

Corticospinal excitability during motor preparation: a comparison among execution, voluntary inhibition, and observation of an interceptive task

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 Corticospinal excitability during motor preparation: a comparison among execution, voluntary inhibition, and observation of an interceptive task

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ABSTRACT

The present work evaluated in human subjects, by transcranial magnetic stimulation, the modulation of corticospinal excitability during execution, voluntary inhibition, and observation of an interceptive task. To this purpose, the time-course of corticospinal excitability was measured before (-200 ms), at the instant of (0 ms), and after (+100 ms, +200 ms) the releasing of a to-be-caught target, before any recordable muscle activity. The motor task didn't require any reaching movement and the time-to-contact was predictable on the basis of target releasing instant. Results showed that the modulation of the corticospinal activity is different in the three experimental conditions. In particular, during execution, corticospinal activity increased with respect to baseline at -200 ms and +200 ms but not in the period immediately following target release (0 ms, +100 ms), probably because of a readiness to react effect. During voluntary inhibition, corticospinal activity never differed from baseline except for an inhibition present at +200 ms, a result commonly found in no-go experiments, likely due to the necessity to prevent actual execution. Finally, no modulation of corticospinal excitability was found during observation, thus supporting the idea that the involvement of the motor system during action observation (mirror-neuron mechanism) is functionally different from motor preparation.



INTRODUCTION

The idea that the motor system plays an important role in cognitive phenomena has been largely developed in the last fifteen years. In particular, the discovery in monkey's premotor cortex of visuomotor neurons coding not only action execution but also action observation (mirror neurons), and the evidence that, in humans, action observation and action execution share a similar network of cortical areas (see Rizzolatti & Craighero, 2004) have led to the hypothesis that motor representations are always addressed during the perception of others' action (Rizzolatti et al., 2001). Evidence in favor of this idea comes from a long series of psychophysical (Brass et al., 2000; Craighero et al., 2002), brain imaging (Rizzolatti et al., 1996; Buccino et al., 2001), and electrophysiological (Hari et al., 1998; Cochin et al., 1999) studies on humans. However, the only experimental technique allowing to demonstrate that the motor cortex dynamically replicates the observed actions, as if they were executed by the observer, is transcranial magnetic stimulation (TMS). TMS instantaneously estimates corticospinal (CS) excitability by measuring motor evoked potentials (MEPs) from the activated muscles and by comparing their amplitude among various experimental conditions. TMS has been extensively used to address this issue and results indicate that, when we observe another individual acting, our motor system replicates, under threshold, the observed action in a strictly congruent fashion (Fadiga et al, 1995; Montagna et al., 2005) and this facilitation is temporally coupled with the dynamics of the observed action (Gangitano et al., 2001). In this direction points an interesting experiment by Borroni and colleagues (Borroni et al., 2005) which analytically investigates the time course and the phase relation between observed movement and observer's motor facilitation. The authors asked subjects to watch a cyclic flexion-extension movement of the wrist, executed at a constant frequency. During observation, observers' MEPs were modulated with identical period as the observed movement and the modulation was anticipated in phase, of the same amount of time by which electrical activation of muscles anticipates the actual movement. The interpretation of these results was that, during observation, corticospinal pathways are modulated and replicate with high temporal fidelity the motor commands needed to execute the observed movement. An alternative explanation of these results is that the anticipated MEP modulation does not indicate a specific effect due to the observation of a cyclic movement, but could be due to a more unspecific involvement of the observer's motor system, reflecting the preparatory phase of the observed action. This hypothesis is supported by electroencephalographic data showing that a readiness potential, a typical marker of motor preparation, can be recoded over the scalp of subjects observing predictable grasping movements even before movement initiation (Kilner et al., 2004).

To test these alternative explanations, we estimated individuals' corticospinal facilitation at different time intervals during the phase immediately preceding an interceptive task of a falling object, in three different experimental conditions: when participants were required to catch a falling object, when they were asked to observe an agent catching it, and when they had to voluntarily refrain from catching it. The interceptive task was chosen because the preparatory phase is intrinsically well separated from the executive one and the time-to-contact is constantly related to the instant of release of the falling object.

MATERIALS AND METHODS

Participants

Fourteen right-handed participants (4 males, 10 females) with age between 22 and 29 (mean age: 23.4) participated in the study. All volunteers were right handed, according to the Oldfield handedness inventory (Oldfield, 1971), did not present any neurological, muscular or cognitive disorder, and gave their written informed consent. The study conformed to the principles of the Declaration of Helsinki and was approved by the local Ethical Committee.

Procedure

Participants were comfortably seated on an armchair with their right forearm and wrist reposing on the armrest. They were requested to maintain their right hand semipronated and shaped in a vertical grip posture with their thumb opposing the other fingers (reference posture). Participants were asked to maintain the reference posture, keeping their hand as much relaxed as possible, during the whole experiment, independently from the experimental condition.

The motor task consisted in grasping at its horizontal midline a 0.5 m aluminum tube (diameter = 2 cm), sliding down with few friction (velocity at interception about 4.4m/s) along а 2 m staff located between individual's thumb and fingers (see Fig. 1). Therefore, to catch the tube no reaching movement was required but only the closing of the fingers with the correct timing to intercept it. The target was maintained at the top of the staff by a computer-driven electromagnet so that its horizontal midline, marked with a black line, was placed at 1 m above participant's hand.

At the beginning of each trial, the positioning of the tube at the top of the staff indicated the beginning of the ready-state (variable duration between 1 and 10 seconds) and participants were waiting the release of the target which was actuated by the experimenter by pressing a keyboard key. Independently from the experimental condition, the release of the target was always accompanied by a beep generated by the computer. Since the distance covered by the falling tube was fixed, time-to-contact was constant (about 400 ms) with respect to its release

The experiment consisted in a mapping session, followed by an experimental session subdivided into three blocks:

Execution, Observation and No-go conditions. The Execution block was always presented first while the order of the two others was randomized.

In the experimental session, for each experimental condition, we used four stimulation times (STs) relative to target release (-200 ms, 0 ms, +100 ms and +200 ms) (see Fig. 2). Each ST was repeated eight times and randomly presented. Fifteen trials without stimulation (No TMS) were inter-mixed with the other trials to avoid TMS expectation. The *Execution* condition was always presented first, while the order of presentation of the other two conditions was counterbalanced among participants. At the beginning of each experimental condition, eight magnetic pulses were delivered to obtain a baseline estimation of corticospinal activation level, while participants were asked to maintain their eyes closed and to keep their hand relaxed in the reference posture.

In sum, each participant was submitted to 165 trials: 3 experimental conditions x 55 trials [8 baseline trials + (4 ST x 8 repetitions) + 15 No TMS trials].

Execution condition: The staff was located between participant's thumb and fingers. Participants were asked to catch the falling tube in correspondence of its horizontal midline.

Observation condition: Participants were asked to carefully observe an actor catching the falling tube. The distance between the participant and the actor was set to allow the participant to see the entire scene (1.5 m). The staff was located between actor's thumb and fingers, and participants were asked to maintain their right hand as much relaxed as possible in the reference posture. To ensure that participants were really focusing their attention on the agent's action, at the beginning of the *Observation* condition they were informed that occasionally they would be requested to report on agent's catching accuracy. Participants had to answer by saying "yes" (correct) or "no" (not correct) trying to maintain a fixed head. The demands occurred in no more than a couple of times for each participant (to avoid as much as possible movement artifacts) and they were concentrated at the beginning of the experimental block (to deceive subjects on the number of demands)

No-go condition. The staff was located between participant's thumb and fingers. Participants were asked to pay attention to the falling tube but to refrain from catching it, continuing to maintain their hand as much relaxed as possible in the reference posture.

TMS and EMG recordings

During mapping and experimental sessions participants' left primary motor cortex was stimulated using a Magstim 200 Mono Pulse magnetic stimulator (Magstim Co., Whitland, Wales, UK). Monophasic magnetic stimuli were

delivered through a figure of eight coil with external loop diameter of 7cm. Motor-evoked potentials (MEPs) were recorded from the right First Dorsal Interosseus (FDI) muscle by using 6 mm Ag-AgCl surface electrodes (Kendall GmbH, Germany) glued to the participants' skin according to a tendon-belly bipolar disposition.

During the mapping session, magnetic stimuli were applied on predetermined positions of a one-centimeter grid drawn on a latex swimming cap worn by participants. The coordinate origin was located at the Cz reference point determined according to the International 10–20 EEG system. The cortical representation of FDI was initially assessed with the stimulator intensity regulated at 70% of its maximum power (2.2T). After detecting the point showing the highest evoked FDI response (hot-spot), the intensity of stimulation was gradually reduced and the FDI rest motor threshold (the minimum stimulation intensity that produce a MEP on half of the trials, see (Rossini et al., 1994)) was established.

During the experimental session, the coil was placed tangentially to the skull with the handle pointing medially and it was stably maintained at the FDI hot-spot by an articulated arm (Manfrotto, Italy). Stimulation intensity was set at 120% of the rest motor threshold. At least 10s separated two successive TMS pulses. Such a rate insures that no long term changes in corticospinal excitability are induced by the TMS pulse repetition, as demonstrated by Chen et al. (1997).

For all the experimental conditions, we recorded EMG signals from -400 ms to +600 ms relative to target release. The EMG patterns were band-pass filtered (50-1000Hz), digitized (2000Hz) and stored on a computer for off-line analysis. To assess the possible presence of an EMG activity before TMS, the amplitude of the rectified EMG signal recorded in the interval from -20 ms to -5 ms relative to the TMS pulse was computed.

Only for the Execution condition a Friedman repeated measures ANOVA on ranks applied on background activity revealed a significant difference in pre-pulse EMG activity (p < 0.05). Post-hoc analysis showed that this effect was explained by a high level of EMG background activity 200 ms after target release. In consequence, six out of the fourteen subjects that presented a significant increase in background EMG activity at 200 ms relative to rest (P<0.05, T-test or Mann-Whitney rank sum test when normality or equal variance tests failed) were removed from the analysis. No significant difference in background EMG activity was found in the other experimental conditions.

Therefore, data are reported on eight participants for the Execution condition and on fourteen participants for the other experimental conditions.

Finally, we checked for MEPs values that could be considered as outliers independently of a high level of EMG activity. For each participant, outliers were defined as values exceeding a threshold computed as: $Q3 + 1.5 \times (Q3 - Q1)$ (with Q1 and Q3 respectively the lower and the upper quartiles of the distribution) and were removed from the averaging.

Data analyses

Catching accuracy (CA) gives an indication on participant's performance in catching the target, relatively to the position of the hand with respect to the black line marking target's horizontal midline (i.e., below, above, in correspondence of). It was trial by trial on-line visually judged by the experimenter.

Reaction time (RT) corresponds to the time interval between target release and the onset of FDI muscle activity. EMG onset was defined as the instant at which, proceeding backwards from the time at which maximal EMG amplitude was recorded, amplitude decreased below background activity plus two standard deviations.

Contact time (CT) corresponds to the time interval between target release and the contact between the hand and the target. The instant of contact was provided by the closing of an electrical circuit including the participant and the target, powered by a 4.5V battery.

MEPs are defined as the area underlying the EMG rectified signal recorded from 21 ms to 36ms after single TMS pulse administration. For each participant, we firstly calculated the MEP relative to each trial and then the averaged individual normalized values (Z scores) for each experimental condition.

CA, RT and CT have been computed for Execution condition only, while MEPs have been calculated for all three experimental conditions.

RESULTS

Catching accuracy

Participants grasped the target in about 96% of trials. In average, they caught the bar too early in about 52% of trials (fingers below the black line), too late in about 21% (fingers above the black line), and successfully in about 23% of the trials (in correspondence of the black line). Catching accuracy was not significantly influenced by the different stimulation times.

Reaction time

RTs were computed for conditions in which TMS-related artefacts and evoked potentials did not interfere with the computation (No TMS, -200 ms ST, 0 ms ST).

For No TMS, RTs were 236 ± 12 ms, for -200 ms ST, RTs were 258 ± 16 ms and for 0 ms ST, RTs were 232 ± 13 ms. Within-subjects one-way ANOVA (three levels: No TMS, -200 ms, 0 ms,) revealed a significant effect (F(4,47) = 2.73, p<0.05) of stimulation on RTs; however, post-hoc analysis (Bonferroni T-tests) failed to show any significant

differences between conditions (for all comparisons p > 0.05).

Contact time

Within-subjects one-way ANOVA (five levels: -200 ms, 0 ms, +100 ms, +200 ms, No TMS) revealed a significant effect of stimulation time on CT (F(4,52)=3.28; p<0.05). Post-hoc analysis (Bonferroni T-test) showed that contact time relative to -200 ms ST (410 ± 3ms) was significantly longer (p < 0.05) than contact time relative to No TMS trials (398 ± 2 ms). Contact time relative to 0 ms ST (404 ± 3 ms), +100 ms ST (404 ± 3 ms) and +200 ms ST (403 ± 3 ms) did not significantly differ each other (p > 0.05) and they did not significantly differ from -200 ms ST and No TMS contact time (p > 0.05).

Motor Evoked Potentials

Examples of representative individual MEP traces and their corresponding average traces are plotted in Fig. 3. A quantification modulation of the MEP amplitude visible on this figure is shown on Fig. 4 that presents the average values of MEPs area (z-scores) for the different experimental conditions. For the *Execution* condition, within-subjects one-way ANOVA (Five levels: -200 ms, 0 ms, +100 ms, +200 ms, No TMS) revealed a significant main effect of stimulation time on MEPs (F(4,28) = 4.53; p<0.006). Post-hoc analysis (Bonferroni T-test, p<0.05) revealed that MEPs recorded at -200 ms ST and +200 ST were significantly larger (p > 0.05) than those recorded during baseline, while MEPs recorded at 0 ms ST and +100 ms ST did not significantly differ from baseline (p>0.05). Despite there was a trend for a decrease of MEP amplitude from -200 ms ST to +100 ms ST, the other comparisons did not reach the significant level (p>0.05).

For the *No-go* condition, a main effect of stimulation time on MEPs area was also significant (F(4,52) = 2.86, p < 0.05). The amplitude that initially was above baseline level decreased continuously from -200 ms ST to +200 ms ST. However, post-hoc analysis (Bonferroni T-test, p<0.05) showed that only MEPs recorded at +200 ST were significantly smaller (p<0.05) than those recorded at -200 ms ST.

For the *Observation* condition, no significant effect of stimulation time on MEPs area was found (F(4,52) = 1.53, p > 0.05).

DISCUSSION

The main aim of the present study was to investigate if during observation of the preparatory phase of an action, immediately preceding its execution, the corticospinal system of the observer is modulated as it happens during action execution. This question is important to understand the dynamics underlying motor representation activation during action observation, and to clarify their functional properties. To this purpose we tested corticospinal excitability during

execution, observation and voluntary inhibition of the catching of a falling tube, sliding down a vertical staff placed in the space between participant's fingers. From target releasing, time-to-contact was constant, since the distance covered by the target was fixed. Consequently, the employed motor task dealt with the decision to move upon an uncertain event (the target releasing instant) to which a fixed event (the time-to-contact instant) was associated.

It has been proposed that overt actions are the last part of a continuum that would contain a covert phase during which action is internally simulated (Jeannerod, 2001). The generation of this "internal" action would share all the characteristics of the overt one except the execution phase. The experimental evidence indicating that the motor system is not activated only during action execution but also during any cognitive activity related to action performance, such as motor imagery and observation of others' actions (see Fadiga & Craighero, 2004), has led to the idea that these motor-related mental states could be functionally equivalent to motor preparation (Jeannerod, 1994). In other words, the involvement of the motor system during action observation is a consequence of an unconscious will to prepare to act, successively inhibited. A different interpretation of the motor system involvement during "cognitive" motor-related tasks is that its role in visuomotor transformations is crucial for the perception and understanding of goal-directed action. Every time the idea or the goal of an action is evoked, action-related motor representations are automatically addressed, allowing the individual to have access to his/her own motor knowledge to motorically understand the event (Fadiga & Craighero, 2004; Rizzolatti & Craighero, 2004).

Therefore, if during action observation the involvement of the motor system is due to a motor preparation successively inhibited, observer's corticospinal excitability should be modulated also during the actor's motor preparation phase, especially in a task, like object interception, in which to have a successful performance the agent necessarily needs to prepare it in advance (see Lacquaniti & Maioli, 1989). Furthermore, no many differences should be present between action execution and voluntary inhibition of action execution. On the contrary, if motor system involvement is due to its automatic activation in consequence of visuomotor transformations, not necessarily the execution, the voluntary inhibition and the observation of an interceptive task, during its preparatory phase, should modulate the corticospinal system in the same way, since corticospinal modulation is estimated when no visible movement is present, yet. There are, however, some indications that the role of the motor system during action observation is not that of a "passive perceiver" but more that of an "active interpreter" (Fadiga & Craighero, 2006), and that the actual visual input is not strictly necessary to evoke the motor representation of the action. One example of this interpretative role of the motor system is given by a single neuron recording experiment (Umilta *et al.*, 2001) demonstrating that mirror neurons in monkeys still fire during observation of object grasping even when the contact between the hand and the object is hidden and only the reaching movement is visible. However, neuron activity is present only when the goal of the action is plausible. Therefore, this last interpretation of the role of the motor system

during action-related cognitive functions is less dramatic than the alternative one in predicting similarities or differences in corticospinal modulation between execution and observation during the preparatory phase of the action.

Present results show that corticospinal excitability estimated during the preparatory phase of an object interception is modulated during action execution and voluntary inhibition, but not during action observation. Furthermore, corticospinal excitability recorded during action execution and inhibition present a very different pattern of modulation, indicating that to prepare to execute when going to actually execute can't be equated to prepare to execute when no actual execution is followed.

In particular, our results show that, during action execution, corticospinal excitability is differently modulated with respect to the instant of target releasing. It increased with respect to baseline while waiting for target releasing (-200 ms ST), it decreased immediately after it (0 ms, +100 ms ST), and it increased again just before the initiation of muscle contraction (+200 ms ST). The decrease in excitability found immediately after target release is in accord with previous studies showing that the excitability of the corticospinal structures is minimal when the subject is optimally ready to react (Hasbroucq et al., 1997). This decrement in corticospinal excitability has been interpreted as an adaptive mechanism to increase the sensitivity of the corticospinal tract to the forthcoming voluntary command (Davranche et al., 2007). Moreover, the increase in excitability recorded just before voluntary muscle contraction is in accord with recent results by Nikolova et al. (2006). These authors tested the effect of TMS on motor cortex excitability in the premovement period at different delays after a visual command for isometric right hand index finger abduction. The MEPs recorded from the right first dorsal interosseous were strongly augmented in a period of 90-100 ms before the voluntary EMG onset. This result confirmed previous findings (Rossini et al., 1995; Leocani et al., 2000) indicating that in a simple reaction time paradigm, progressive increments of MEPs amplitude are detectable 80-120 ms before the onset of EMG activity. It is to note that, in the present task, muscle contraction was not a mere response to a go-signal, as in simple reaction time paradigms, but its onset was determined by the subject according to time-to-contact estimation. Our findings suggest that this internal signal would occur between 100 (+100 ms ST decreasing) and 200 ms (+200 ms ST increasing) after target releasing. Given the fact that EMG onset was around 240 ms after target releasing, this indicates that the internal signal to execute the fingers closure should occur in the temporal window comprised between 40 ms and 140 ms before EMG onset.

Regarding contact time, a delay was observed especially when TMS pulse was delivered 200 ms before target releasing (-200 ms ST). This result is in agreement with several studies indicating that the execution of the motor response in a simple reaction time task can be delayed by transcranial magnetic stimulation (Day *et al.*, 1989; Rothwell *et al.*, 1989; Palmer *et al.*, 1994; Ziemann *et al.*, 1997).

In the No-go condition, in which subjects were asked to pay attention to the falling tube but to refrain themselves

from catching it, MEPs recorded at +200 ST were significantly smaller than those recorded at -200 ST. The time at which we found MEPs inhibition corresponded approximately to the mean EMG onset during Execution condition (240 ms after target releasing). This result is in accord with papers evaluating corticospinal excitability during reaction time in no-go paradigms. Leocani et al. (2000) asked subjects to extend their right or left thumb in response to a specific tone and to abstain from responding when a different tone was presented. In the no-go trials, MEPs were inhibited, both in the muscle involved in the task and in its homologous one, 200-300 ms after the acoustic signal, corresponding approximately to the mean RT found in the go trials. The authors interpreted this finding as evidence that in no-go trials there is not just a lack of efferent activation, but the inhibition of both the agonist and the antagonist muscle of the same spinal segment. These results are in agreement with those previously reported by Hoshiyama et al. (1997) showing that MEPs of both wrist extensor and flexor muscles were significantly attenuated during the period of 100-200 ms after the no-go signal, in a task requiring the extension of the right wrist according to the go, no-go and control signals. Both studies suggest that the inhibitory effect in a no-go task is non-specific to the target muscles. Leocani et al. (2000) proposed that reduced MEPs in no-go trials could result from inhibition of the corticospinal output by control centres such as the premotor area, or could be mediated by descending inhibitory pathways at the spinal level.

Regarding the *Observation* condition, in which participants where asked to observe the interceptive task executed by an actor, our results indicate no significant modulation of MEPs amplitude during observation of the preparation phase of the action. It is to note that at the instant at which TMS was applied, subjects were observing the agent ready to catch the target, but absolutely immobile. In fact, the latest ST was +200 ms, and the EMG onset (when, however, the movement was not yet visible) was around 240 ms after target releasing. This results suggest that, in order to activate motor representations during action observation the actual execution of the action, even if not visible (see Umilta *et al.*, 2001), is necessary, further supporting that observer's motor system involvement is temporally strictly related to the specific phase of the movement actually perceived (Gangitano *et al.*, 2001; Gangitano *et al.*, 2004; Borroni *et al.*, 2005).

Therefore, present results indicate that the involvement of the motor system during the preparatory phase of an interceptive task differs according to the tested experimental conditions. In particular, the execution and the voluntary inhibition of this action determine a completely different modulation of the motor system. During *Execution* condition corticospinal activity is almost always increased with respect to the baseline, a part from the period immediately after target releasing. This decreasing in excitability is considered, on the basis of previous studies, an indication of the readiness to react. During *No-go* condition corticospinal activity doesn't differ from baseline a part from a significant inhibition at the time approximately corresponding to the mean EMG onset during actual execution, indicating that

participants were effortfully paying attention to the falling target. Finally, the mere observation of an agent preparing to execute an interceptive task, when the exact instant of action execution is perfectly known by the observer, is not sufficient to elicit a corticospinal modulation. Consequently, present results do not support the hypothesis that the motor system involvement during action observation is functionally equivalent to motor preparation, furthermore, they suggest that motor representation activation is present in the observer only during the perception of the actual execution of another individual's action.

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FIGURE LEGENDS

Figure 1. Experimental set-up. A tube was sliding along a vertical staff, passing between the participants thumb and fingers. The participants had to intercept (*Execution* condition) the bar, to observe a real actor intercepting the bar (*Observation* condition) or just looking at the falling of the tube (*No-go* condition).

Figure 2. Schematic representation of the time course of experimental events. Arrows indicate the four stimulation times (ST) during *Observation*, *Execution* and *No-go* conditions. The baseline (BL) of the EMG activity was calculated before each ST and the area of the Motor Evoked Potential (MEP) after each ST. They are presented only once on the figures for clarity.

Figure 3. Representative examples of individual motor evoked potentials for each stimulation time and each experimental condition. For each experimental condition, the overlays of all trials of one subject are presented on the top raw with the corresponding average traces on the bottom raw. The right part of the figure present the rectified population average traces for each condition.

Figure 4. Time course relative to bar release (t = 0 ms) of Z-score of averaged FDI MEP area during execution (left), inhibition (middle) and observation (right) of target interception. Vertical bars represent standard error. Isolated asterisks denote statistically significant difference (p < 0.05) relative to respective baseline.



Figure 1. Experimental set-up. A tube was sliding along a vertical staff, passing between the participants thumb and fingers. The participants had to intercept (Execution condition) the bar, to observe a real actor intercepting the bar (Observation condition) or just looking at the falling of the tube (No-go condition). 191x215mm (72 x 72 DPI)



Figure 2. Schematic representation of the time course of experimental events. Arrows indicate the four stimulation times (ST) during Observation, Execution and No-go conditions. The baseline (BL) of the EMG activity was calculated before each ST and the area of the Motor Evoked Potential (MEP) after each ST. They are presented only once on the figures for clarity. 397x196mm (72 x 72 DPI)



Figure 3. Representative examples of individual motor evoked potentials for each stimulation time and each experimental condition. For each experimental condition, the overlays of all trials of one subject are presented on the top raw with the corresponding average traces on the bottom raw. The right part of the figure present the rectified population average traces for each condition. 797x846mm (150 x 150 DPI)



Time of stimulation (ms)

Figure 4. Time course relative to bar release (t = 0 ms) of Z-score of averaged FDI MEP area during execution (left), inhibition (middle) and observation (right) of target interception. Vertical bars represent standard error. Isolated asterisks denote statistically significant difference (p < 0.05) relative to respective baseline.

676x308mm (150 x 150 DPI)

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