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Parallel fast and slow motor inhibition processes in Joint Action coordination

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ABSTRACT

Motor inhibition is essential to adapt to an ever-changing environment and to noise in state prediction. As a consequence, inhibitory motor control must also play a key role during Joint Action (JA) tasks, where the motor system has to further integrate inferences about others' action. Yet, very little research has been carried out on the contribution of motor inhibition in JA tasks. Here, we used an interactive task in which subjects were required to open a bottle with one hand. The bottle was held and stabilized by a co-actor (JA) or by a mechanical holder (vice clamp, no-JA). A first motion capture study characterized the reaching and grasping kinematics of the two conditions. In a second study, by means of Transcranial Magnetic Stimulation (TMS), we measured (i) corticospinal excitability (CSE), (ii) cortical silent period (cSP) and (iii) short-interval intracortical inhibition (sICI), during the reaching phase of the task. These latter two indexes respectively reflect slow corticospinal (GABAb-mediated) and fast intracortical (GABAa-mediated) inhibition. We found no modulation for CSE, while cSP was increased and intracortical inhibition was downregulated during JA. Interestingly, the cSP correlated with partners' predictability as a whole and with partners' behaviour in the previous trial. These results, beside showing clear dissociation between fast and slow inhibition during JA, also shed new light on the predictive role played by corticospinal inhibitory mechanisms in online mutual behavioural co-adaptation.

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1. Introduction

Behavioral cooperation requires continuous and reciprocal exchange of information mediated via bodily movements. Sensorimotor communication is central to cooperative behaviors in which two or more agents coordinate their actions in time and space, to achieve a common goal (Pezzulo, Roche, & Saint-Bauzel, 2019; Lucia M. Sacheli, Aglioti, & Candidi, 2015; Sebanz, Bekkering, & Knoblich, 2006). Joint Actions (JAs) require online inter-individual mutual motor adaptation (D'Ausilio et al., 2012; Konvalinka & Roepstorff, 2012) and a shared cognitive representation of a given task (Gallotti, Fairhurst, & Frith, 2017; Konvalinka, Vuust, Roepstorff, & Frith, 2010). This highly interactive process enables the emergence of interpersonal coupling at behavioral (Richardson, Marsh, Isenhower, Goodman, & Schmidt, 2007), psychological (Mitkidis, McGraw, Roepstorff, & Wallot, 2015; Müller & Lindenberger, 2011) and neural levels (Konvalinka & Roepstorff, 2012; Novembre, Knoblich, Dunne, & Keller, 2017).

As far as the neural underpinnings of JA are concerned, it has recently been shown that single neurons in the monkey left dorsal premotor (lPMd) cortex discharge during JA tasks (Ferrari-Toniolo, Visco-Comandini, & Battaglia-Mayer, 2019). Specifically, a class of lPMd neurons are active only when the two monkeys have to coordinate their force pulses on an isometric joystick but not when the same action was performed individually. These results agree with human neuroimaging data showing that activity of premotor regions might code higher-order "joint" motor representations (L. M. Sacheli et al., 2019).

Indeed, the motor system supports others' action anticipation (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004) via specific modulations of corticospinal excitability (Amoruso & Finisguerra, 2019; D'Ausilio, Bartoli, & Maffongelli, 2015; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Naish, Houston-Price, Bremner, & Holmes, 2014) that are driven by premotor cortex activations (Avenanti, Candidi, & Urgesi, 2013). During JA instead, the motor system has to integrate inferences about others' action while also organizing appropriate self-action. Although this process of integration might be reflected in modulation of corticospinal inhibitory mechanisms (Cardellicchio, Dolfini, Hilt, Fadiga, & D'Ausilio, 2020), no direct demonstration has been provided yet.

The aim of the present study was to directly elucidate whether motor inhibition is modulated in JA tasks. To explore this issue, we used a novel experimental task in which subjects were required to open a bottle with one hand. The JA component relies on the fact that, with one hand, the bottle needs to be stabilized to accomplish the task. The bottle was held by a co-actor (Joint Action, JA) or by a mechanical holder (vice clamp, no-JA). This JA task requires an online and ecological interaction between two participants via haptic exchange of forces. However, even before haptic interaction, both the participant and the actor have to adapt to each other to accomplish the task. In fact, the actor will likely apply anticipatory pressure to the bottle to prepare for the haptic interaction. On the other hand, the participant will likely adjust his/her reaching strategy depending on prior history of haptic interactions and thus by building a prediction on the behavior of the confederate.

The first Kinematic study was developed to fully characterize the two conditions (JA and no-JA) in terms of movement features (e.g., reaching and grasping components of movements). In the second study we investigated, by means of Transcranial Magnetic Stimulation (TMS), the recruitment of excitatory and inhibitory neural mechanisms. We delivered the TMS pulse during the reaching phase to avoid any confound driven by somatosensory activation during haptic interaction with the bottle. TMS, online triggered by electromyography, was delivered to the primary motor cortex (M1) representation of the Opponens Pollicis (OP) muscle. We measured (i) corticospinal excitability (CSE), (ii) cortical silent period (cSP) and (iii) short-interval intracortical inhibition mechanisms (sICI). While CSE provides an instantaneous read-out of the net excitation directed to the target muscles, cSP and sICI probe different inhibitory circuits. The sICI, associated to the activation of low threshold inhibitory interneurons in M1 (Cardellicchio, Hilt, Olivier, Fadiga, & D'Ausilio, 2018; V.; Di Lazzaro et al., 2000; Ilić et al., 2002; C.; Tandonnet, Garry, & Summers, 2010) and mediated GABAa receptors, is considered an index of inhibition required in fast motor adaptation (Neubert, Mars, Olivier, & Rushworth, 2011). The cSP is a GABAb-mediated neurophysiological index of inhibition (Cardellicchio et al., 2020; Tergau et al., 1999) that is considered as a marker of slow corticospinal inhibition required for response selection (Davranche et al., 2007; Tandonnet et al., 2012).

In the main TMS experiment we do not expect any CSE modulation because this index is mostly influenced by muscular contraction, that is kept constant for the two conditions. Instead, considering that our task forces participants to co-adapt via small but temporally accurate corrections, we predict modulation of intracortical and corticospinal inhibitory mechanism. These modulations would suggest that the delicate negotiation of motor performance, as it is required in our JA task, is best characterized by the fine-tuning of motor inhibition rather than excitation.

2. Materials and methods

2.1. Subjects

A total of 52 healthy naive volunteers took part in the study (25 males: mean age 27.47, SD ± 4.50). 36 subjects (17 males, mean age 26.9, SD: 4.47) participated in the first Kinematic study and the remaining 16 (8 males; mean age 23.75, SD ± 3.08) participated in the second Transcranial Magnetic Stimulation study. Sample sizes of both studies was aligned with previous similar literature (Becchio, Sartori, Bulgheroni, & Castiello, 2008; Cardellicchio et al., 2018, 2020; Sartori, Becchio, Bara, & Castiello, 2009). None of the subjects participated in more than one experiment. All subjects were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). Participants were informed about the experimental procedure and gave their written consent according to the 1964 Helsinki Declaration, as revised in 1983. None of the participants reported neurological, psychiatric or other contraindications to TMS (Rossi et al., 2009). The experiment was approved by the ethical committee "Comitato Etico Unico

della Provincia di Ferrara" (approval N. 170592), and participants were compensated for their participation with 12,50 €.

2.2. Kinematic study

2.2.1. Stimuli and procedures

Participants were seated in a comfortable armchair with their forearm pronated and the right-hand resting on a button-box on a table in front of them (length = 110 cm; width = 80 cm). A deformable plastic bottle was positioned on the table at a distance of 45 cm (about 2/3 of participant's arm length) from participants' chest along his/her midline. The bottle height was 25 cm, with a rough plastic texture, and a cap diameter of 5 cm. Each experimental trial began with the presentation of a 300 ms sine-wave tone (800 Hz), instructing participants to reach the bottle and open its screw cap. After completing the action, participants returned to the initial position. The length of the inter-trial interval (ITI) was 7 s with a randomized jitter of ±500 ms. All the participants started in the same initial position with the same hand/arm posture.

To open a bottle, we normally need to stabilize it with the other hand. Instead, to successfully open a screw cap bottle with one hand only, we need another way to stabilize it. Here participants were presented with two conditions. In the first, an actor sat in front of the subject and held the bottle with his/her right hand (Joint Action condition; JA). In the second one, the actor was seated in front of the subject, but the bottle was held by a mechanical holder (no Joint Action—no-JA; Fig. 1A). Considering that sex pairing effects have been reported in JA tasks (Gaggioli et al., 2019; Mussi, Marino, & Riggio, 2015; van der Weiden, Aarts, Prikken, & van Haren, 2016), half of the trials were run with a male (age: 35) and half with a female (age: 30) co-actor. Four blocks of 15 trials were administered, one for each combination of condition and co-actor (2 conditions: JA and no-JA; 2 co-actors: male and female). The order of blocks presentation was counterbalanced across participants. The experiment was run in a single session of ~20 min.

A near-infrared camera motion capture system with seven cameras (Vero v2.2, Vicon Motion Systems Ltd.; set-up frame rate: 100 Hz), an analog/digital (A/D) converting station (Lock+, Vicon Motion Systems Ltd.; set-up frame rate: 2000 Hz) and a dedicated software (Nexus 2.8.2, Vicon Motion Systems Ltd.) were used to track the subjects' movements (Fig. 1C). Participants' right arm and hand were outfitted with 11 lightweight infrared reflective markers (4 mm in diameter). These markers were attached on the following anatomical locations: (I) thumb, radial side of the nail, (II) thumb, radial side of the proximal phalange, (III) index, radial side of the nail (IV) index, radial side of the proximal phalange (V) wrist, dorso—distal aspect of the radial styloid process, (VI) lower part of the right arm, (VII) elbow, (VIII) middle of the right upper arm, (IX) right shoulder, (X) left shoulder, (XI) manubrium of sternum. Three additional markers were positioned, respectively, on the bottle-cap, on the center and on the bottom of the bottle (Fig. 1B). One capacitive sensor was positioned on the bottle-cap to record the moment in which participants reached and touched the cap. A force sensor inside the bottle quantified the grip force exerted by the co-actor. The start button signal and the sensors analog data was fed to the VICON analog-to-digital converter.

2.2.2. Data processing and analysis

We recorded the kinematics of each block in a continuous mode. Each trial was individually inspected off-line for correct marker identification. Kinematic data were segmented considering the reach-to-grasp phase of the movement, from the reach onset (thumb velocity larger than 10 mm/sec after the go signal) to the reach offset (thumb velocity below a 10 mm/sec threshold). All trials in which participants started their movement before the go signal (false start) were excluded as incorrect trials (12 trials excluded in total, .45%). Kinematic trajectories in each trial was first inspected for correct marker identification, and then run through a low-pass Butterworth filter with a 10 Hz cutoff. For data processing and analysis, a custom software (Matlab; The MathWorks, 2015) was used to extract the following indexes:

A. Reaction Time (RT), defined as the time between the go-signal and movement onset (thumb velocity threshold);
B. Movement Time (MT), defined as the time between movement onset (thumb velocity threshold) and bottle-cap touch (capacitive sensor);
C. Thumb Mean Velocity (Vmean), defined as the absolute mean velocity of the thumb marker (mm/sec);
D. Thumb Maximum Velocity (V_{max}), defined as the maximal velocity of the thumb marker (mm/sec);
E. Thumb Time to Peak Velocity (TPV), defined as the time elapsed to reach maximal thumb velocity during the reaching movement;
F. Maximum Grip Aperture (MGA), defined as the maximal distance between the thumb and index markers (mm);
G. Path Length (PL), defined as the sum of Euclidean distance of the thumb x-, y- and z-coordinates between reaching onset and offset.

For each of the above-mentioned dependent measures, the individual grand mean in each condition was calculated. Values 2 SD above or below each individual mean for each kinematic indexes were excluded as outliers (RTs: 4.4%; MT: 3.8%; Vmean: 3.8%; V_{max}: 3.8%; TPV: 5%; MGA: 4.5%; PL: 3.4%). In order to test the interaction between participants and co-actors in terms of sex differences and tasks, values of each dependent variable were entered in a separate repeated measure ANOVA. Experimental conditions were arranged according to a 2 × 2 factorial design with sex pairing between participants (Sex: pair, unpair), and task type (Task: JA, no-JA) as within subject factors. Significant main effects or interactions were further explored with Newman Keuls post-hoc tests.

In JA trials, the actor is also supposed to stabilize the bottle by increasing grip force before subjects has reached the bottle-cap. We thus calculated force at the time of reaching onset and at bottle touch timing to test whether the co-actor employed a cooperative strategy. We performed a two-tails t-test between these two values, to evaluate whether the actor increased squeezing force to stabilize the bottle. To verify

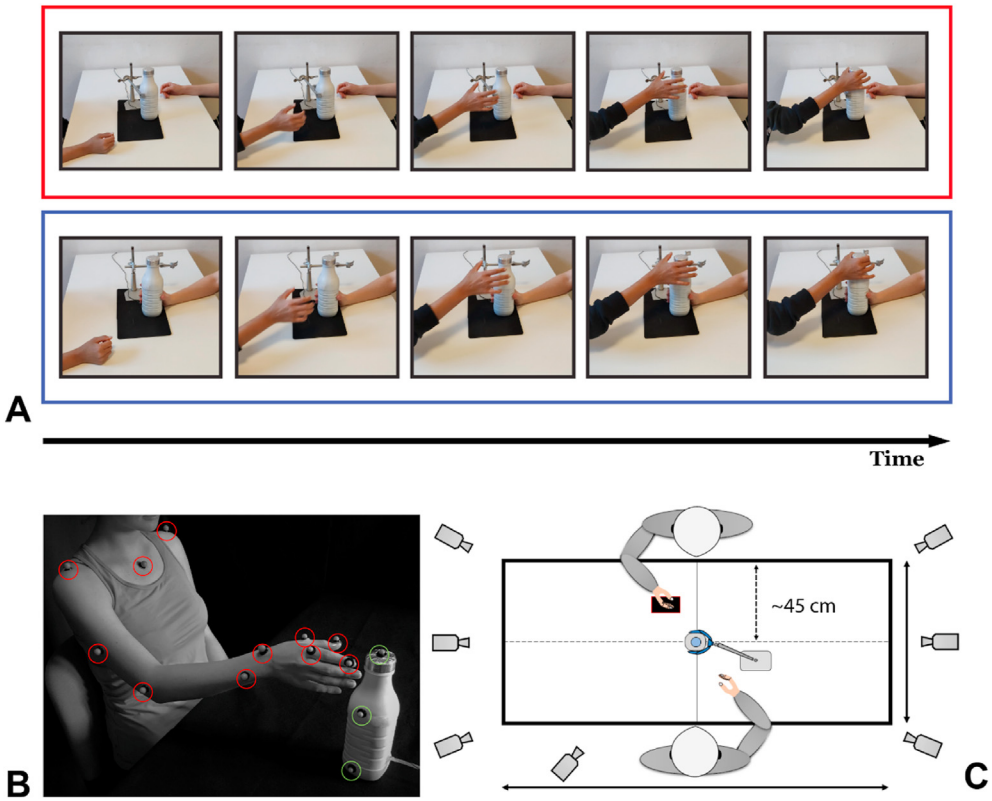

Fig. 1 – Panel A shows the timeline of the experimental trials in the two experimental conditions (JA and no-JA). Red square indicates no-JA condition, the blue square indicates the JA. In both conditions, after the go-signal participants were instructed to reach for the bottle and open the cap. The bottle was held by a co-actor or by a mechanical holder. In the no-JA condition the actor was seated in the same position but kept her hand resting on the table (C). In both conditions the mechanical holder and the co-actor were constantly present and visible to participants. Panel B shows markers position. Panel C shows the experimental setting and position of each infrared camera.

whether co-actor stabilization depended on subject-actor sex pairing we employed an ANOVA with factors Sex (paired, unpaired) and Force (movement onset, bottle touch) and dependent variable the grip force values. Finally, to describe the amount of co-actor anticipation, the bottle stabilization onset was computed with a first-derivative-based methods. We first computed the first derivative of the pressure exerted on the bottle by the co-actor. Once the peak of the derivative is extracted, we used a 5% threshold to determine onset and offset of the pressure signal (D'Amico & Ferrigno, 1992, 1990; Lanshammar, 1982). This anticipation timing was compared across the sex pairings with a two-tails *t*-test.

2.2.3. *Results*

In the JA condition, the co-actor exerted a stabilizing force on the bottle that was significantly larger when participants touched the cap as opposed to baseline values ($t(14) = -5.5$; $p < .01$; Cohen's $d = 1.42$). The increase in grip force however did not interact with sex pairing in the experiment ($F(1,14) = .39$, $p = .54$). Grip force grew before cap touch (mean: 319.74 mV ± 277.9) but there was no difference in anticipation depending on subject-actor sex pairing ($t(14) = .35$; $p = .7$).

The 2 × 2 repeated-measure ANOVAs on RT, MT and TPV did not show any significant main effect or interaction. A significant main effect of the Task was present in Vmean ($F(1,35) = 5.13$, $p = .02$, $\eta^2p = .12$), V_{max} ($F(1,35) = 5.84$, $p = .020$, $\eta^2p = .14$), MGA ($F(1,35) = 9.82$, $p = .003$, $\eta^2p = .21$) and PL ($F(1,35) = 8.64$, $p = .005$, $\eta^2p = .19$). In general, we can exclude that co-actors sex pairing affect coordination in our task. Table 1 contains mean and standard deviation values for each variable in both conditions.

Table 1 – Mean and standard deviation of Kinematic measures. Asterisks indicate significant main effect of Task in 2 × 2 ANOVA between JA and no-JA conditions.

	JA	No-JA
Reaction Time (RT) (sec)	.539 ± .116	.536 ± .106
Movement Time (MT) (sec)	.593 ± .137	.586 ± .147
Thumb Mean Velocity (Vmean)*(cm/sec)	41.67 ± 12.23	40.4 ± 11.66
Thumb Maximum Velocity (Vmax)* (cm/sec)	84.32 ± 24.22	81.51 ± 22.91
Thumb Time to Peak Velocity (TPV) (sec)	.45 ± .03	.45 ± .04
Maximum Grip Aperture (MGA)* (cm)	10.09 ± .561	10 ± .542
Path Length (PL)* (cm)	38.6 ± .36	38.1 ± .40

2.3. TMS study

2.3.1. Stimuli and procedures

Participants were asked to do the same task of the Kinematic study (Fig. 1A). Since the results of the kinematic study showed no relevant interaction between sex pairing and task, only the female actor participated in this study. Here we recorded movement onset with the release of the button-box, bottle touch via the capacitive sensor on the cap and actor anticipatory cooperation via the force sensor in the bottle. All the participants started in the same initial position.

For both experimental conditions (JA; no-JA), two TMS protocols were used: 1) a single pulse (SP-TMS) TMS protocol and 2) a paired pulse protocol (PP-TMS). The first allows the recording of the corticospinal excitability (CSE) and the cortical Silent Period (cSP). The second, with an inter-pulse interval of 3 ms was employed to investigate the Short Interval Intracortical Inhibition (sICI). Each condition (JA, no-JA) contained respectively 60 trials, of which 15 were SP-TMS, 15 PP-TMS and 30 without TMS (catch trials included to eliminate TMS expectation effects). We thus obtained a total of 120 trials randomized in 4 blocks (2 blocks for JA and 2 for no-JA) in a counter-balanced across participants order. Additionally, at the beginning and at the end of the experimental session we also collected additional 15 SP-TMS and 15 PP-TMS as baseline. The task required about ~20 min per participant and was implemented in MATLAB (MATLAB R2015b, The MathWorks Inc., Natick, MA, 2000).

2.3.2. TMS and EMG

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. OP was chosen because it is critical in grasping and in the rotating movement required to open a screw cap. The OP Optimal Scalp Position (OSP) was located by moving the coil in .5 cm steps around the left primary motor cortex hand area and using a slightly suprathreshold stimulus. The TMS coil was held tangentially to the scalp with the handle pointing backward and laterally form a 45° angle with the midline. The OSP was marked on a cap, and the resting motor threshold (rMT) was established as the lowest stimulus intensity eliciting Motor Evoked Potentials (MEPs) on the right OP muscle, greater than 50 μV amplitude, in at least 5 trials out of 10 (Rossini et al., 1994). SP-TMS was delivered at the intensity of 120% of rMT. For the PP-TMS the conditioning stimulus (CS) was set at 80% of rMT while the test stimuli (TS) was set at 120%, with an inter-stimulus intervals (ISIs) of 3 ms. The rMT ranged from 40% to 60% (mean = 51.6%; SD = 4.9%) of the maximum stimulator output.

The EMG signal was recorded through a wireless EMG system (Zerowire EMG, Aurion, Italy) with a tendon-belly montage. EMG data, collected from 3000 ms before and after the TMS pulse, were digitized (2 kHz) and acquired by a CED power1401 board to be stored on a PC for offline analysis (Signal 3.09 software; Cambridge Electronic Design, Cambridge, UK).

TMS timing during each trial, was triggered by OP muscle activity. In fact, reaching length could vary significantly between and within subjects, making it difficult to lock TMS timing to a specific movement landmark. Instead, here TMS was delivered depending on the activation the muscle of interest. Specifically, a moving average procedure with a sliding window of 50 ms was run on-line during the reaching actions on the rectified surface EMG. We defined OP onset as when the EMG signal exceeded by 100% the average EMG recorded in a 100 ms window before the reaching started. TMS pulses were then delivered 100 ms after OP onset (Fig. 2).

2.3.3. Analysis

For JA trials without TMS we calculated actor's cooperative anticipation on the force sensor as we did in the kinematic study. We similarly calculated grip force at movement onset and at the time of bottle touch. We performed a two-tails *t*-test between these two values, in order to verify whether the co-actor stabilized the bottle during the reaching phase. Finally, to describe the amount of co-actor anticipation, the bottle stabilization onset was computed as in the kinematic study.

We then examined participant's behavioral performances in JA and no-JA tasks. Trials with MT over 3000 ms were discarded (none of subjects had null trials). RTs (interval between the go signal and button-box release) and MTs (from button-box release to the touch of the bottle-cap) were calculated in catch trials (without TMS), to exclude the movement perturbation introduced by TMS. Values that fell 2 SD above or below each individual mean were excluded as outliers (RTs: 2.8%; MTs: 4.3%). Furthermore, we computed the MTs percentage in which the TMS pulse would have been delivered (based on EMG signal). Considering that TMS timing was driven by OP activation on trial by trial basis, we intended to control if TMS was delivered in the same phase of the reaching action.

In TMS trials we first verified if the amount of pre-TMS EMG activity of the OP muscle was comparable between the two conditions. We ran a two-tailed *t*-test on the root mean square (RMS) of EMG signal in a time window of 100 ms before the TMS pulse. We then proceeded with the analyses of CSE, sICI and cSP values. We discarded from the analysis trials with either no visible cSP or a MEP below 50 μV (mean .72%, SD = 1.48), and trials in which the subjects touched the cap before the TMS pulse (mean 5.6%, SD = 7.6).

Raw MEPs were extracted computing peak to peak amplitudes in a window of 60 ms following the TMS pulse. CSE was then normalized as the ratio between the mean MEPs size within each condition and the baseline MEPs size. sICI values were expressed as the ratio between the mean conditioned MEPs amplitude and the mean single pulse MEPs amplitude. Silent period durations (cSP) were measured for each trial as the time between the offset of the MEPs and the return of EMG activity, according to standard procedures (Cardellicchio et al., 2020; Farzan et al., 2010, 2013; Säisänen et al., 2008). The end of the cSP was determined on each individual trial as the resumption of at least 2 SD of EMG-activity to the level of pre TMS stimulus (end of cSP >2SD of the 50 ms pre-stimulus signal).

Offline semi-automated extraction of MEPs amplitude and cSP durations was carried out with Signal 6.05 software (Cambridge Electronic Design, Cambridge, UK). Since each index (CSE, cSP and sICI) measures different neurophysiological processes, we compared Joint and non-Joint actions via separated paired-samples two-tailed *t*-tests comparisons.

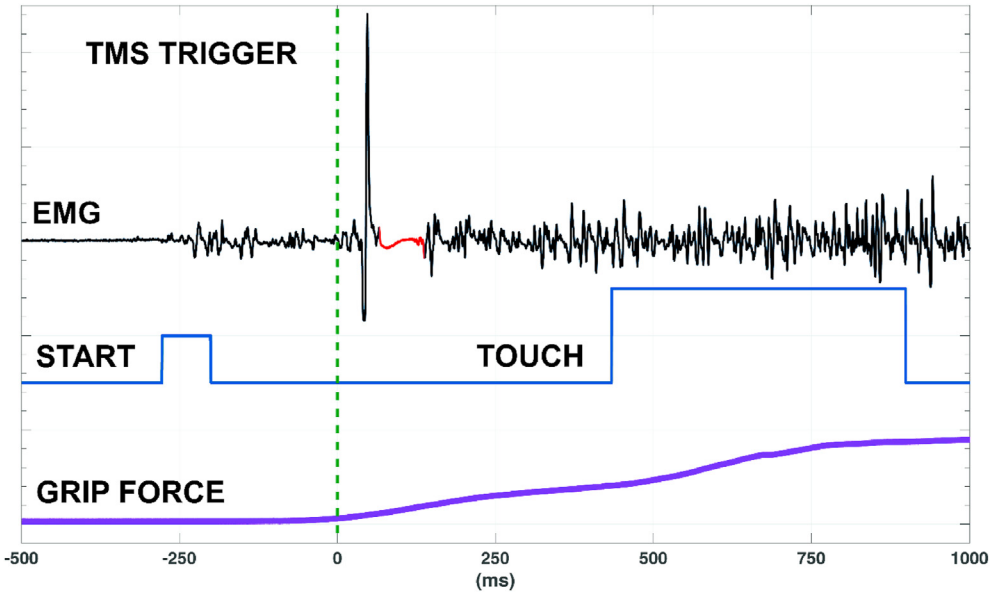

Fig. 2 – Example of one trial timeline and all signals recorded. The black line shows the EMG of the OP muscle in a single participant in one trial. TMS was triggered by the OP's muscular activity (see methods). Please note in red the cSP following the MEP and that the time axis is centred upon the delivery of TMS (vertical dashed green line). The thin blue line represents the release of the button (first square wave) and later the touching of the bottle-cap (second square wave). The thick blue line shows the bottle grip force produced by the co-actor. Please note that the force increases during the reaching phase to anticipate participant's grasping.

Finally, in order to explore the effect of mutual behavioral adaptation on neurophysiological indexes, we run a series of correlational analyses between TMS indexes and the force exerted by the partner (see Fig. 2 for a visual depiction of the signals recorded in each trial). Firstly, we extracted the area (P_area) and the maximum (P_max) value of the pressure signal between reaching movement onset (release of the button) and offset (touch of the cap). We then calculated the correlation across trials between significantly modulated TMS indexes (cSP and sICI) and force data (P_area and P_max) in the same (n) or in the previous trial (n-1). We then performed a non-parametric test (two-tailed permutation test) to evaluate if the correlation indices (Fischer normalized) were significantly different from zero.

Moreover, in order to test whether actor's variability could explain our pattern of results, we computed the standard deviation across trials of P_area and P_max, separately for each experimental session. The standard deviation of force indexes can be considered as a proxy of actor's behavioral predictability. These values were correlated across participants with the significant TMS indexes (cSP and sICI). Parametric analyses were run with STATISTICA 9 (StatSoft, Inc.), non-parametric analyses were implemented in MATLAB (MATLAB R2015b, The MathWorks Inc., Natick, MA, 2000).

3. Results

In the JA condition, the co-actor produced a stabilizing force on the bottle that was significantly larger when participants touched the cap as opposed to baseline values ($t(15) = -6.94$; $p < .01$; Cohen's $d = 1.73$). Grip force increased before cap touch (mean: 431.9 ± 107.9). Behavioral performance between the two conditions, in no TMS trials, didn't show any significant difference on RTs ($t(15) = .64$; $p = .53$; JA: 555 ms ± .88 SD; no-JA: 560 ms ± .86 SD) and on MTs ($t(15) = 2.03$; $p = .06$; JA: 715 ms ± .14 SD; no-JA: 728 ms ± .14 SD). The EMG-based criteria to deliver TMS, in no TMS trials, was met at comparable movement phase across conditions ($t(15) = .11$; $p = .91$; JA: 53% of MTs ± 11.9 SD; no-JA: 54% of MTs ± 11.7 SD), potentially excluding any confound due to unequal timing of stimulation during the reaching movement.

In stimulated trials, the amount of pre-TMS EMG activity of the OP muscle was comparable during the execution of JA and no-JA actions. The paired sample *t*-test showed that there was no significant difference between the two tasks in the time window preceding the TMS pulse ($t(15) = 1.06$; $p = .30$). This result allowed us to compare CSE, sICI and CSP across conditions excluding any evident confound due to unequal muscle activation.

CSE did not differ across conditions ($t(15) = 1.15$; $p = .26$; JA: 2.25 ± .61 SD; no-JA: 2.29 ± .69 SD; Fig. 3A), while sICI was reduced during JA ($t(15) = 2.98$; $p < .01$; $\eta^2p = 0{,}75$; JA: .84 ± .13 SD; no-JA: .80 ± .15 SD; Fig. 3B) and cSP was greater in JA ($t(15) = 2.88$; $p = .01$; $\eta^2p = 0{,}72$; JA: 70 ms ± 23 SD; no-JA: 66 ms ± 22 SD; Fig. 3C).

The single-trial correlation between P_area and P_max and cSP and sICI in the same trial (trial n) did not show any significant effect. Instead, correlation with the previous trial (trials n-1) was significant for the cSP for both P_area and P_max. Table 2 contains p-values and effect sizes for each correlation. The correlations across participants between TMS indexes (cSP and sICI) and the standard deviation of confederate's force, show only a significant relation (R2 = .30;

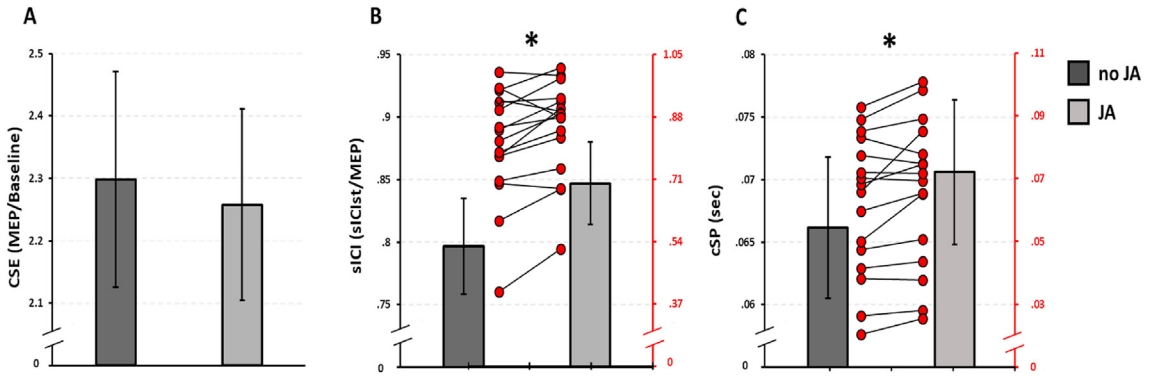

Fig. 3 – Corticospinal excitability and inhibitory indexes (mean and SE). The figure represents the TMS measures recorded during the movement. (A) Corticospinal Excitability (CSE) shows no significant differences between the JA and no-JA conditions. Otherwise, we observed less inhibition in JA with sICI (B) and the opposite effect with cSP length (C). Asterisks denote significant effects. Right's vertical axes in the significant graphs show in red the participant's distributions by means individual data points connected across the conditions.

Table 2 – Single trial correlation results between P_area, P_max and cSP, sICI in the same or the previous trials. The table reports p-values and effect sizes while asterisks indicate significant effects on the permutation tests.

cSP	P_area p-value	P_area Effect size	P_max p-value	P_max Effect size
Trial (n)	.85	.0015	.73	.31
*Trial (n-1)**	.01*	1.36	.03*	1.16
sICI				
Trial (n)	.14	.75	.23	.66
Trial (n-1)	.58	.27	.65	.27

p = .026) between cSP and the maximal force exerted by the confederate (Fig. 4 B). No other significant correlations were found (Fig. 4 A, C, D).

4. General discussion

The present work investigated the kinematic and the neural underpinnings of sensorimotor-interaction during a real-time Joint Action coordination. However, inherent in JA is a larger degree of behavioral variability which may turn into reduced predictability. This is indeed a key point in JA research. In fact, a true comparison should be with an equally unpredictable and perfectly matched time-varying force exerted by a non-human artifact. Still, this synthetized behavior would then be imbued with key human-like properties—though missing a human-like appearance. Although partner's appearance is important, our task was designed to have participants focus on a shared goal that could only be achieved by the spatio-temporal alignment of complementary actions. Participants had to open a bottle held by another individual (JA) or by a mechanical holder (no-JA). As expected, the first study shows that motor performance was different in JA, as demonstrated by a greater mean and peak transport velocity, grip aperture and by a longer path.

In agreement with the current modulations, coordination is often altered in JA tasks with shared motor goals, as for instance in the control of isometric force (Masumoto & Inui, 2013, 2014), reaching the same fixed (Reed et al., 2006; Takagi, Beckers, & Burdet, 2016) or moving target (Ganesh et al., 2014; Takagi, Ganesh, Yoshioka, Kawato, & Burdet, 2017; Takagi, Usai, Ganesh, Sanguineti, & Burdet, 2018), or operating a tool (Van der Wel, Knoblich, & Sebanz, 2011). During JA, performance is generally better than that of a person doing the same task alone (Ganesh et al., 2014; Reed et al., 2006). In fact, participants adjust their kinematics to facilitate coordination (Coco et al., 2017; D'Ausilio et al., 2015; Pezzulo, Donnarumma, & Dindo, 2013; Lucia M. Sacheli, Tidoni, Pavone, Aglioti, & Candidi, 2013; Vesper & Richardson, 2014), often by reducing motor variability to be more predictable (P. Hilt et al., 2019). More importantly, these subtle variations in movement kinematics can be picked up by the observer to support inferences about other's action goals (Ansuini et al., 2016; Soriano, Cavallo, D'Ausilio, Becchio, & Fadiga, 2018).

In the TMS study we used three protocols to investigate corticospinal and intracortical excitability modulations when actions have to be co-regulated between agents. We showed the specific recruitment of different inhibitory processes during JA and no modulation of corticospinal excitability. Our results suggest the concurrent operation of two distinct forms of inhibition: corticospinal inhibition was increased while intracortical inhibition was downregulated.

4.1. *Inhibitory mechanisms during JA*

Neural inhibition is regulated by GABAergic (GABA) neuromodulation, which alters polarization of neural membranes via fast acting GABAa receptors and slow acting GABAb receptors (Krnjević, 1997). The first, measured by sICI, provides an index of quasi-instantaneous inhibition mediated by fast ionotropic postsynaptic GABAa receptors (V. Di Lazzaro et al., 2000; Vincenzo Di Lazzaro et al., 2006; Hanajima et al., 1998; Kujirai et al., 1993; Ziemann, Lönnecker, Steinhoff, & Paulus, 1996). The second, indexed by cSP length, provides a measure of slow metabotropic postsynaptic GABAb-mediated inhibition (Hallett, 2007; Werhahn, Kunesch, Noachtar, Benecke,

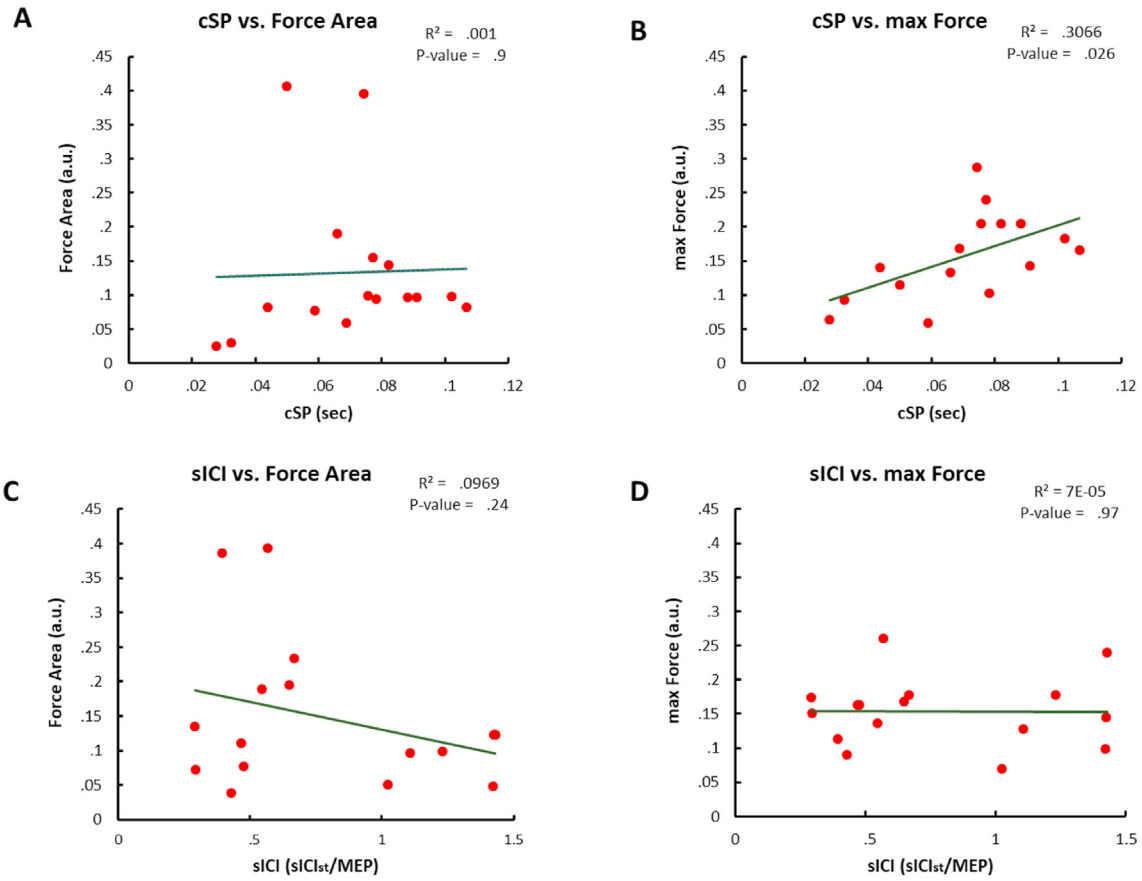

Fig. 4 – Correlations between TMS indices (cSP and sICI) and the standard deviations of force (area and max force) exerted on the bottle by the actor. The relationship between cSP length and maximal force was significant.

& Classen, 1999). The properties of these receptor subtypes appear to serve different functional roles. In fact, the flexibility of GABAergic neurotransmission contributes to the regulation of motor activities via parallel fast and slow modulatory signaling (Tamás, Lörincz, Simon, & Szabadics, 2003; Tritsch, Granger, & Sabatini, 2016).

The fast recruitment of GABAa receptors, makes it a potential candidate for rapidly regulating or gating neuronal firing (Heubl et al., 2017; Kang, Kaneko, Ohishi, Endo, & Araki, 1994; Nicoll, 2004). In this way, it may regulate cortical gamma oscillations (Cardin et al., 2009; Kujala et al., 2015; Sohal, Zhang, Yizhar, & Deisseroth, 2009; Whittington, Traub, Kopell, Ermentrout, & Buhl, 2000), as well as the temporal fidelity of neuronal output (Lamsa, Heeroma, & Kullmann, 2005). Intracortical inhibition, as measured via ppTMS, is substantially reduced during muscle activation (Ridding, Taylor, & Rothwell, 1995), suggesting its role in suppressing voluntary activity (Liepert, Classen, Cohen, & Hallett, 1998; Sohn, Wiltz, & Hallett, 2002). Specifically, modulation of sICI may serve the regulation of muscle synergies during complex hand actions, by selectively activating (sICI decrease) or not (sICI increase) specific muscles (Gagné & Schneider, 2007). For example, sICI of the relaxed abductor pollicis brevis muscle is increased in phase with the index finger flexion (Stinear & Byblow, 2003, 2004a, 2004b). Moreover, newly required actions are selected through a progressive sICI release from inhibition in the execution of the response (Neubert et al., 2011). As a consequence, sICI modulation seems to reflect how motor inhibitory circuits shape the motor command towards "meaningful behavioral outcomes" (Byblow & Stinear, 2006). Intracortical inhibition is also reduced when subtle motor errors are shown in the observed action (Cardellicchio et al., 2018). During our JA task, co-actors need to monitor others' action to extract potential deviations from their expectations. The reduction of intracortical inhibition observed in the present study, may reflect both the process of monitoring other's action as well as the implementation of small motor adjustments to optimize JA interaction. Yet intracortical inhibition did not correlate at the single trial level with the force produced by the co-actor nor with her predictability as a whole. These results suggest that sICI do not seem to reflect specific and online adaptations to the partner. Rather, these results seem to suggest that sICI may describe a general readiness to adapt more than a proper marker of behavioral adaptation during JA.

GABAb-based inhibition is slower and requires associative neuronal firing to generate enough GABA pooling (Brown, Davies, & Randall, 2007; Cash, Ziemann, Murray, & Thickbroom, 2010; Nicoll, 2004; Poncer, McKinney, Gáhwiler, & Thompson, 2000; Scanziani, 2000). This characteristic attribute to GABAb inhibition a role in the coordination of neuronal assemblies (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; Christophe Tandonnet et al., 2012), suppression of voluntary motor drive (Tergau et al., 1999) and is reduced when action observation does not match a concurrent executed action (Cardellicchio et al., 2020). In the JA condition, participants had to cooperate with the actor to achieve a shared goal, while in the no-JA condition activity of the two were dissociated. As a consequence, the increase we show in corticospinal inhibition could reflect goal sharing in JA, while the shortening of cSP in the no-JA condition may index goal misalignment across partners. Interestingly, cSP length was correlated at the single-trial level with the force produced by the partner in the previous trial, not in the current one. This is highly suggestive of the fact that action control is here informed by past interactions and this information is reflected in cSP modulations. Additionally, cSP was also (weakly but significantly) correlated with the partner's predictability as expressed by the variability of the force produced on the bottle. All these results together seem to suggest that differently from sICI, cSP may provide a more specific index of motor inhibition during JA that is sensible to both past interaction and task predictability.

4.2. *Hierarchical predictive mechanisms in JA*

JA can be conceived as motor control for the purpose of negotiating behavioral change in another individual, in function of a common goal. In fact, JA coordination requires the parallel processing of self and other's action (Lucia M. Sacheli et al., 2013) to integrate them into a shared goal representation (Clarke et al., 2019; Sebanz & Knoblich, 2009). Specifically, a joint goal representation might be instantiated as a hierarchical predictive model of the interaction (Friston, 2008; Kilner, Friston, & Frith, 2007) and the computation of prediction errors across all levels might be essential to adjust and adapt to our partner (Pesquita, Whitwell, & Enns, 2018).

During action observation, error signals are computed as a distance between one's own motor template and the observed action (P. Hilt et al., 2020). At the same time, when people are engaged in JA, they also flexibly modulate their movements to establish an effective channel of sensorimotor communication (Pezzulo et al., 2019). Through this channel, key information is shared across multiple levels, for example about the content (i.e., goals) of an action as well as about finer kinematic cues necessary to achieve spatial and temporal action coordination (P. Hilt et al., 2019).

The present study was directed towards the investigation of motor inhibition during JA, by employing two well-known measures of intracortical and corticospinal inhibition. We provide evidence for two parallel modes of inhibition acting during JA and possibly indexing complementary phenomena. The first one, the sICI, seems to reflect an unspecific preparation to coordinate, while the results obtained in cSP might underline the fact that participants build predictive models of their partner to improve interaction success.

Authors contribution

P.C., A.D had the idea and design the experiments. P.C., E.D. prepared the experimental setup and collected the data. P.C. and E.D. analyzed the data. All authors participated in interpretation of data and helped draft the manuscript; L.F. and A.D. supervised the project. All authors gave final approval for publication.

Open practices

The study in this article earned Open Materials and Open Data badges for transparent practices. Materials and data for the study are available at: https://osf.io/aw9g4/.

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

No part of the study procedures neither study analyses were pre-registered prior to the research being conducted.

Declaration of competing interest

The authors have no conflict of interest to declare.

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REFERENCES

Amoruso, L., & Finisguerra, A. (2019). Low or high-level motor coding? The role of stimulus complexity. *Frontiers in Human Neuroscience, 13*, 1–9. https://doi.org/10.3389/fnhum.2019.00332 (October).

Ansuini, C., Cavallo, A., Koul, A., D'Ausilio, A., Taverna, L., & Becchio, C. (2016). Grasping others' movements: Rapid discrimination of object size from observed hand movements. *Journal of Experimental Psychology. Human Perception and Performance, 42*(7), 918–929. https://doi.org/10.1037/xhp0000169

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 (APR 2013).

Becchio, C., Sartori, L., Bulgheroni, M., & Castiello, U. (2008). Both your intention and mine are reflected in the kinematics of my reach-to-grasp movement. *Cognition*. https://doi.org/10.1016/j.cognition.2007.05.004

Brown, J. T., Davies, C. H., & Randall, A. D. (2007). Synaptic activation of GABAB 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

Byblow, W. D., & Stinear, C. M. (2006). Modulation of short-latency intracortical inhibition in human primary motor cortex during synchronised versus syncopated finger movements. *Experimental Brain Research, 168*(1–2), 287–293. https://doi.org/10.1007/s00221-005-0205-9

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*. https://doi.org/10.1016/j.neuroimage.2019.116445 (November 2019).
Cardellicchio, P., Hilt, P. M., Olivier, E., Fadiga, L., & D'Ausilio, A. (2018). Early modulation of intra-cortical inhibition during the observation of action mistakes. *Scientific Reports, 8*(1), 1–9. https://doi.org/10.1038/s41598-018-20245-z
Cardin, J. A., Carlén, M., Meletis, K., Knoblich, U., Zhang, F., Deisseroth, K., et al. (2009). Driving fast-spiking cells induces gamma rhythm and controls sensory responses. *Nature*. https://doi.org/10.1038/nature08002
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
Clarke, S., McEllin, L., Francová, A., Székely, M., Butterfill, S. A., & Michael, J. (2019). Joint action goals reduce visuomotor interference effects from a partner's incongruent actions. *Scientific Reports*. https://doi.org/10.1038/s41598-019-52124-6
Coco, M. I., Badino, L., Cipresso, P., Chirico, A., Ferrari, E., Riva, G., et al. (2017). Multilevel behavioral synchronization in a joint tower-building task. *IEEE Transactions on Cognitive and Developmental Systems, 9*(3), 223–233. https://doi.org/10.1109/TCDS.2016.2545739
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
Di Lazzaro, V., Oliviero, A., Meglio, M., Cioni, B., Tamburrini, G., Tonali, P., et al. (2000). Direct demonstration of the effect of lorazepam on the excitability of the human motor cortex. *Clinical Neurophysiology, 111*(5), 794–799. https://doi.org/10.1016/S1388-2457(99)00314-4
Di Lazzaro, V., Pilato, F., Dileone, M., Ranieri, F., Ricci, V., et al. (2006). GABAA receptor subtype specific enhancement of inhibition in human motor cortex. *Journal of Physiology, Paris, 575*(3), 721–726. https://doi.org/10.1113/jphysiol.2006.114694
D'Amico, M., & Ferrigno, G. (1990). *Technique for the evaluation of derivatives from noisy biomechanical displacement data using a model-based bandwidth-selection procedure. Medical & Biological Engineering & Computing*. https://doi.org/10.1007/BF02441963
D'Amico, M., & Ferrigno, G. (1992). *Comparison between the more recent techniques for smoothing and derivative assessment in biomechanics. Medical & Biological Engineering & Computing*. https://doi.org/10.1007/BF02446130
D'Ausilio, A., Badino, L., Li, Y., Tokay, S., Craighero, L., Canto, R., et al. (2012). Leadership in orchestra emerges from the causal relationships of movement kinematics. *Plos One*. 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
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
Farzan, F., Barr, M. S., Hoppenbrouwers, S. S., Fitzgerald, P. B., Chen, R., Pascual-Leone, A., et al. (2013). The EEG correlates of the TMS-induced EMG silent period in humans. *Neuroimage, 83*, 120–134. https://doi.org/10.1016/j.neuroimage.2013.06.059
Farzan, F., Barr, M. S., Levinson, A. J., Chen, R., Wong, W., Fitzgerald, P. B., et al. (2010). Reliability of long-interval cortical inhibition in healthy human subjects: A TMS-EEG study. *Journal of Neurophysiology, 104*(3), 1339–1346. https://doi.org/10.1152/jn.00279.2010
Ferrari-Toniolo, S., Visco-Comandini, F., & Battaglia-Mayer, A. (2019). Two brains in action: Joint-action coding in the primate frontal cortex. *Journal of Neuroscience, 39*(18), 3514–3528. https://doi.org/10.1523/JNEUROSCI.1512-18.2019
Friston, K. (2008). Hierarchical models in the brain. *Plos Computational Biology*. https://doi.org/10.1371/journal.pcbi.1000211
Gaggioli, A., Falletta, E. M., Ferrise, F., Graziosi, S., Gallace, A., D'Ausilio, A., et al. (2019). Effects of interpersonal sensorimotor synchronization on dyadic creativity: Gender matters. *Frontiers in Psychology, 9*(FEB), 1–12. https://doi.org/10.3389/fpsyg.2018.02604
Gagné, M., & Schneider, C. (2007). Dynamic changes in corticospinal control of precision grip during wrist movements. *Brain Research, 1164*(1), 32–43. https://doi.org/10.1016/j.brainres.2007.06.014
Gallotti, M., Fairhurst, M. T., & Frith, C. D. (2017). *Alignment in social interactions*. Consciousness and Cognition. https://doi.org/10.1016/j.concog.2016.12.002
Ganesh, G., Takagi, A., Osu, R., Yoshioka, T., Kawato, M., & Burdet, E. (2014). Two is better than one: Physical interactions improve motor performance in humans. *Scientific Reports, 4*, 1–7. https://doi.org/10.1038/srep03824
Hallett, M. (2007). Transcranial magnetic stimulation: A primer. *Neuron, 55*(2), 187–199. https://doi.org/10.1016/j.neuron.2007.06.026
Hanajima, R., Ugawa, Y., Terao, Y., Sakai, K., Furubayashi, T., Machii, K., et al. (1998). Paired-pulse magnetic stimulation of the human motor cortex: Differences among I waves. *Journal of Physiology, Paris, 509*(2), 607–618. https://doi.org/10.1111/j.1469-7793.1998.607bn.x
Heubl, M., Zhang, J., Pressey, J. C., Al Awabdh, S., Renner, M., Gomez-Castro, F., et al. (2017). GABAA receptor dependent synaptic inhibition rapidly tunes KCC2 activity via the Cl–sensitive WNK1 kinase. *Nature Communications, 8*(1). https://doi.org/10.1038/s41467-017-01749-0
Hilt, P., Badino, L., D'Ausilio, A., Volpe, G., Tokay, S., Fadiga, L., et al. (2019). Multi-layer adaptation of group coordination in musical ensembles. *Scientific Reports*. https://doi.org/10.1038/s41598-019-55965-3
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*, 1–11. https://doi.org/10.1093/cercor/bhaa006
Ilić, T. V., Meintzschel, F., Cleff, U., Ruge, D., Kessler, K. R., & Ziemann, U. (2002). Short-interval paired-pulse inhibition and facilitation of human motor cortex: The dimension of stimulus intensity. *Journal of Physiology, Paris*, 545(1), 153–167. https://doi.org/10.1113/jphysiol.2002.030122
Kang, Y., Kaneko, T., Ohishi, H., Endo, K., & Araki, T. (1994). Spatiotemporally differential inhibition of pyramidal cells in the cat motor cortex. *Journal of Neurophysiology, 71*(1), 280–293. https://doi.org/10.1152/jn.1994.71.1.280
Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). *Predictive coding: An account of the mirror neuron system, 8 Cognitive Processing §*. Springer-Verlag. https://doi.org/10.1007/s10339-007-0170-2
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
Konvalinka, I., & Roepstorff, A. (2012). The two-brain approach: How can mutually interacting brains teach us something about social interaction? *Frontiers in Human Neuroscience, 6*(JULY), 1–10. https://doi.org/10.3389/fnhum.2012.00215
Konvalinka, I., Vuust, P., Roepstorff, A., & Frith, C. D. (2010). Follow you, follow me: Continuous mutual prediction and adaptation in joint tapping. *The Quarterly Journal of Experimental*

Psychology: QJEP, 63(11), 2220–2230. https://doi.org/10.1080/17470218.2010.497843

Krnjević, K. (1997). Role of GABA in cerebral cortex. In *Canadian journal of physiology and pharmacology*. https://doi.org/10.1139/y97-030

Kujala, J., Jung, J., Bouvard, S., Lecaignard, F., Lothe, A., Bouet, R., et al. (2015). Gamma oscillations in V1 are correlated with GABAA receptor density: A multi-modal MEG and Flumazenil-PET study. *Scientific Reports, 5*, 1–12. https://doi.org/10.1038/srep16347 (June).

Kujirai, T., Caramia, M. D., Rothwell, J. C., Day, B. L., Thompson, P. D., Ferbert, A., et al. (1993). Corticocortical inhibition in human motor cortex. *The Journal of Physiology, 471*(1), 501–519.

Lamsa, K., Heeroma, J. H., & Kullmann, D. M. (2005). Hebbian LTP in feed-forward inhibitory interneurons and the temporal fidelity of input discrimination. *Nature Neuroscience, 8*(7), 916–924. https://doi.org/10.1038/nn1486

Lanshammar, H. (1982). On practical evaluation of differentiation techniques for human gait analysis. *Journal of Biomechanics*. https://doi.org/10.1016/0021-9290(82)90041-0

Liepert, J., Classen, J., Cohen, L. G., & Hallett, M. (1998). Task-dependent changes of intracortical inhibition. *Experimental Brain Research, 118*(3), 421–426. https://doi.org/10.1007/s002210050296

Mann, E. O., & Paulsen, O. (2007). Role of GABAergic inhibition in hippocampal network oscillations. *Trends in Neurosciences, 30*(7), 343–349. https://doi.org/10.1016/j.tins.2007.05.003

Masumoto, J., & Inui, N. (2013). Two heads are better than one: Both complementary and synchronous strategies facilitate joint action. *Journal of Neurophysiology, 109*(5), 1307–1314. https://doi.org/10.1152/jn.00776.2012

Masumoto, J., & Inui, N. (2014). Effects of speech on both complementary and synchronous strategies in joint action. *Experimental Brain Research, 232*(7), 2421–2429. https://doi.org/10.1007/s00221-014-3941-x

Mitkidis, P., McGraw, J. J., Roepstorff, A., & Wallot, S. (2015). Building trust: Heart rate synchrony and arousal during joint action increased by public goods game. *Physiology & Behavior, 149*, 101–106. https://doi.org/10.1016/j.physbeh.2015.05.033

Müller, V., & Lindenberger, U. (2011). Cardiac and respiratory patterns synchronize between persons during choir singing. *Plos One, 6*(9). https://doi.org/10.1371/journal.pone.0024893

Mussi, D. R., Marino, B. F. M., & Riggio, L. (2015). The influence of social and nonsocial variables on the Simon effect. *Experimental Psychology*. https://doi.org/10.1027/1618-3169/a000292

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 (November).

Neubert, F. X., Mars, R. B., Olivier, E., & Rushworth, M. F. S. (2011). Modulation of short intra-cortical inhibition during action reprogramming. *Experimental Brain Research, 211*(2), 265–276. https://doi.org/10.1007/s00221-011-2682-3

Nicoll, R. A. (2004). My close encounter with GABAB receptors. *Biochemical Pharmacology, 68*(8), 1667–1674. https://doi.org/10.1016/j.bcp.2004.07.024

Novembre, G., Knoblich, G., Dunne, L., & Keller, P. E. (2017). Interpersonal synchrony enhanced through 20 Hz phase-coupled dual brain stimulation. *Social Cognitive and Affective Neuroscience Electronic Resource, 12*(4), 662. https://doi.org/10.1093/scan/nsw172

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

Pesquita, A., Whitwell, R. L., & Enns, J. T. (2018). Predictive joint-action model: A hierarchical predictive approach to human cooperation. *Psychonomic Bulletin & Review*. https://doi.org/10.3758/s13423-017-1393-6

Pezzulo, G., Donnarumma, F., & Dindo, H. (2013). Human sensorimotor communication: A theory of signaling in online social interactions. *Plos One, 8*(11). https://doi.org/10.1371/journal.pone.0079876

Pezzulo, G., Roche, L., & Saint-Bauzel, L. (2019). *Haptic communication optimises joint decisions and affords implicit confidence sharing*.

Poncer, J. C., McKinney, R. A., Gáhwiler, B. H., & Thompson, S. M. (2000). Differential control of GABA release at synapses from distinct interneurons in rat hippocampus. *Journal of Physiology, Paris*. https://doi.org/10.1111/j.1469-7793.2000.00123.x

Reed, K., Peshkin, M., Hartmann, M. J., Grabowecky, M., Patton, J., & Yishton, P. M. (2006). Haptically linked dyads are two motor-control systems better than one? *Psychological Science, 17*(5), 365–366. https://doi.org/10.1111/j.1467-9280.2006.01712.x

Richardson, M. J., Marsh, K. L., Isenhower, R. W., Goodman, J. R. L., & Schmidt, R. C. (2007). Rocking together: Dynamics of intentional and unintentional interpersonal coordination. *Human Movement Science, 26*(6), 867–891. https://doi.org/10.1016/J.HUMOV.2007.07.002

Ridding, M. C., Taylor, J. L., & Rothwell, J. C. (1995). The effect of voluntary contraction on cortico-cortical inhibition in human motor cortex. *The Journal of Physiology, 487*(2), 541–548. https://doi.org/10.1113/jphysiol.1995.sp020898

Rossi, S., Hallett, M., Rossini, P. M., Pascual-Leone, A., Avanzini, G., Bestmann, S., et al. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical Neurophysiology, 120*(12), 2008–2039. https://doi.org/10.1016/j.clinph.2009.08.016

Rossini, P. M., Barker, A. T., Berardelli, A., Caramia, M. D., Caruso, G., Cracco, R. Q., et al. (1994). Non-invasive electrical and magnetic stimulation of the brain, spinal cord and roots: Basic principles and procedures for routine clinical application. Report of an IFCN committee. *Electroencephalography and Clinical Neurophysiology, 91*(2), 79–92. https://doi.org/10.1016/0013-4694(94)90029-9

Sacheli, L. M., Aglioti, S. M., & Candidi, M. (2015). *Social cues to joint actions: The role of shared goals. Frontiers in Psychology*. https://doi.org/10.3389/fpsyg.2015.01034

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

Sacheli, L. M., Verga, C., Arcangeli, E., Banfi, G., Tettamanti, M., & Paulesu, E. (2019). How task interactivity shapes action observation. *Cerebral Cortex, 29*(12), 5302–5314. https://doi.org/10.1093/cercor/bhz205

Säisänen, L., Pirinen, E., Teitti, S., Könönen, M., Julkunen, P., Määttä, S., et al. (2008). Factors influencing cortical silent period: Optimized stimulus location, intensity and muscle contraction. *Journal of Neuroscience Methods, 169*(1), 231–238. https://doi.org/10.1016/j.jneumeth.2007.12.005

Sartori, L., Becchio, C., Bara, B. G., & Castiello, U. (2009). Does the intention to communicate affect action kinematics? *Consciousness and Cognition*. https://doi.org/10.1016/j.concog.2009.06.004

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

Sebanz, N., Bekkering, H., & Knoblich, G. (2006). Joint action: Bodies and minds moving together. *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2005.12.009

Sebanz, N., & Knoblich, G. (2009). Prediction in joint action: What, when, and where. *Topics in Cognitive Science, 1*(2), 353–367. https://doi.org/10.1111/j.1756-8765.2009.01024.x

Sohal, V. S., Zhang, F., Yizhar, O., & Deisseroth, K. (2009). Parvalbumin neurons and gamma rhythms enhance cortical circuit performance. *Nature*. https://doi.org/10.1038/nature07991

Sohn, Y. H., Wiltz, K., & Hallett, M. (2002). Effect of volitional inhibition on cortical inhibitory mechanisms. *Journal of Neurophysiology, 88*(1).

Soriano, M., Cavallo, A., D'Ausilio, A., Becchio, C., & Fadiga, L. (2018). Movement kinematics drive chain selection toward intention detection. *Proceedings of the National Academy of Sciences of the United States of America, 115*(41), 10452–10457. https://doi.org/10.1073/pnas.1809825115

Stinear, C. M., & Byblow, W. D. (2003). Role of intracortical inhibition in selective hand muscle activation. *Journal of Neurophysiology, 89*(4), 2014–2020. https://doi.org/10.1152/jn.00925.2002

Stinear, C. M., & Byblow, W. D. (2004a). Impaired modulation of intracortical inhibition in focal hand dystonia. *Cerebral Cortex, 14*(5), 555–561. https://doi.org/10.1093/cercor/bhh017

Stinear, C. M., & Byblow, W. D. (2004b). Modulation of corticospinal excitability and intracortical inhibition during motor imagery is task-dependent. *Experimental Brain Research, 157*(3), 351–358. https://doi.org/10.1007/s00221-004-1851-z

Takagi, A., Beckers, N., & Burdet, E. (2016). Motion plan changes predictably in dyadic reaching. *Plos One, 11*(12), 1–15. https://doi.org/10.1371/journal.pone.0167314

Takagi, A., Ganesh, G., Yoshioka, T., Kawato, M., & Burdet, E. (2017). Physically interacting individuals estimate the partner's goal to enhance their movements. *Nature Human Behaviour*. https://doi.org/10.1038/s41562-017-0054

Takagi, A., Usai, F., Ganesh, G., Sanguineti, V., & Burdet, E. (2018). Haptic communication between humans is tuned by the hard or soft mechanics of interaction. *Plos Computational Biology, 14*(3), 1–17. https://doi.org/10.1371/journal.pcbi.1005971

Tamás, G., Lörincz, A., Simon, A., & Szabadics, J. (2003). Identified sources and targets of slow inhibition in the neocortex. *Science, 299*(5614), 1902–1905. https://doi.org/10.1126/science.1082053

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

Tandonnet, C., Garry, M. I., & Summers, J. J. (2010). Cortical activation during temporal preparation assessed by transcranial magnetic stimulation. *Biological Psychology, 85*(3), 481–486. https://doi.org/10.1016/j.biopsycho.2010.08.016

Tergau, F., Wanschura, V., Canelo, M., Wischer, S., Wassermann, E. M., Ziemann, U., et al. (1999). Complete suppression of voluntary motor drive during the silent period after transcranial magnetic stimulation. *Experimental Brain Research, 124*(4), 447–454. https://doi.org/10.1007/s002210050640

The MathWorks, I. (2015). *MATLAB*. MA, USA: Natick. https://doi.org/10.1201/9781420034950

Tritsch, N. X., Granger, A. J., & Sabatini, B. L. (2016). Mechanisms and functions of GABA co-release. *Nature Reviews Neuroscience, 17*(3), 139–145. https://doi.org/10.1038/nrn.2015.21

Van der Wel, R. P. R. D., Knoblich, G., & Sebanz, N. (2011). Let the force Be with us: Dyads exploit haptic coupling for coordination. *Journal of Experimental Psychology. Human Perception and Performance, 37*(5), 1420–1431. https://doi.org/10.1037/a0022337

Vesper, C., & Richardson, M. J. (2014). Strategic communication and behavioral coupling in asymmetric joint action. *Experimental Brain Research*. https://doi.org/10.1007/s00221-014-3982-1

van der Weiden, A., Aarts, H., Prikken, M., & van Haren, N. E. M. (2016). Individual differences in action co-representation: Not personal distress or subclinical psychotic experiences but sex composition modulates joint action performance. *Experimental Brain Research, 234*(2), 499–510. https://doi.org/10.1007/s00221-015-4475-6

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, Paris, 517*(2), 591–597. https://doi.org/10.1111/j.1469-7793.1999.0591t.x

Whittington, M. A., Traub, R. D., Kopell, N., Ermentrout, B., & Buhl, E. H. (2000). Inhibition-based rhythms: Experimental and mathematical observations on network dynamics. *International Journal of Psychophysiology*. https://doi.org/10.1016/S0167-8760(00)00173-2

Ziemann, U., Lönnecker, S., Steinhoff, B. J., & Paulus, W. (1996). The effect of lorazepam on the motor cortical excitability in man. *Experimental Brain Research, 109*(1), 127–135. https://doi.org/10.1007/BF00228633