWLEDGE (K, no_K) and TIMING (Go, EMG, Grip) as within-subject factors, and STRATEGY (Early, Late) as a between-subject factor. Significant interactions were further explored with Newman-Keuls post-hoc tests.

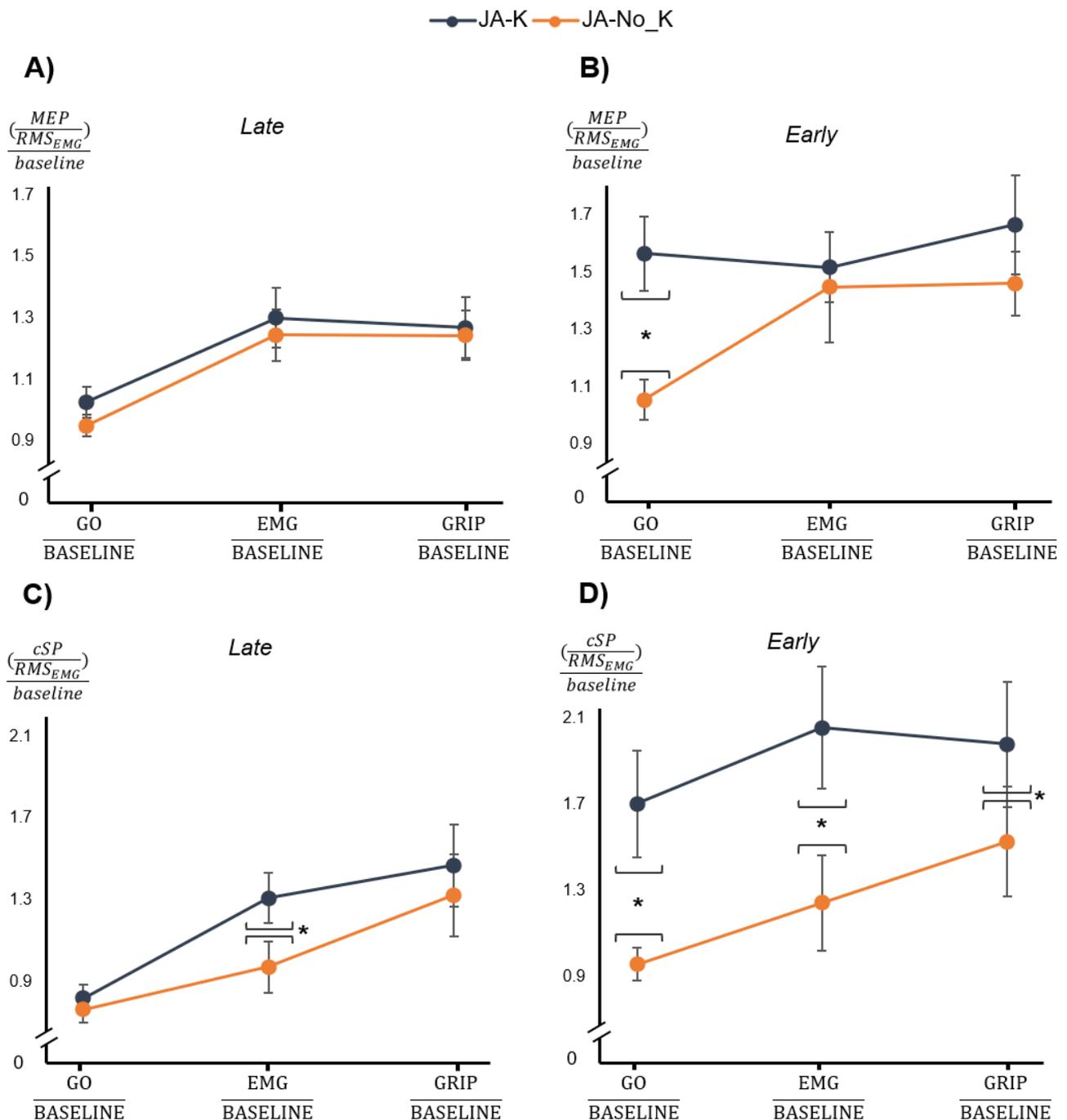


Figure 4. Neurophysiological modulations depending on JA coordination strategy. (A) CSE results in Late group. **(B)** CSE results in Early group. **(C)** cSP results in Late group. **(D)** cSP results in Early group. Parentheses and asterisks show statistically significant results according to Newman-Keuls post-hoc test.

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 (Fig.4A), while larger modulation during JA-K in the Go timing was present for the Early group (Fig.4B; see Table S7 for the full table of effects). 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 do not show any CSE modulation.

In contrast, a different pattern of results was found for cSP: the Late group showed larger inhibition for JA-K only in the EMG timing (Fig.4C) whereas the Early group showed effects in the same direction but spread across all three time points (Fig.4D; see Table S8 for the full table of effects). Here, cSP is modulated in both groups but with a very different degree of temporal specificity. Participants anticipating their squeeze show a tonic modulation of inhibition throughout the task (Go, EMG and Grip), possibly indicating a prolonged focus on sampling kinematic cues. The Late group, instead, show a temporally selective change in cSP, precisely when kinematic information starts to become available (EMG).

Confederate's behaviour did not influence coordination strategy

Finally, we performed some control analyses to rule out that differences between the Early/Late group 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} ; time between go signal and Mov_{onset}) and mean movement time (MT; time between Mov_{onset} and Mov_{offset}). We also analysed the confederate's hand acceleration profile (see STAR methods for analyses).

The confederate showed comparable RT_{led} (Early: $515.03 \pm 17.35ms$; Late: $520.95 \pm 45.41ms$; $p=0.67$) and MT (Early: $920.8 \pm 59.73ms$; Late: $881.5 \pm 65.02ms$; $p=0.16$) during interaction with participants from both groups (mean RT_{led} and MT are reported for all participants in table S3).

Similarly, no difference was observed in the acceleration profile (at any time point) of confederate's movements between Early and Late groups (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 S2-5. Overall, we can rule out that the adoption of a particular strategy was driven by confederate's behaviour.

DISCUSSION

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

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, Dolfini and D'Ausilio, 2021). In agreement with earlier studies, we find larger CSE and longer cSPs (more inhibition) in JA than no_JA (Cardellicchio, Dolfini, Fadiga, *et al.*, 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; Figure 5). 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 (Słowiński *et al.*, 2016; Hilt *et al.*, 2020). 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 (Figure 5).

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 and Rothwell, 1997; Spampinato *et al.*, 2023). The activity sampled via single-pulse TMS, however, is not only related 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 and 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, Valls-Solé and Kumru, 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 corticospinal excitability, possibly reflects reactivation of motor circuits in a sort of simulative mode (Fadiga *et al.*, 1995; Flanagan and Johansson, 2003; Naish *et al.*, 2014; D'Ausilio, Bartoli and Maffongelli, 2015). 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 (Avenanti, Candidi and Urgesi, 2013; Amoruso and Urgesi, 2016; Amoruso, Finisguerra and Urgesi, 2018). Overall, these results converge toward the idea that CSE is highly prone to top-down modulation (Barchiesi and Cattaneo, 2013; Liuzza *et al.*, 2015; Ubaldi, Barchiesi and Cattaneo, 2015; Amoruso, Finisguerra and Urgesi, 2018).

In line with this, Kilner *et al.* (Kilner *et al.*, 2004) have shown that the 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's else action) is sufficient to excite one's own motor system. Hence, modulation of corticospinal excitability could reflect 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 corticospinal excitability during action observation/execution encodes far more than the low-level motor details of actions (Sartori *et al.*, 2011; Amoruso, Finisguerra and Urgesi, 2018; Hilt *et al.*, 2020). Indeed, we find modulation before the onset of movement (observed and executed), based on cues that anticipate whether interpersonal haptic coordination will occur.

cSP modulation reflects the monitoring of kinematic features

cSP length provides a measure of slow metabotropic postsynaptic GABA_b-mediated inhibition (Werhahn *et al.*, 1999; Hallett, 2007). The specific attribute of GABA_b-mediated inhibition is that it requires associative neuronal firing to generate enough GABA pooling (Poncer *et al.*, 2000; Scanziani, 2000; Nicoll, 2004; Brown, Davies and Randall, 2007; Cash *et al.*, 2010), thus revealing its role in the coordination of neuronal ensembles (Scanziani, 2000; Nicoll, 2004; Brown, Davies and Randall, 2007; Mann and Paulsen, 2007; Cash *et al.*, 2010). 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” (Aron *et al.*, 2016; Alamia *et al.*, 2019; Derosiere and 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, *et al.*, 2020). Along these lines, cSP lengthening could reflect goal sharing in JA, while its shortening could indicate goal misalignment between partners (Cardellicchio, Dolfini, Fadiga, *et al.*, 2020). According to the active inference framework (Friston, Daunizeau and Kiebel, 2009; Friston, 2010; Donnarumma *et al.*, 2017), 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.

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, Loewenstein and Prelec, 2005; Levy and Glimcher, 2012; O'brien and 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* to engage 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 individual motor signature (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 temporally non-specific modulation of cSP associated with early modulation of CSE, while the Late group showed temporally specific modulations of cSP but no modulation of CSE (Figure 5). 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.

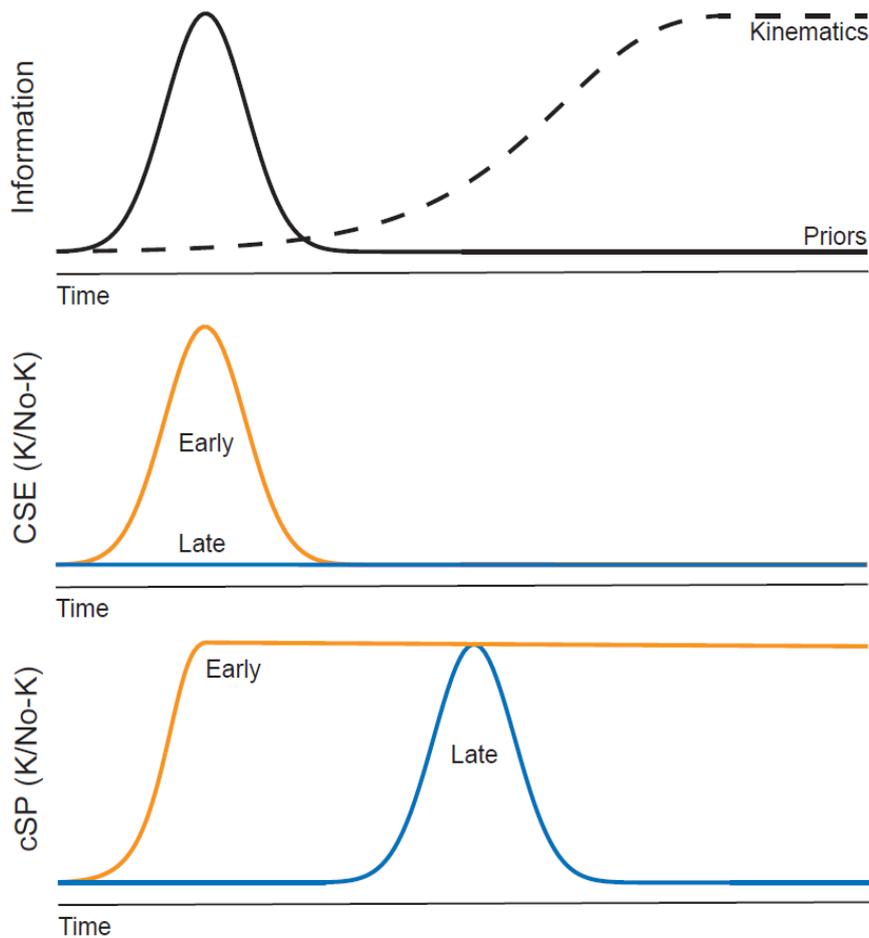


Figure 5. Neurophysiological modulations according to different coordination strategy. The upper panel shows the temporal relationship between prior information (top-down) and kinematic cues (bottom-up) during the course of the action. The temporal development of CSE (middle panel) and cSP (lower panel) comparing the presence of prior information (K) and its absence (No_K) in the two groups. The Early and Late strategies show marked differences in both the early modulation of excitation and the temporal tuning of inhibition.

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 proper selection of the motor program and eventual switching between different possible motor options. Central to the implementation of these processes is dopamine (DA), whose neuromodulatory activity is known to complement excitatory and inhibitory signals in generating the chosen motor output (Doya, 2008; Rogers, 2011). For example, mesolimbic DA neurons signalling in the nucleus accumbens (NAc) appears to mediate decision-making related to risk-taking behaviour by promoting appropriate action selection when faced with risky alternatives

(Sugam *et al.*, 2012). Indeed, impaired activity of DA neurons is associated to several pathological conditions (Grace, 2016) and reveals an altered evaluation of costs and risks of potential actions (i.e., risk-prone decision-making; (St. Onge and Floresco, 2009; Young *et al.*, 2011)). Here, we show that the tendency to choose riskier options (i.e., participants belonging to the Late group) is also reflected by distinct patterns of motor inhibition and excitation, which it is reasonable to assume might be implemented in conjunction with dopaminergic neuromodulations. Therefore, we believe that exploring the modelling role of DA over sensorimotor activity is a *conditio sine qua non* for a better understanding of action control.

In this regard, it should be highlighted that DA neurons involved in value-based decision-making are embedded in a large neural circuit which also involves the prefrontal cortex (PFC). The PFC plays a central role in working memory, which allows us to transiently hold and manipulate information needed to generate an upcoming action (Durstewitz and Seamans, 2002), and its impaired activity underlies some cognitive deficits in schizophrenia (Winterer and Weinberger, 2004). Interestingly, dopamine modulates both working memory performance and task-dependent neuronal firing rates within the PFC in a complex manner (Sawaguchi, Matsumura and Kubota, 1990; Zahrt *et al.*, 1997; Seamans, Floresco and Phillips, 1998; Arnsten, 2007). Dopamine exerts its impact through multiple effects, which include also GABA_A (Seamans *et al.*, 2001) and N-methyl-D-aspartate (NMDA; (Zheng *et al.*, 1999)) currents modulation mediated by D1-class and D2-class receptors. In particular, it has been hypothesized that PFC network dynamics exist on a continuum where the general regime at any given time is determined by prevailing D1 versus D2 receptor activation (i.e., the D1/D2 activation ratio; (Durstewitz and Seamans, 2008)). D1 state refers to a condition characterized by high energy barrier among different network states (in PFC) which implies robust online maintenance of information for working memory (but with the disadvantage of less flexible switching among activity states). On the other hand, D2 state is characterized by low energy barrier that is beneficial for flexible and fast switching among (information) representational states (Durstewitz and Seamans, 2008).

Given 1) the centrality of the PFC in top-down modulation of forthcoming actions (Durstewitz and Seamans, 2002), 2) the influence of D1/D2 state on the PFC (Durstewitz and Seamans, 2008), and 3) the importance of top-down and bottom-up mixing in the formation of IMSs (presented here), we believe it is crucial to further explore the role that DA exerts on sensorimotor circuits in shaping IMS during JA. In addition, investigating the relationship between DA dynamics and IMS emergence could provide valuable information to describe normal and pathological (goal-directed) interactive motor behaviours beyond their phenomenological aspect.

In fact, a significant interest is emerging towards 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 (Haraldsson *et al.*, 2004; Frantseva *et al.*, 2014; Rossini *et al.*, 2015; Howes *et al.*, 2017; Rossi *et al.*, 2021). 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). In this context, 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 IMS also in psychiatric patients. In fact, 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, E.V., P.C., A.D.; Investigation, E.V. and P.C.; Methodology, E.V., P.C., A.T., A.D.; Software, E.V. and P.C.; Formal Analysis, E.V.; Writing – Original Draft, E.V.; Writing – Review & Editing, E.V., P.C., A.T., L.F., A.D.; Supervision, A.D.; Project Administration, L.F. and A.D.; Funding Acquisition, L.F. and A.D.

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