Title: The effect of type and context of sensorimotor information on corticospinal excitability

Running title: Different effects of sensorimotor information on corticospinal excitability

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Abstract

During skilled hand-object interactions, the human sensorimotor system generates predictive motor commands based on visual information and sensorimotor memories established from previous experience. Here we investigated whether predictive force scaling could be adapted to context-dependent information that is not always explicitly available. We probed the effect of motor prediction mechanisms on corticospinal excitability (CSE) with transcranial magnetic stimulation (TMS). In experiment 1, participants performed a continuous force tracking task by squeezing a manipulandum. We varied the type of visual information for predicting motor output by displaying either the actual target force curve participants had to match (sinusoidal curve condition) or the visual error between the required and exerted force (horizontal line condition). CSE was modulated by the rate of change of forces (speed) in both conditions. Force direction changes further modulated CSE but in the sinusoidal curve condition only. These findings indicate that the corticospinal output mainly reflects the ongoing motor command, but can also be modulated by less explicit contextual information. In experiment 2, we tested whether participants could accurately predict the required force scaling in a standard random weight object lifting task, which also included series of small weight increments. Results showed that participants were unable to generate accurate force predictions by extrapolating weight from the implicit series, which failed to modulate CSE, unsurprisingly. Altogether, these findings suggest that corticospinal output is modulated based on context-dependent information when mediated by explicit visual cues, but not when sensorimotor cues are presented in an implicit manner.

Highlights

- Visual cues and sensorimotor experience are key for hand-object interactions
- We investigated the underlying corticospinal excitability (CSE) changes
- Visual cues improved motor performance and modulated CSE
- CSE was partly modulated by less explicit information
- Implicit information did not improve motor performance and nor modulate CSE

Introduction

Dextrous hand object interactions necessitate appropriate and predictive planning of fingertip forces adjusted to the properties of the object (Gordon et al., 1993) as, for instance, a fragile object may be damaged when exerting too much force. When visual information indicates object weight, this allows

individuals to predictively scale their fingertip forces. For example, individuals scale their forces on well-established 'priors', such as object size (Gordon et al., 1991) and material (Baugh et al., 2012), indicating object weight. In contrast, when such visual information is absent, individuals predictively scale their forces based on prior interactions with the same or similar objects (Baugh et al., 2012; Fu et al., 2010; Gordon et al., 1993; Johansson & Westling, 1988; van Polanen & Davare, 2015), an effect that has been termed the 'sensorimotor memory'.

In daily life, motor control mechanisms might benefit from finetuning their sensorimotor predictions based on relevant environmental information instead of solely relying on object-specific properties. For instance, when moving luggage or having someone pour water into a glass you are holding, motor control mechanisms may optimize performance by relying on the most recently performed action (i.e., the sensorimotor memory, Baugh et al., 2012), but also by integrating contextual information. For instance, Mawase & Karniel (2010) argued that an individual's sensorimotor system can use information the individual is not aware of: The authors showed that individuals predictively scale their fingertip forces to a non-existent heavier weight after lifting a series of increasing weights that were implicitly presented within larger sequences primarily consisting of random weights. In Cashaback et al. (2017), participants were required to lift an object with varying weights according to a skewed probability distribution. The authors showed that participants would not scale their fingertip forces based on the previously lifted object, but rather would strategize to minimize their prediction error over many trials. In line with the latter study, other studies on hand actions have evidenced that motor control mechanisms can adapt their sensorimotor predictions towards environmental variability for minimizing the general prediction error across multiple trials (Hadjiosif & Smith, 2015; Körding et al., 2004; Landy et al., 2012; Zhang et al., 2015).

The primary motor cortex (M1) plays a pivotal role in controlling hand-object interactions. When disrupting M1 activity transiently with repetitive Transcranial Magnetic Stimulation (rTMS), individuals fail to predictively scale their fingertip forces based on sensory feedback (Chouinard et al., 2005; Parikh et al., 2020; Schabrun et al., 2008). In addition, Loh et al. (2010) showed that corticospinal excitability (CSE), probed with TMS over M1 during lift planning, reflects the weight of the previously lifted object but becomes reflective of a forthcoming weight when indicated by a visual cue. In previous work from our group, we showed that CSE modulation can reflect an object's weight distribution when indicated through action observation (Rens et al., 2021). Arguably, these studies (Loh et al., 2010; Rens et al., 2021) investigated how task requirements, indicated by visual cues, are mapped directly onto the corticospinal output while performing hand-object interactions. For instance, when visual cues indicate a heavy object,

this can be directly mapped into an increased CSE. Therefore, it is likely that, in both studies, CSE directly reflected task requirements.

To our knowledge, it is not well understood how CSE encodes hand-object interactions when task requirements cannot be directly mapped onto the motor command due to environmental uncertainty. For instance, in the study of Mawase & Karniel (2010), the question arises whether CSE modulation would represent force predictions based on an implicit series of increasing weights. Noteworthy, using different behavioral modalities, CSE has been shown to be modulated by probabilistic information. For instance, using a reaction time task, Van Elswijk et al. (2007) showed that CSE modulation increases with increasing response signal expectancy. That is, the longer it takes for the cue to appear, the more likely it is to appear, which increases CSE modulation. Using a similar reaction time paradigm, Bestmann et al. (2008) showed that CSE modulation increases in case of low entropy (i.e., low uncertainty about sampling one trial from all possible trials) and low surprise (i.e., probability of the upcoming trial on itself). Finally, using finger tapping tasks, other studies (Nojima et al., 2019; Wilkinson et al., 2010, 2016) have shown that CSE modulation is affected by probabilistic information during finger tapping tasks.

In sum, it has been shown that (a) task requirements can be mapped directly, through visual cues, to the corticospinal output for grasping actions (Loh et al., 2010; Parikh et al., 2014; Rens et al., 2021), and (b) CSE modulation can be altered by probabilistic information in both reaction time (Bestmann et al., 2008; Van Elswijk et al., 2007) and finger tapping tasks (Wilkinson et al., 2010, 2016). However, it is unknown how CSE reflects sensorimotor predictions for hand-object object interactions when environmental information cannot be directly mapped onto motor output. To address this issue, we performed two separate experiments exploring how explicit and implicit information can modulate CSE during both continuous (experiment 1) and discrete (experiment 2) hand-object interactions.

For experiment 1 we used a force tracking task and manipulated the type of visual information participants received about their ongoing motor performance. Participants were instructed to track a sinusoidal force curve by exerting increasing and decreasing force at different rates of change (slope of the curve) with their fingertips on force sensors. The type of the visual feedback was varied by displaying either the task goal, i.e. the actual force target (sinusoidal curve) participants had to match or the visual error between the required and exerted force (horizontal line). Importantly, in the sinusoidal curve condition participants could rely on both predictive mechanisms, by observing the curve's slope, and feedback-driven mechanisms, by observing their performance error (i.e., distance between the target curve and the line representing their performance). If participants would perform the task perfectly, their performance would overlap with the force target (sinusoidal curve). If they would not generate force at

all, their performance would show as a horizontal line. In this way, we argued that both prediction- and feedback-related visual cues would directly map task requirements onto the corticospinal output. In contrast, in the horizontal line condition, participants tracked the same sinusoidal force changes although the actual force target was hidden from the participants. Instead, they could only see their performance error (i.e., deviation from the sinusoidal curve) as deviations from a horizontal line. Thus, in this condition, if participants would perform the sinusoidal force tracking task perfectly, their performance would show as a horizontal line. Conversely, if participants would not exert force at all, their performance would be represented as the inverse of the sinusoidal target curve. As such, we argued that in this horizontal line condition, task requirements could not be directly mapped onto the corticospinal output as (a) force scaling requirements could not be predicted due to the force gradients (curve slope) not being visible and (b) performance error was shown in an inverse manner. Finally, TMS was applied to probe CSE during different phases (speed: fast or slow rate of change; target line: sinusoidal or horizontal; direction: up- or downscaling of fingertip forces). We argued that by manipulating the type of visual information, we could investigate how direct vs. indirect mapping of visuomotor contextual information could affect CSE modulation during continuous hand-object interactions.

Using a similar paradigm, Kimura et al. (2003) asked participants to contract and relax their elbow in a sinusoidal manner. They found that CSE increased during the contraction compared to relaxation phase, even though TMS was applied when the participants exerted the same amount of force in both phases. In line with Kimura et al. (2003), we hypothesised that, in both conditions, CSE would be larger during increasing compared to decreasing force exertion. To extend on the work of Kimura et al. (2003), we also manipulated the slope of the sinusoidal curve, resulting in slower or faster scaling of fingertip forces, to investigate sensorimotor involvement in the rate of force changes. We hypothesized that CSE modulation would be larger in the fast compared to slow condition. Importantly, if CSE modulation reflects ongoing task performance, independent of the type of visual information, CSE would be modulated similarly in the sinusoidal curve and horizontal line conditions. However, Bestmann et al. (2008) showed that CSE modulation is larger during low uncertainty. Accordingly, we hypothesized that, due to differences in the type of visual information between the target line conditions, CSE modulation would be larger when contextual information can be directly mapped onto motor output, i.e. in the sinusoidal curve condition.

For experiment 2 we used a behavioral task that was similar to Mawase & Karniel (2010). Participants lifted intermixed series of increasing and randomly ordered weights while TMS was applied during lift planning. In this experiment, we argued that sensorimotor control mechanisms could

extrapolate force requirements after the series of increasing weights, which would be reflected in changes in corticospinal output. That is, motor performance and CSE would not reflect a direct encoding of force scaling based on the last trials (i.e., the sensorimotor memory) but rather would reflect an extrapolation process for predicting force scaling based on the implicit weight increase series. As such, we hypothesized that participants would use more force when lifting the same weight after the implicit series compared to after the random series. Similarly, we hypothesized that CSE would reflect the extrapolated weight based on the series of increasing weights and not the weight of the previously lifted object (akin to Loh et al., 2010).

Methods

Participants

Thirty healthy right-handed volunteers were recruited for the experiment, of which 15 took part in experiment 1 (12 females, mean age 22±2 years) and 15 in experiment 2 (11 females, mean age 22±3 years). Two participants (one for each experiment) were excluded from analysis, causing us to have 14 participants for each experiment. The first one (female) was excluded during data processing as the motor evoked potentials (MEPs; see below) during the experiment (and thus after defining stimulation intensity) exceeded the range of our electromyography (EMG) system. The second participant (female) was excluded as even during baseline assessment of CSE she was not able to relax their hand.

All participants were right-handed (self-reported). TMS eligibility was assessed by the TMS safety screening questionnaire (Rossi et al., 2011). Participants had no known neurological or sensory impairments and had normal or corrected-to-normal vision. The study was approved by the ethical committee of UZ/KU Leuven and all participants signed an informed consent before the experiment.

Acquisition of force data

Forces were measured using a grip(-lift) manipulandum (see Figure 1). The manipulandum consisted of two force/torque sensors (ATI Nano17, ATI Industrial Automation) that were mounted on a custom-made carbon fiber basket. The total weight of the manipulandum was 1.2 N. The graspable surface (17 mm diameter and 45 mm apart) of the force sensors was covered with fine sandpaper (P600) to increase friction. In the manipulandum's basket, small objects could be placed. Force sensor data was sampled at 1 kHz frequency through a NI-USB 6343X (National Instruments, USA) which was connected to a personal computer. Measurement of forces in both experiments was performed using custom written Labview scripts (National Instruments, USA) and transferred for off-line analysis.

Figure 1. *The (grip-lift) manipulandum consisting of force sensors mounted on a carbon fibre basket as used in the experiments. In experiment 1, participants squeezed the force sensors to track a curve on a computer screen. In experiment 2, small visually identical cubes with different weights were placed in the basket to be lifted by the participants.*

Transcranial magnetic stimulation procedures

For both experiments, two Ag-Al electrodes were placed on the first dorsal interosseus muscle (FDI) in a typical belly-tendon montage. A third reference electrode was placed on the ulnar styloid processus. Electrodes were connected to a NL824 AC preamplifier (Digitimer) and a NL820A isolation amplifier (Digitimer), which in turn was connected to a micro140-3 CED (Cambridge Electronic Design). The CED was connected to a personal computer. Electromyography (EMG) recordings were amplified with a gain of 1000, high pass filtered with a frequency of 3 Hz, sampled using Signal and Spike2 software (Cambridge Electronic Design, UK) and were stored for off-line analysis. Spike2 was used for data collection in experiment 1 and Signal was used for data collection in experiment 2. The sample frequency was 1 kHz and 5 kHz in Experiment 1 and 2, respectively. A 70 mm figure-of-eight TMS coil [experiment 1: Magstim rapid 200 (Magstim Co Ltd, United Kingdom); experiment 2: DuoMag XT-100 (Deymed Diagnostic, Czech Republic)] was used to apply TMS. In both experiments, participants received TMS over M1 only. For M1 stimulation, the coil was tangentially placed over the head to induce a posterior-anterior current flow and to elicit motor evoked potentials (MEPs) in the FDI muscle. Before the experiment, we defined the optimal stimulation site (i.e., 'hotspot') and the stimulation intensity to be used in the experimental task for each participant. The hotspot was defined as the position from which MEPs with maximal amplitude were produced in the FDI muscle. The hotspot was marked on the scalp. The stimulation intensity (1mV threshold) was defined as the lowest stimulation intensity that produced MEPs equal to or greater than 1 mV in the FDI muscle in at least five out of ten consecutive trials when stimulating at the predetermined hotspot.

Specific procedures for experiment 1. The behavioural task of experiment 1 consisted of continuous force production (i.e., 'squeezing' on the F/T sensors; see below). We assessed the 1 mV threshold while participants produced a constant total grip force of 2.5 N (sum of horizontal forces applied by thumb and index finger on the force sensors). As such, the 1 mV threshold was not defined during 'rest' but during active contraction. The 1 mV threshold for experiment 1 was 42 ± 11 % (group mean ± standard error) of the maximal stimulator output.

Specific procedures for experiment 2. The behavioural task of experiment 2 consisted of an object-lifting task and TMS was applied during lift planning (i.e., before the reaching phase, thus while the hand was still relaxed on the table; see below). Accordingly, the stimulation intensity for experiment 2 was defined while participants kept their hand relaxed on the table. The 1 mV threshold was 56 ± 8 % (group mean ± standard error) of the maximum stimulator output.

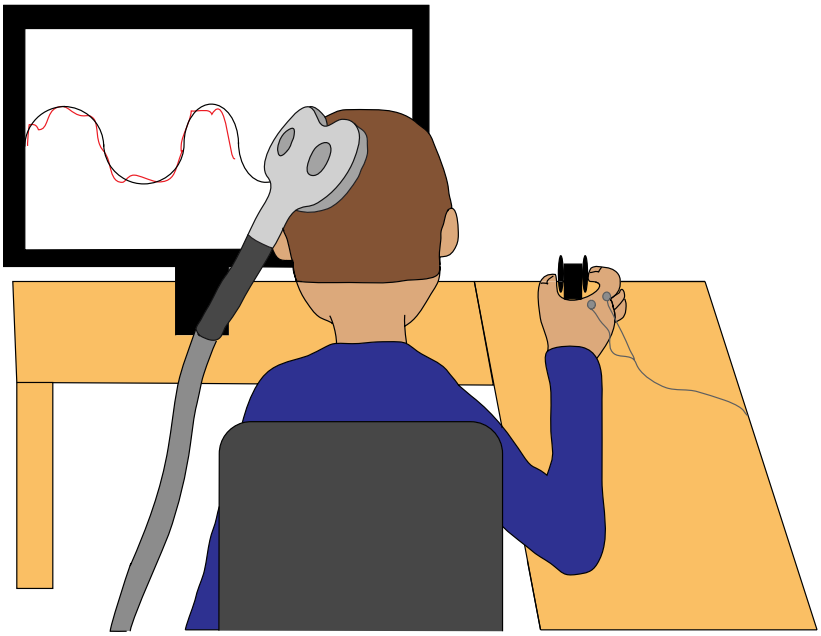

Figure 2. *Drawing of the experimental setup in experiment 1. Participants squeezed the force sensors to track a target curve on the screen with their right hand. During the task, transcranial magnetic stimulation was applied over the left motor cortex and electromyography was measured with electrodes placed on the right first dorsal interosseus muscle.*

Experiment 1

<u>Task and procedures</u>

After initial preparations (i.e., consent, questionnaires and TMS preparations), participants performed the experimental task. Participants were comfortably seated in a chair. A table was positioned

in front of them on which a computer screen was placed and the grasp-lift manipulandum was placed on another table on their right side. Participants were instructed to rest their right arm on the table and grasp the two force sensors of the manipulandum using their right thumb and index finger (precision grip). The manipulandum itself was fixed on the table to ensure it would not move during the experiment. During the experiment, the TMS-coil was held above the hotspot by an experimenter (see Figure 2 for a drawing of the set-up).

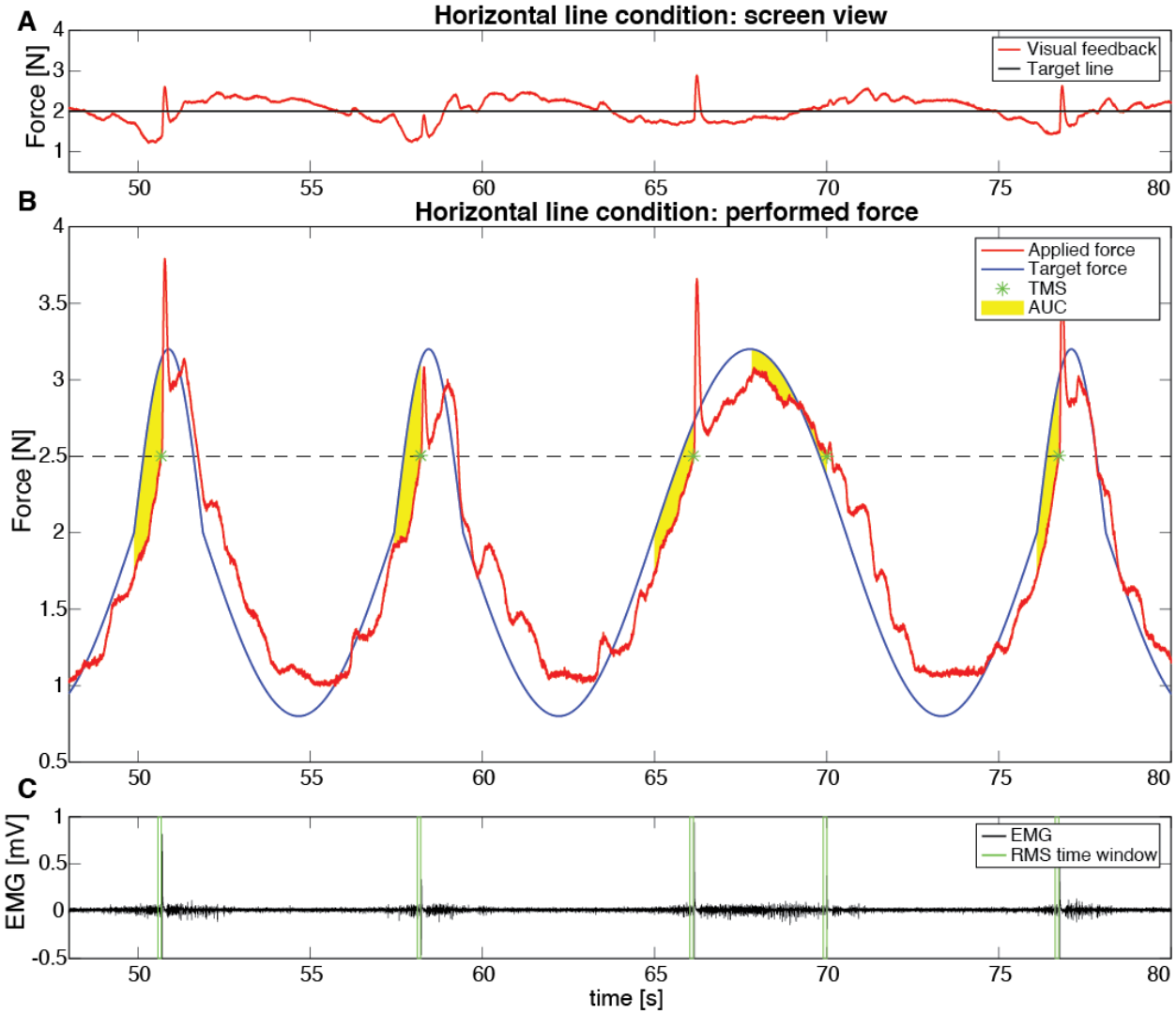

Figure 3. *Representative example of a part of a trial in the horizontal line condition.* ***A.*** *Screen view as shown to the participant during performance of the task. The black line indicates the target line and the red line represents the participant's performance as deviation in exerted force from the target line (in N).* ***B.*** *Actual performed force (red) and actual target force which was hidden from the participant (blue). The black dashed line represents the force level at which TMS was applied. A TMS event is indicated with a green asterisk. Yellow shadings indicate the area under the curve (AUC) as a measure of performance. Note that in the sinusoidal condition, the screen view looked like the blue (target) and red (performance) lines.* ***C.*** *Electromyography (EMG) data (black). The time window of 100 ms before TMS that was used to calculate the background EMG (RMS100) is indicated with green vertical lines.*

Sinusoidal curve condition. On the screen a sinusoidal target line was projected with the x- and y-axis representing time and amount of exerted force, respectively (Figure 3 top row). The target sinusoid had an amplitude of 1.2 N and was centred around 2 N. A cursor moved over the target line indicating the participant's location over time. The cursor produced a red line providing visual feedback of performance over time. Participants controlled the cursor's vertical displacement by exerting force on the force sensors. Participants could not control the cursor's horizontal displacement as the cursor moved with a constant speed over the screen. The sinusoid could have a frequency of either 0.09 ('slow' condition) or 0.25 Hz ('fast' condition) over the positive and negative half cycles which was indicated by a 'wider' or 'smaller' sinusoidal wave thus causing a more gradual or steep slope, respectively. The frequency (thus the sinusoid's width) changed pseudo-randomly when crossing the midpoint (i.e., when exerting a force equal to 2 N). In this way, four different conditions could be identified, being fast up (upscaling of forces; 0.25 Hz), fast down (downscaling; 0.25 Hz), slow up (upscaling; 0.09 Hz) and slow down (downscaling; 0.09 Hz). Participants were instructed to stay as close as possible to the target line by controlling the vertical displacement of the cursor and, thus, by sinusoidally changing the amount of force they were exerting on the force sensors. As participants could see where they were on the target line, they could anticipatorily plan to up- or downscale their forces and their speed. Optimal performance in this task would consist of sinusoidally scaling fingertip forces and would show the red trace (produced by the cursor's movement) to perfectly overlap with the sinusoidal target line. Last, TMS was applied when participants exerted 2.5 N (Figure 3B, green asterisk). As such, TMS was only applied during the positive half-cycle (considering that the sinusoid was centered around 2 N). The interval between two TMS pulses was minimally 3.5 seconds to avoid carry-over effects (Hannah, 2020).

Horizontal line condition. The experimental design was nearly identical to the sinusoidal curve condition. As such, we will only discuss those things that differed. In this task, the sinusoidal target line was not shown on the screen, but only a horizontal line was shown (Figure 3 middle row). Participants had to perform the same task of sinusoidally scaling their forces although the depicted target line was a straight horizontal line. The cursor showed the deviation from the 'hidden' sinusoidal target curve as a deviation from the horizontal line. Accordingly, participants could not perceive where they were (e.g., positive, or negative half cycle of sinusoidally scaling their forces), but they could still perceive the red trace produced by the cursor's movement. As such, participants could not anticipatorily plan their forces (e.g., by seeing that they were at the peak of the positive half cycle or whether they were performing a cycle in the slow or fast condition) but they still received on-line feedback about their performance.

Optimal performance in this task would consist of sinusoidally scaling fingertip forces but would show the red trace (produced by the cursor's movement) to overlap with the straight horizontal target line.

The top row (Figure 3A) shows a representative example of a participant's on-screen view and their performance in the horizontal line condition. The sinusoidal curve was hidden (i.e., only a target horizontal line was shown) although participants still received visual feedback about their ongoing performance. The second row of Figure 3 (Figure 3B) shows the actual sinusoidal curve, that was hidden from the participants, and the participant's performance relative to this sinusoidal curve. When a participant would perform the sinusoidal curve condition, the target curve and the feedback of the participant's performance would look like the example in Figure 3B. On this figure it can also be seen that in this example the first two and last cycles are part of the 'fast' condition, whereas the third cycle is part of the 'slow' condition.

The sinusoidal curve and horizontal line conditions were presented in a blocked design which were counterbalanced across participants. In each block, 13 trials of 30 seconds were performed (6 participants) or 5 trials of 120 seconds (9 participants). The length of the trial was changed after it became apparent that participants could easily perform trials of longer durations. Each trial consisted of a random sequence of the four conditions (frequency: slow-fast; direction: down-up).

Table 1. Events included in the analysis for each condition on average (after removal of incorrect events). Mean ± SD over participants for each condition.

	Slow up	Fast up	Slow down	Fast down
Sinusoidal curve	25.3±4.8	28.9±5.6	24.0±7.2	18.7±6.6
Horizontal line	26.1±6.0	26.2±8.3	21.7±8.6	17.5±5.0

At the start of each trial, a preparatory target line at the 2 N level was shown. The cursor took between 5 to 8 seconds (randomized) to allow participants to move the cursor to the midpoint force level at the start of the trial. This preparatory target line would transition into the experimental sinusoidal curve or horizontal line. The transition between the preparatory and experimental target line was indicated with a vertical line. Before starting the experimental task, 2 practice trials of 30 seconds were performed, and a short break was presented between the two blocks.

Data analysis

Several parameters were extracted when TMS was applied (i.e., when participants generated 2.5 N); the MEP amplitude (as defined above) was extracted in a window of 5 to 45 ms after the TMS pulse. From the EMG, we also extracted muscle activity using peak-to-peak amplitude and root mean squared activation (RMS100) in a 100 ms interval before the TMS pulse (105-5 ms before the TMS pulse) as a measure of background EMG before TMS.

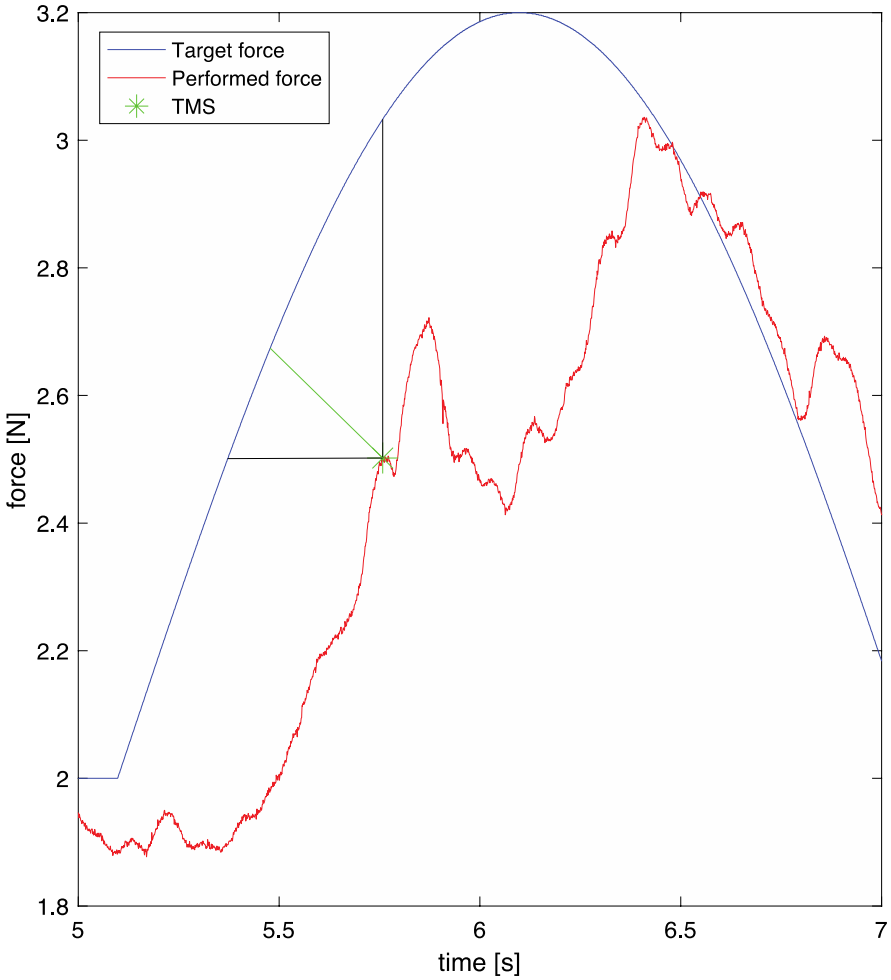

Figure 4. *Example of calculation of Euclidian distance to determine erroneous trials. The blue and red line represent the target and performed force, respectively. From the point at which the TMS was applied (green asterisk) the shortest distance to the target force was determined, which was done in 2D space incorporating both the deviation in time and force. Black lines indicate distances to the target curve if only force or time were considered.*

Although participants were instructed to keep the cursor as close as possible to the target line, they often made errors. Particularly in the horizontal line condition, participants could not rely on visual information regarding the upcoming force requirements as they could only rely on their ongoing performance (as indicated by increasing/decreasing deviations from the target horizontal line).

Accordingly, participants sometimes scaled their fingertip forces not in line with the current event (e.g., up- instead of downscaling or fast instead of slow scaling). To assess (i) which event should have been performed (up/down – fast/slow) and (ii) performance on this event, we did the following: we calculated the total error in 2D space (force-time space). This allowed us to include errors in force (too much/too little force applied at any given give) and time (where participants should have been on the curve when applying a certain amount of force). The total error for each event was defined as the shortest Euclidean distance between the target curve and the participant's force generation at the TMS event (see Figure 4). Specifically, in Figure 4, the TMS event is indicated with a green asterisk on the actual performed force (red line). The shortest distance from this asterisk to the target curve (i.e., between current performance and the target sinusoidal curve in blue) was determined. Note that in the horizontal line condition, even though participants perceived a straight horizontal target curve, we used the 'hidden' sinusoidal curve to investigate performance (i.e., participants saw on-screen Figure 3A, but their performance was quantified as in Figure 3B). We decided to include both dimensions (force and time) for assessing general performance as, for instance, participants could have been generating the appropriate amount of force although they were performing the incorrect event (e.g., up- instead of downscaling forces). As the TMS pulse was automatically triggered when participants generated 2.5 N (with a minimum 3.5 s delay between two consecutive stimulations), we had no direct control over when TMS was applied. We reasoned that if participants deviated too much in force-time space, the MEP would not reflect the current event and thus needed to be removed from analysis. Based on visual inspection of all trials, a criterion of 0.55 was used for this total error. This value of 0.55 was chosen as it closely matched the visual judgement of two observers that independently rated the individual trials. Using this criterion, 2% of all MEPs were removed. Note that we did not include this parameter (the Euclidian total error) to assess participants' overall performance but rather to reject incorrectly performed events. In addition, we also removed MEPs that were smaller than the peak-to-peak EMG in the 100 ms interval before TMS (134 trials, 4%), as such MEPs lower than background EMG activity likely reflect noise.

Last, MEPs were obtained from TMS applied at the same force level. Since EMG amplitude depends on the amount of force that is applied, the RMS100 should not differ between the conditions. However, we found that this was not always the case (see Results). To control for differential force activation, we also divided the MEP values by the RMS100 before the TMS pulse and analysed this corrected value (MEP_{EMG}) separately.

To investigate actual participants' performance, we relied on force-related parameters. The average force rate (time differentiated force) was determined between 300 ms before the TMS pulse and the TMS

pulse. Furthermore, to examine the deviation from the target line for a longer period, the difference between the target force and the generated force was calculated from the midpoint of the curve (start of a condition) until the time point TMS was applied. The absolute area under the curve of this difference (AUC) was calculated as a measure of deviation from the target curve. To correct for possible different time durations the AUC was divided by the number of samples included in its calculation. In this way, the AUC represented the average deviation between the executed force and the target force from the start of the curve to the time of TMS in a specific condition.

Statistical analysis

All variables (MEP, RMS100, average speed, AUC) were calculated for each condition (i.e., fast up, fast down, slow up or slow down) and each task (sinusoidal curve or horizontal line). Since TMS was applied 3.5 s apart and always at the performed force level, the number of events in each condition differed among participants (as shown in Table 1 and explained in calculating the total Euclidian error in 'Data Analysis'). A repeated measures analysis of variance (ANOVA) was performed on the variables with factors direction (up, down), speed (slow, fast) and task (sinusoidal curve or horizontal line). In line with previous work of our group (Rens et al., 2020), we z-scored MEP and RMS100 data for each participant separately before calculating participant averages and performing statistics. Post-hoc tests were performed with Bonferroni corrected t-tests. A significance level of 0.05 was used and effect sizes for the factors are reported using partial eta squared (η_p^2). Only if otherwise denoted, Data in text is reported as mean ± standard error.

Experiment 2

Task and procedure

After initial preparations (i.e., consent, questionnaires and TMS preparations), participants performed the experimental task. The behavioural task of experiment 2 comprised of an object-lifting task based on Mawase & Karniel (2010). Participants were comfortably seated in front of a table with their right arm resting on the tabletop. The experimenter was seated in front of the participant. Participants were instructed to grasp and lift the manipulandum on the table and received the following instructions: (1) Lift the manipulandum to a height of approximately 5 cm at a smooth pace that is natural to you. (2) Only place thumb and index finger on the graspable surfaces (i.e., use precision grip). (3) After lifting, keep the manipulandum in the air until the switchable screen (see below) turns opaque. Only then replace the object on the table. (4) Only start reaching towards the manipulandum after you have received the TMS

pulse. Accordingly, one trial consisted of one reach-grasp-lift-replace action. Before the start of the experiment, five practice trials were performed with a random sequence of objects included in the experimental task.

A switchable screen (MagicGlass) was placed between the participant and the table. The screen could become transparent or opaque to enable/block vision on the manipulandum, respectively. When the screen was opaque between trials, the experimenter could change the cube in the manipulandum's basket out of the participant's view. Five possible objects could be placed in the manipulandum with approximate weights of 1.04, 2.55, 3.11, 3.56 and 5.15 N, which will be referred to as (weight) 1-5. As mentioned before, the manipulandum weighted approximately 1.2 N, thus giving total weights of approximately 2.23, 3.75, 4.31, 4.75 and 6.34 N to be lifted. Total weight was assessed by holding the cube-loaded manipulandum steady in the air for a few seconds which was repeated 5 times for each weight. These cubes were 3D printed, visually identical and measured 5×5×5 cm. In addition, all objects were hidden below the same paper cover to ensure that participants could not rely on visual cues indicating object weight.

Each trial started with the switchable screen becoming transparent. After 400 ms (± 100 ms jitter), a TMS pulse was applied over M1. The TMS pulse served as the 'go' cue for participants to initiate their action of grasping, lifting, and replacing the manipulandum. The timing of the TMS pulse during lift planning was in line with previous work of our group (Rens et al., 2020, 2021). Four seconds after the screen becoming transparent, it turned opaque again indicating the end of the trial and indicating participants to replace the manipulandum on the table. Force data was only sampled when the screen was transparent, EMG data was continuously sampled but only an epoch of 5 seconds (from 2 seconds before to 3 seconds after the TMS pulse) was stored.

Similar to the task of Mawase & Karniel (2010) the weights were presented in an apparently random order although we used both series of increasing weights and of random weights. A series of increasing weights consisted of the weights 1, 2, 4 and 5 (i.e., four trials). After this series of increasing weights, weight 3 was presented in the fifth trial as a 'catch' trial'. The series of random weights varied between 4 and 9 trials of which a randomly chosen trial comprised of lifting weight 3 (weight 3 was presented earliest trial 2 and latest trial 9). This was to ensure that participants would not anticipate that the catch trial was the fifth trial after the series of increasing weights.

As weight 3 was presented after both the series of increasing and of random weights, we could compare force scaling in catch trials between these two conditions. Accordingly, we could investigate whether participants would predictively scale their forces differently for the same weight based on

421 implicit information (i.e., increasing vs. random series). Importantly, to ensure that predictive force scaling
422 differences for weight 3 between series were not driven solely by the previous lift (Johansson & Westling,
423 1988), we decided that the weight immediately before weight 3 in the series of random weights was the
424 same as the last weight in the series of increasing weights (i.e., weight 5) (for an example sequence of the
425 object lifting task see Figure 5). For experiment 2, we decided on 15 catch trials per condition, thus
426 resulting in 15 series of increasing weights and 15 series of random weights which was close to double the
427 amount of trials in Mawase & Karniel (2010).

428 A different experimental sequence was generated for each participant. As the total amount of trials
429 depended on the random trials, participants performed on average 181 trials. Participants received a
430 break after approximately 60 and 120 trials which varied as the break took place after completing a series
431 (thus after lifting weight 3). After completing the experiment, participants performed a short
432 questionnaire (akin to Mawase & Karniel, 2010), which contained questions about their experience of the
433 objects:

434 1) Did you experience a change in the weight of the objects?
435 2) Did you experience this change in object weights as random?
436 3) Did you experience a pattern or series in the change of object weights?
437 4) Did you feel like some weights appeared more often or less frequent, or was this equally divided?

438

439 Data analysis

440 *EMG data.* From the EMG recordings, we extracted the MEPs, which were defined as the peak-to-peak
441 amplitude in the EMG signal, using a custom-written MATLAB script. MEPs were determined between 5
442 ms to 45 ms after the TMS pulse. Trials were visually inspected for background noise related to muscle
443 contractions. Trials that showed visual contamination of EMG activity prior to TMS were flagged and
444 removed from analysis (3.6 %). In addition, MEPs were also considered noise and removed when they
445 were smaller than 50 µV or smaller than the peak-to-peak EMG signal in the 100 ms before TMS (1.7 %).

446 *Force data.* Trials in which the incorrect object was lifted (i.e., experimenter placing the wrong
447 weight), or in which the object was not lifted or lifted twice in one trial (e.g., when the participant's
448 fingertips slipped from the force sensors) were removed from the force analysis (0.3%). The force data
449 was filtered with a fourth order low-pass bidirectional Butterworth filter with a cut-off frequency of 15
450 Hz. (Total) load force (LF) and (total) grip force (GF) were the sum of the forces parallel and perpendicular
451 to the gravitational force, respectively. Load and grip force rates (LFR and GFR) were defined as the first
452 time-derivatives of LF and GF. Peak values of the force rates were determined between object contact

(defined as GF > 0.1 N) and 50 ms after lift-off (LF > object weight). We decided to use the peak values, and in particular the first peak values (peak1 LFR and peak1 GFR), of the force rates (and not the forces) as this has been considered a more sensitive measure of predictive force scaling (Johansson & Flanagan, 2009; Johansson & Westling, 1988). In line with Van Polanen et al. (2020), we extracted the first peak that was at least 30% of the maximum value to avoid noise extraction. Finally, the loading phase duration (LPD) was determined as the latency between LF onset (LF > 0.1 N) and object lift-off (defined above). To end, we also calculated grip force at lift-off (GFatLO). GFatLO was extracted as this was the behavioural parameter used in (Mawase & Karniel, 2010). This allowed us to directly compare our findings with theirs.

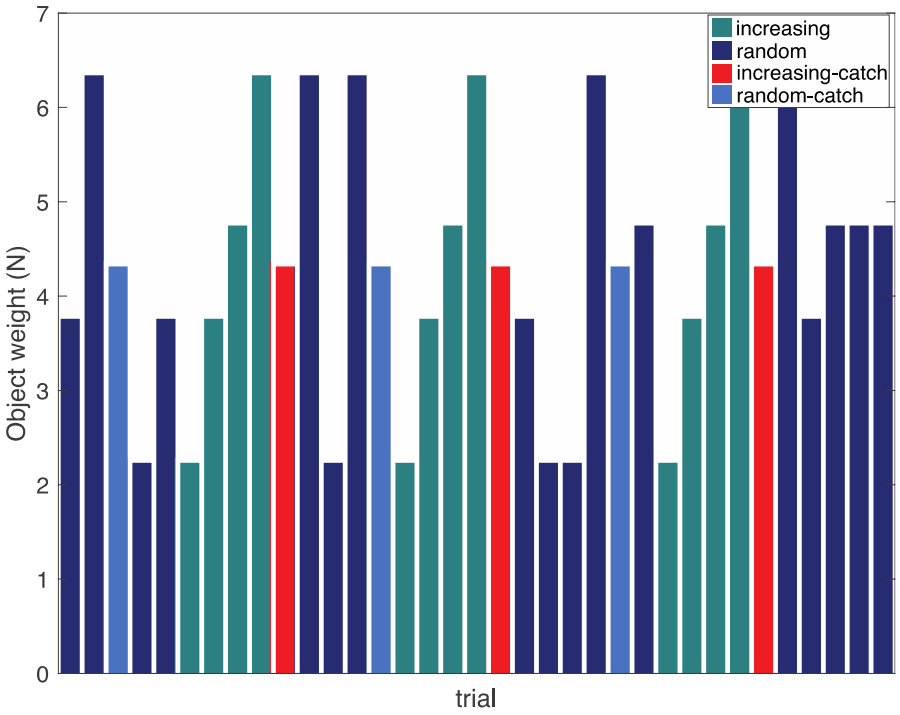

Figure 5. *Example of trial sequence in experiment 2. Trials consisted of a series of increasing weights (turquoise) or random order (dark blue). A catch trial was presented in each series: at the end of an increasing series (red) or at a random position in the random series (light blue). Note that a catch trial was always preceded by the heaviest weight in the object set.*

Statistical analysis

We extracted all parameters (MEP, peak1 LFR, peak 1 GFR, LPD, GFatLO) for catch trials after the series of increasing and random weights. For each parameter, outliers, defined as being smaller or larger than the mean ± three standard deviations, were removed from the analysis (< 2 % for any parameter). Analyses were performed on the averaged participant data. In line with (Rens et al., 2020) , MEP and behavioural data were converted to z-scores for each parameter of each participant to take inter-subject variability in

account. Z-scored data were then averaged per parameter for each participant and condition and then used for statistical analysis. Catch trials in the series and random conditions were compared with paired sample t-tests. Only if otherwise denoted, all values reported in text are mean ± standard error of the mean. As sample size was relatively small, we decided on Hedges' g to report effect size for between-condition comparisons.

Results

Experiment 1

In the first experiment, participants tracked a curve by applying force on two sensors. TMS was applied when a force of 2.5N was crossed, which could occur when moving up or down on the curve and at a fast or slow speed.

Corticospinal excitability. The MEPs were compared for all conditions to test whether CSE differed depending on the task that had to be performed. Results are shown in Figure 6A. The repeated measures ANOVA showed that MEPs were larger when moving up (up = 0.42 ± 0.04) compared to moving down (down = -0.42 ± 0.07) on the curve (effect direction, $F(1,13) = 74.8$, $p<0.001$, $\eta_p^2 = 0.85$). Furthermore, MEPs were also larger when the movement was fast (fast = 0.08 ± 0.03) compared to slow (slow = 0.03 ± 0.04) (effect speed, $F(1,13) = 23.0$, $p<0.001$, $\eta_p^2 = 0.64$). However, an interaction effect between speed and direction ($F(1,13) = 7.9$, $p = 0.015$, $\eta_p^2 = 0.38$) indicated that the speed effect was only seen in upwards movements (up fast = 0.57 ± 0.06; up slow = 0.27 ± 0.03; $p = 0.002$), but not in downwards movements (down fast = -0.40 ± 0.07; down slow = -0.44 ± 0.09; $p = 1.00$). The difference between moving up and down was visible within both the fast (up fast compared to down fast) and slow (up slow compared to down slow) movements (both $p<0.001$). Finally, an interaction between direction and task was found ($F(1,13) = 7.1$, $p = 0.020$, $\eta_p^2 = 0.35$), but post-hoc tests only showed differences between up and downward movements within tasks (sinusoidal curve: up = 0.47 ± 0.06; down = -0.48 ± 0.03; $p < 0.001$; horizontal line: up = 0.37 ± 0.07; down = -0.36 ± 0.1; $p < 0.001$), but no differences within direction between tasks (e.g., upward movement compared between the sinusoidal curve and horizontal line conditions) were found (both $p = 1.00$).

Background EMG. Since MEPs also depend on background EMG, we also compared the RMS of the EMG obtained 100ms before the TMS was applied (RMS100). Here, an effect of direction ($F(1,13) = 114.4$, $p<0.001$, $\eta_p^2 = 0.90$) was found. RMS100 was higher when going up (up = 0.28 ± 0.04) compared to going down (down = -0.44 ± 0.04). No effects of speed or task were found for RMS100.

Together, these results suggest that MEPs differ depending on movement direction and speed, but not on visibility of the target curve. However, the direction effect as observed in the MEPs were also seen in the background EMG, which might have contaminated the MEP results.

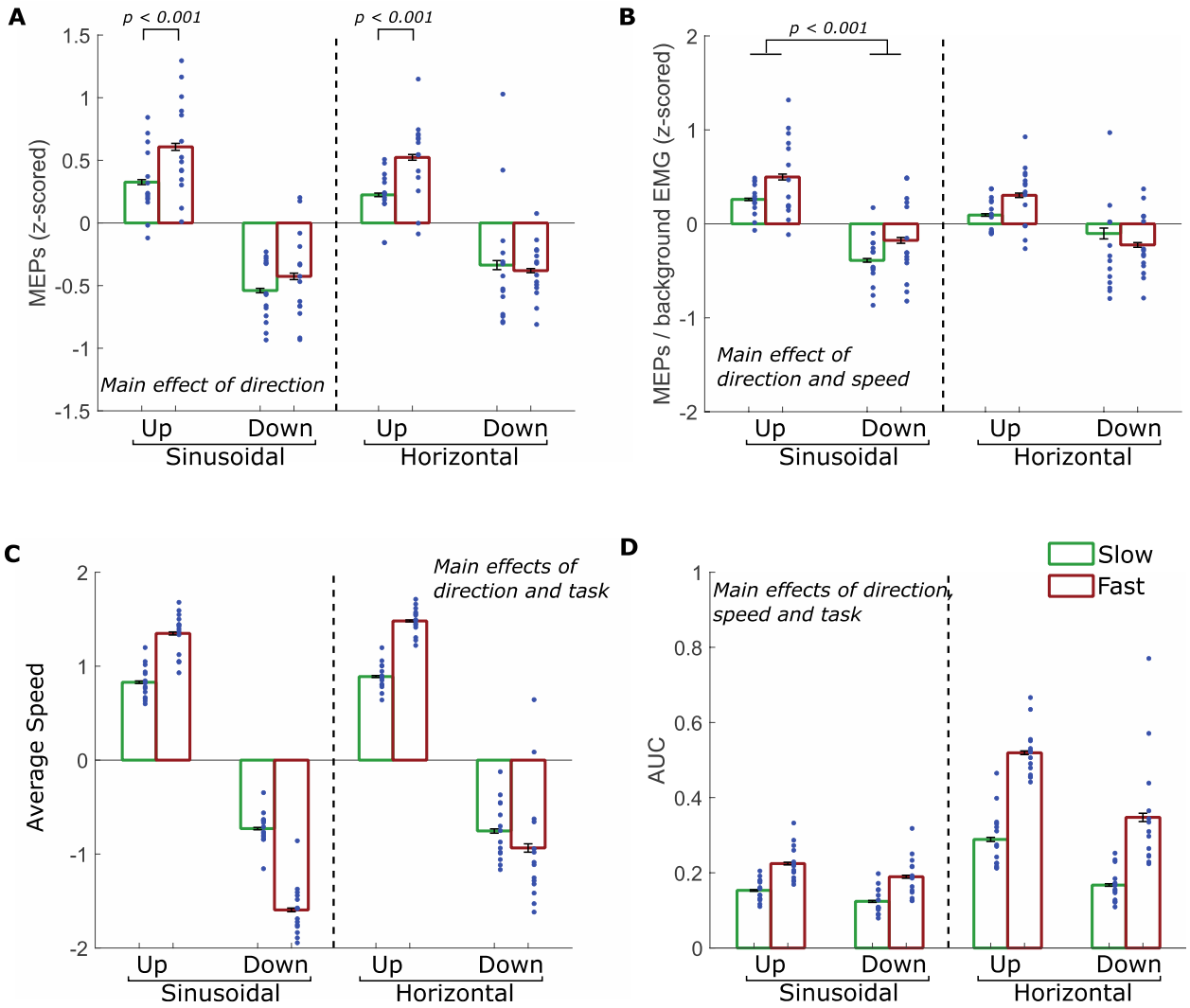

Figure 6. *Results for experiment 1, for both the sinusoidal and horizontal line condition.* ***A.*** *Motor evoked potentials (MEP).* ***B.*** *MEPs divided by background EMG.* ***C.*** *Average speed.* ***D.*** *Area under the curve (AUC). Green and red bars represent slow and fast conditions, respectively. Blue dots represent individual values. Main effects are reported and interactions are indicated with significance bars. Error bars indicate standard errors.*

Corticospinal excitability corrected for background EMG. To correct for background differences in muscle contraction, we divided the MEP of each TMS event by the RMS100 in that event (shown in Figure 6B). For this MEP_{EMG} we found main effects of direction ($F(1,13) = 12.5$, $p = 0.004$, $\eta_p^2 = 0.49$) and speed ($F(1,13) = 11.2$, $p = 0.005$, $\eta_p^2 = 0.46$), indicating that MEPs were still higher when going up compared to going down (up = 0.29 ± 0.05; down = -0.22 ± 0.11) and moving fast compared to slow (fast = 0.10 ± 0.03;

521 down = -0.03 ± 0.05), even when corrected for background EMG. For this analysis we also found an
522 interaction of direction × task ($F(1,13) = 4.8$, $p = 0.048$, $\eta_p^2 = 0.27$). Post-hoc tests indicated that the upward
523 movements were only different from the downward movements in the sinusoidal curve condition (up =
524 0.38 ± 0.07; down = -0.28 ± 0.04; $p<0.001$), not in the horizontal line condition (up = 0.20 ± 0.09; down =
525 -0.16 ± 0.13; $p = 0.292$). No differences were seen between the two conditions (between conditions: both
526 $p > 0.21$).

527 *Rate of force scaling.* To assess whether participants performed the task correctly, we calculated the
528 average speed prior to the TMS (Figure 6C). The ANOVA on the average speed showed a main effect of
529 direction and task, and all two-way interactions and the three-way interaction was also significant (all
530 $F>6.8$, all $p<0.021$, all $\eta_p^2>0.34$). Participants moved faster in the fast conditions compared to the slow
531 conditions (all $p<0.001$), except in the horizontal line condition when making a downward movement
532 where no difference was found ($p = 1.00$). Not surprisingly, the direction also differed based on whether
533 up or down movements were made (all $p<0.001$). There were no notable differences between the
534 sinusoidal curve and horizontal line conditions, except for the fast down condition, which was slower in
535 the horizontal line compared to the sinusoidal curve condition ($p = 0.002$). These measures indicated that
536 participants seemed to perform the task according to the instructions; sinusoidal curve: slow up: 0.83 ±
537 0.047, fast up: 1.35 ± 0.06, slow down: -0.73 ± 0.048, fast down: -1.60 ± 0.075; horizontal line slow up:
538 0.89 ± 0.039, fast up: 1.49 ± 0.039, slow down: -0.76 ± 0.085, fast down: -0.94 ± 0.169).

539 *Motor performance.* To determine whether participants' performance differed between conditions,
540 we measured the AUC of the difference between the target curve and the applied force (Figure 6D). An
541 ANOVA on the AUC showed that the deviation depended on the direction ($F(1,13) = 144.9$, $p<0.001$, $\eta_p^2 =$
542 0.92), speed ($F(1,13) = 161.7$, $p<0.001$, $\eta_p^2 = 0.93$) and task ($F(1,13) = 99.3$, $p<0.001$, $\eta_p^2 = 0.88$). Participants
543 deviated further from the curve when they moved upwards (up = 0.30 ± 0.01) compared to downwards
544 (down = 0.21 ± 0.02). In addition, a larger AUC was seen for fast movements (fast = 0.32 ± 0.02) compared
545 to slow movements (slow = 0.18 ± 0.01). Finally, larger deviations were seen in the horizontal line
546 condition (mean = 0.33 ± 0.02) compared to the sinusoidal curve condition (mean = 0.17 ± 0.01).
547 Furthermore, interactions between direction and task ($F(1,13) = 56.5$, $p<0.001$, $\eta_p^2 = 0.81$) and between
548 speed and task ($F(1,13) = 100.1$, $p<0.001$, $\eta_p^2 = 0.89$) were observed. However, the post-hoc tests of these
549 interactions were all significant (all $p<0.01$), providing no new interpretations to the data.

550 In sum, CSE was modulated according to the direction and speed of the movement, even after
551 correcting for background EMG. This CSE modulation was seen both in the sinusoidal curve and horizontal

552 line conditions, i.e., when the sinusoidal target curve was visible or when only feedback from a straight
553 line was present.
554
555 Experiment 2
556 In experiment 2, participants lifted objects that were presented either in a series of increasing or random
557 weights. After a series of increasing weights or within the random series, a 'catch trial' (weight 3) was
558 presented. Immediately prior to this catch trial, in both the series of random and increasing weights, the
559 heaviest (weight 5) was presented. In addition, we applied TMS prior to object lifting to assess CSE
560 modulation during lift planning. With this experiment, we aimed to investigate whether lift planning (on
561 the behavioral and corticospinal level) reflects implicit information, related to a series of random or
562 increasing object weights, during a discrete object lifting task. For this we investigated differences in
563 predictive force scaling and CSE modulation for the catch trial only.
564 *Debriefing results.* After the experimental task, participants were debriefed and were asked
565 questions using a standardized questionnaire (see methods) related to the experimental task. All
566 participants (Question 1: 15/15) reported that the weights of the object changed between trials. All but
567 one participant (Question 2: 14/15) experienced these changes as random and two participants (Question
568 3: 2/15) reported to experience a pattern in the object presentation. While most participants (Question
569 4: 9/15) reported all weights to appear equally frequent, four answered that there were more heavy
570 objects in the sequence and one participant argued they did not know whether the weights appeared
571 equally frequent.
572 *Behavioral results.* The results for the behavioural parameters are shown in Figure 7B-D. We first
573 looked at the amount of total grip force (GFatLO; z-scored) participants applied at lift-off, which was also
574 used by Mawase & Karniel (2010) as a proxy of predictive force scaling. Our results did not reveal that
575 participants scaled their grip forces at lift-off significantly different when performing the catch trial after
576 a series of increasing (-0.039 ± 0.04) or random weights (mean = -0.003 ± 0.0.04) ($t(1,13) = -0.79$, $p = 0.44$,
577 $g = 0.34$). These findings were similar for peak1GFR (z-scored: increasing = 0.29 ± 0.10; random = 0.27 ±
578 0.08) ($t(1,13) = 0.17$, $p = 0.87$, $g = 0.06$), peak1LFR (z-scored: increasing = 0.21 ± 0.09; random = 0.27 ±
579 0.05) ($t(1,13) = -0.53$, p = 061, $g = 0.18$) and for LPD (z-scored: increasing = -0.04 ± 0.26 ms; random = 0.04
580 ± 0.29 ms) ($t(1,13) = -0.57$, $p = 0.58$, $g = 0.07$). In sum, our findings provide no evidence that participants
581 scaled their forces differently in the catch trial (weight 3) when it was presented after either a series of
582 random or increasing weights. Accordingly, these results suggest that participants did not integrate
583 implicit information related to the series of increasing weights but rather scaled their fingertip forces

based on their previous lift on the preceding weight (i.e., weight 5) which was the same in both series of increasing and random weights.

Corticospinal excitability. Similar to our behavioral findings, we did not find significant differences in CSE modulation when participants planned to lift in the catch trial between the increasing (z-scored: mean = 0.077 ± 0.06) and random condition (z-scored: mean = -0.02 ± 0.09) ($t(1,13) = 0.96$, $p = 0.35$, $g = 0.34$). Results for MEPs are shown in Figure 7A.

In sum, these findings show that neither on the behavioral nor on the corticospinal level, participants planned to lift weight 3 differently when it was presented after a series of increasing or random weights.

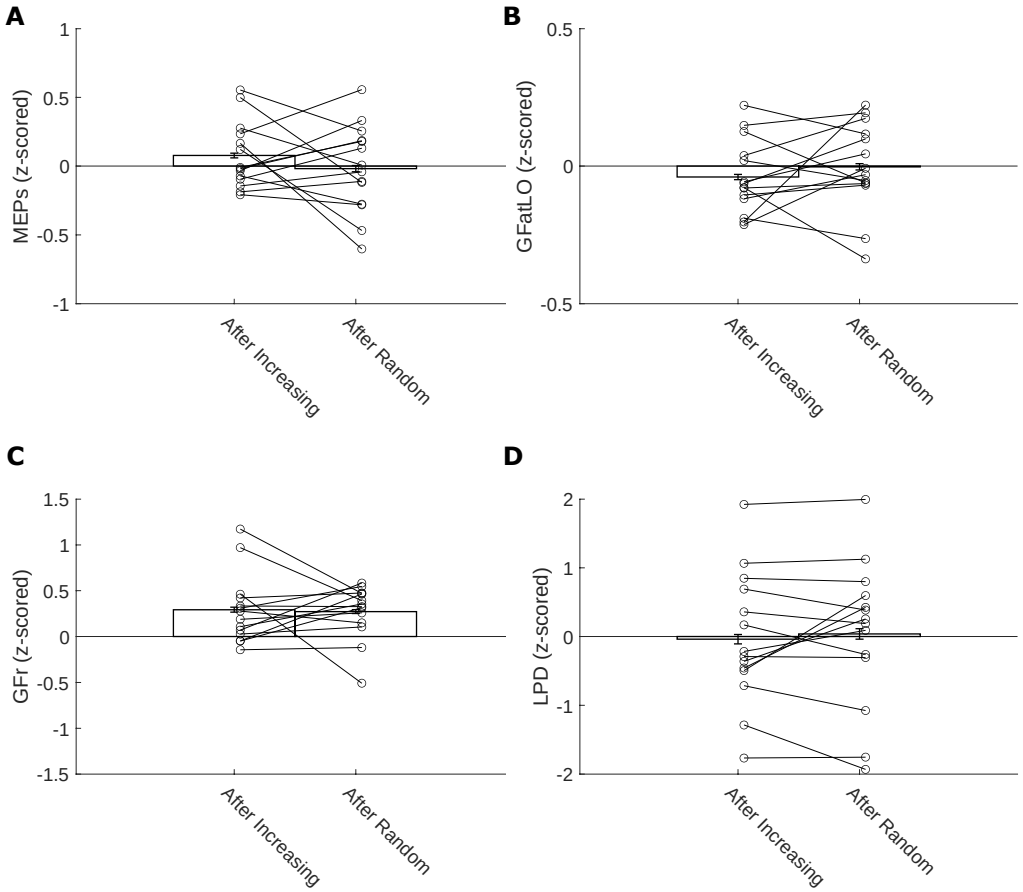

Figure 7. *Results for experiment 2 for the catch trial after a series of increasing weights or in a random order.* ***A.*** *Motor evoked potentials (MEPs).* ***B****. Grip force at lift off (GFatLO).* ***C****. first peak of grip force rate (GFr). Note that values for the first peak of load force rate were similar to GFr.* ***D****. Loading phase durations (LPD). Bars indicate mean and standard errors. Circles and lines represent values for individual participants.*

602 **Discussion**

603 In the present study, we investigated how explicit and implicit contextual information affected force
604 scaling and CSE modulation during hand-object interactions. In experiment 1, participants performed a
605 continuous force tracking task and in experiment 2, other participants performed a discrete object lifting
606 task. In both experiments, motor performance was assessed to investigate how participants scale their
607 fingertip forces during continuous and discrete hand-object interactions. TMS was used to probe the
608 underlying changes in CSE. For experiment 1, we found that when visuomotor cues were indirectly
609 mapped onto the motor output (i.e., absence of prediction and reliance on error-driven feedback),
610 participants performed worse compared to when task requirements could be directly mapped on the
611 motor output (i.e., both prediction and normal feedback). Noteworthy, CSE (when corrected for
612 background EMG; Figure 6B) was modulated by the rate of force scaling (fast vs. slow) in both target
613 display conditions but only by directionality (up- vs. downscaling of fingertip forces) in the sinusoidal curve
614 but not in the horizontal line condition. These findings suggest that CSE is primarily modulated by task
615 requirements that can be directly mapped onto the corticospinal output. However, results also indicate
616 that CSE is modulated by task requirements when these are specified by less readily available information.
617 For experiment 2, we found that when participants lifted a specific weight after a series of increasing
618 weights that neither force scaling nor CSE modulation was different compared to when they lifted the
619 same weight after a series of random weight. These findings indicate that participants did not predictively
620 scale their forces by extrapolating from the implicit weight increasing series.

621 In experiment 1, participants performed a sinusoidal force tracking task when provided with the
622 actual sinusoidal target force (sinusoidal condition) or only received feedback about their performance in
623 the form of a deviation from a horizontal line (horizontal line condition). As can be seen in Figure 6D,
624 participants performed significantly worse (higher AUC value) in the horizontal line condition compared
625 to the sinusoidal curve one. These findings indicate performance suffered when participants could not
626 visually track their location on the sinusoidal curve and thus not predict the required directionality (up- or
627 downscaling of force scaling) and rate of force scaling (the steepness of the curve's slope). Conversely,
628 when the upcoming task requirements could be directly mapped onto the sensorimotor system (i.e.,
629 observing performance relative to the sinusoidal curve), performance was better than when these
630 requirements could not be directly mapped (i.e., observing performance relative to a horizontal line).

631 Please note that we decided to focus on the MEP findings when corrected for background EMG
632 due to the potential confounding effects of background muscle activation. Interestingly, we found that
633 the corrected MEPs depended on the direction and change in force scaling rate (speed), but this also

interacted with the type of visual information. In the sinusoidal curve condition, where the information could be directly mapped to the corticospinal descending drive, CSE was modulated both by direction and rate of change. On the other hand, in the horizontal line condition, CSE was only modulated by rate of change. As such, these findings indicate that CSE encoded ongoing task execution (i.e., rate of force scaling and direction) but that it also depended on the type of visual information about task requirements and performance. In the horizontal line condition, information about the task was less directly available, but corticospinal drive was still modulated by some of the task requirements. On the other hand, when participants were not able to perceive their position on the sinusoidal curve, CSE modulation was decreased compared to when information was more directly available. Note that although the modulation of CSE towards task requirements was decreased when information was less directly available, the corticospinal drive was not generally increased or decreased depending on the type of visual information, even though performance differed between the two tasks. That is, even though the task seemed to be more difficult in the horizontal line condition, this did not lead to an overall increase or decrease in CSE.

It is plausible that CSE modulation was inhibited to some extent in the horizontal line condition as participants could only focus on visual feedback and not their position on the curve. Indeed, Bestmann et al. (2008) showed that CSE modulation becomes smaller when uncertainty increases. From a behavioral point of view, it is plausible that the horizontal line condition induced participants to control their fingertip forces more carefully in an attempt to rapidly switch between up- and downscaling when required thus altering CSE modulation. Noteworthy, using a reaction time task, Young et al. (2000) showed that when individuals respond to stimuli, CSE is not selectively modulated by selective intention ('readiness to respond') and selective attention ('preferential processing of stimuli'). However, as indicated by our results, it is plausible that when attentional strategy has to be altered based on type of visible information that CSE modulation altered as well (during continuous tasks).

Finally, in the sinusoidal curve condition, CSE was larger when participants were upscaling their fingertip forces compared to downscaling (Figure 6A). The latter findings are in line with Kimura et al. (2003) and Li (2013) who showed that CSE is increased when contracting the elbow flexor (compared to relaxation) and when dynamically contracting the muscles of four fingers (without thumb) compared to isometric contraction and relaxation, respectively. These results agree with findings that motoneuron inputs have a greater relative contribution during shortening muscle contractions than relaxations (Semmler et al. 2002) and that CSE decreases prior to muscle relaxation (Suzuki et al. 2015). Our results extend on these studies by showing that (a) CSE is increased when upscaling fingertip forces compared to downscaling during a force tracking task, (b) CSE is also modulated by movement speed, where it is

increased with fast compared to slow changes in force, and (c) that the type of visual information can alter the pattern of CSE modulation. Together, our findings suggest that the corticospinal output is primarily driven by the ongoing motor command based on more directly available visual cues, but can be flexibly modulated based on indirect information, although to a lesser extent.

In support of the continuous motor task in experiment 1, we performed experiment 2 to investigate how implicit information affects CSE modulation in a discrete object lifting task. Previous studies have indicated that the CSE modulation represents task requirements (i.e., object weight) based on the previously lifted object (Loh et al., 2010). In addition, behavioural evidence suggests that the sensorimotor system can adapt predictive force scaling towards other object lifting strategies based on information about several lifts (Mawase & Karniel 2010; Cashaback et al. 2017). Here, we investigated whether these adapted lifting strategies would also be reflected in modulation of the corticospinal drive. Participants performed an object lifting task on differently weighted, but visually identical, cubes. Within the overarching sequence of presented weights (see Figure 5), two types of series were hidden. One consisted of random weights whereas the second one consisted of increasing weights. Importantly, in both the random and increasing weights series, the second to last trial was always performed on the heaviest object and the last trial on a lighter 'catch weight', as in Mawase & Karniel (2010). The second to last weight was standardized across increasing and random series to control for sensorimotor memory effects (Baugh et al., 2012; Castiello, 2005; Johansson & Westling, 1993). With this experiment, we wanted to investigate whether CSE modulation would reflect the weight series (random or increasing). Critically, our results provided no evidence that the sensorimotor system altered predictive force scaling based on the series of increasing weights and hence, no modulation of CSE was observed either. We did not find statistical differences for behavioral parameters and CSE between same-weighted lift after the series of random and increasing weights. Noteworthy, Mawase & Karniel (2010) reported that participants extrapolated their fingertip forces based on the hidden series of increasing weights. There are three major differences between their and our study that could explain why we could not replicate their behavioural results.

First, they relied on a virtual reality set-up whereas we used real hand-object interactions. In a recent review, Snow & Culham (2021) argued substantial differences between how virtual and real objects affect perception, cognition and action. For instance, individuals have a 'real-object preference' when gazing at real objects and 2D representations of the same object. It is possible that in the study of Mawase & Karniel (2010) participants had a different object lifting strategy than the one that is typically used when lifting real objects because the virtual reality set-up induced more uncertainty. For instance, in a virtual

698 reality setup, some tactile information (e.g., friction between object and fingertips) is missing, which
699 contributes to force scaling (Castiello, 2005) thus potentially altering the grasping strategy.
700 Second, as a proxy for predictive force scaling, Mawase & Karniel (2010) relied on grip force at
701 lift-off whereas we relied on multiple dependent proxies (grip force, load force duration and force rates).
702 It has been argued that the force rate provides a higher sensitivity for probing predictive lift planning
703 (Johansson & Westling, 1993). Critically, neither for grip force at lift-off (akin Mawase & Karniel, 2010) nor
704 for the other proxies did we find differences in predictive force scaling when participants lifted the catch
705 weight after the series of random or increasing weights. Our results therefore suggest that predictive force
706 scaling is not sensitive to an implicit series of increasing weights.
707 Third, Mawase & Karniel (2010) did not include a direct comparison between same-weighted lifts
708 after the series of increasing and random weights. We argued that, if we wanted to investigate how
709 predictive force scaling would be altered by the hidden series, a direct comparison between same
710 weighted objects in different conditions should be made. This is the typical approach we used before (for
711 example see: Rens & Davare, 2019; Rens et al., 2020; Van Polanen et al., 2020) and which has been used
712 by other groups in our field as well (for example see Alaerts et al., 2010; Baugh et al., 2012; Buckingham
713 et al., 2014; Cashaback et al., 2017; Gordon et al., 1993; Johansson & Westling, 1993; Loh et al., 2010;
714 Reichelt et al., 2013; Senot et al., 2011). As such, it is unclear whether the results of Mawase & Karniel
715 (2010) reflect force planning driven by the hidden series or sensorimotor effects that are entirely driven
716 by the object weight lifted in only the preceding trial. In sum, in contrast to Mawase & Karniel (2010) we
717 did not find evidence that individuals automatically encode implicit information within a series of
718 increasing object weighs.
719 With respect to CSE, our results provide no evidence that CSE modulation was altered by the
720 hidden series of increasing weights. That is, CSE was not statistically different when participants planned
721 to lift the same weight after lifting a series of increasing or random weights. Loh et al., (2010) showed that
722 when individuals plan to lift an object, CSE was modulated by the previously lifted object. Based on Loh
723 et al. (2010), it seems plausible that CSE modulation in experiment 2 depended entirely on the
724 sensorimotor memory of the previous lift which reflected the heaviest weight that was the same in both
725 the increasing and random series. It is unlikely that this null result is driven by the timing of the TMS pulse
726 during lift planning as we did find CSE modulation in our previous work using the same TMS timing (Rens
727 et al., 2021). In addition, other work reported lift planning effects on CSE modulation when the TMS pulse
728 was applied even longer after object presentation (Parikh et al., 2014). As such, and in support of our

729 behavioral findings, we argue that the null results are caused by sensorimotor control mechanisms not
730 being able to detect the hidden series of increasing weights.

731 In conclusion, in the present study we investigated whether the corticospinal output could be
732 modulated based on the type and context of sensorimotor information during the execution of continuous
733 (experiment 1) and discrete (experiment 2) hand-object interactions. Our results indicate that the
734 corticospinal output is primarily concerned with ongoing force scaling but can also be modulated when
735 available information is not directly mapped onto motor output. When information about task
736 requirements is hidden in discrete events, sensorimotor control mechanisms are unable map implicit
737 information for driving predictive force scaling and the underlying corticospinal output changes are
738 unaffected.

739

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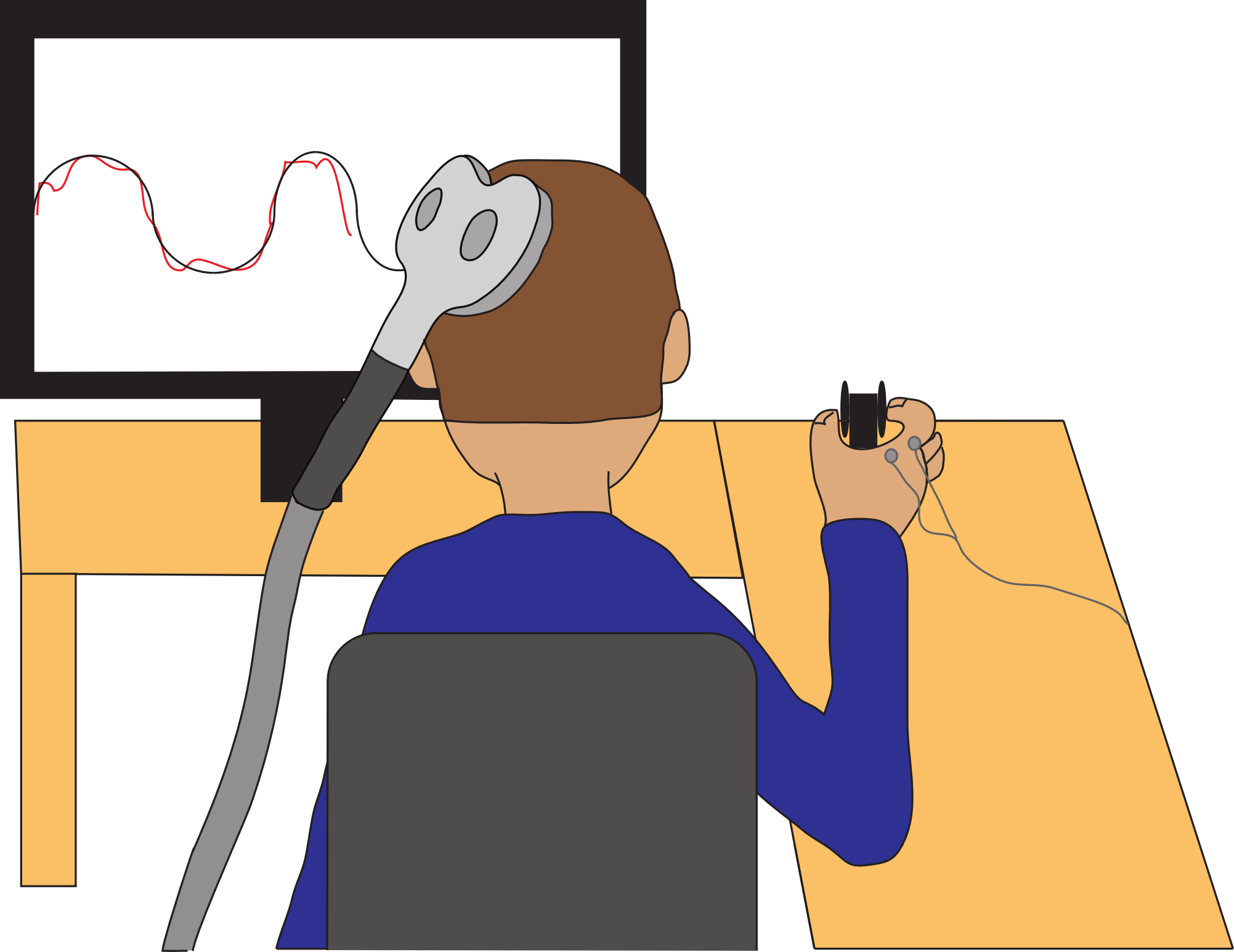

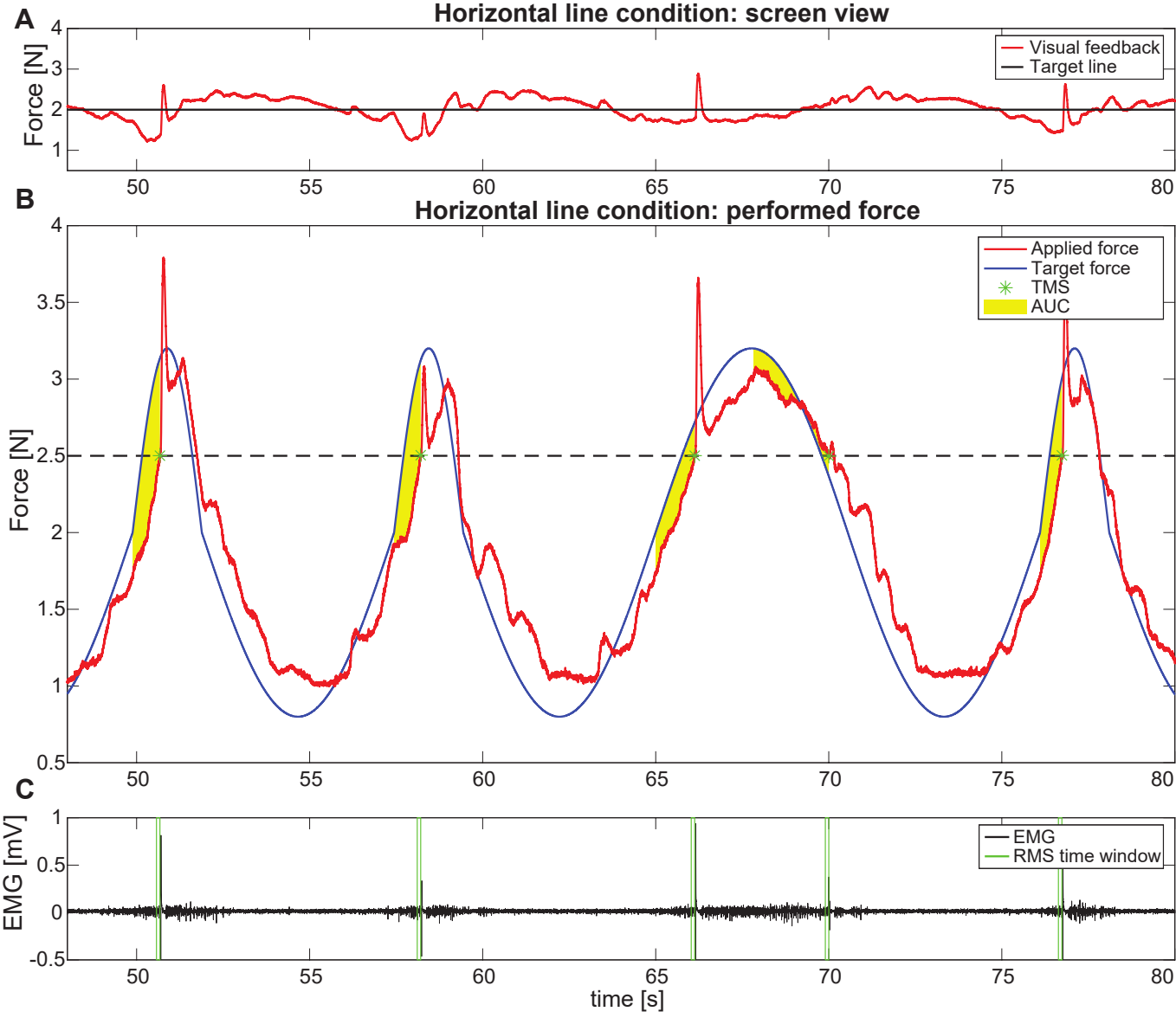
A
Horizontal line condition: screen view
Force [N]
Visual feedback
Target line
B
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AUC
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EMG
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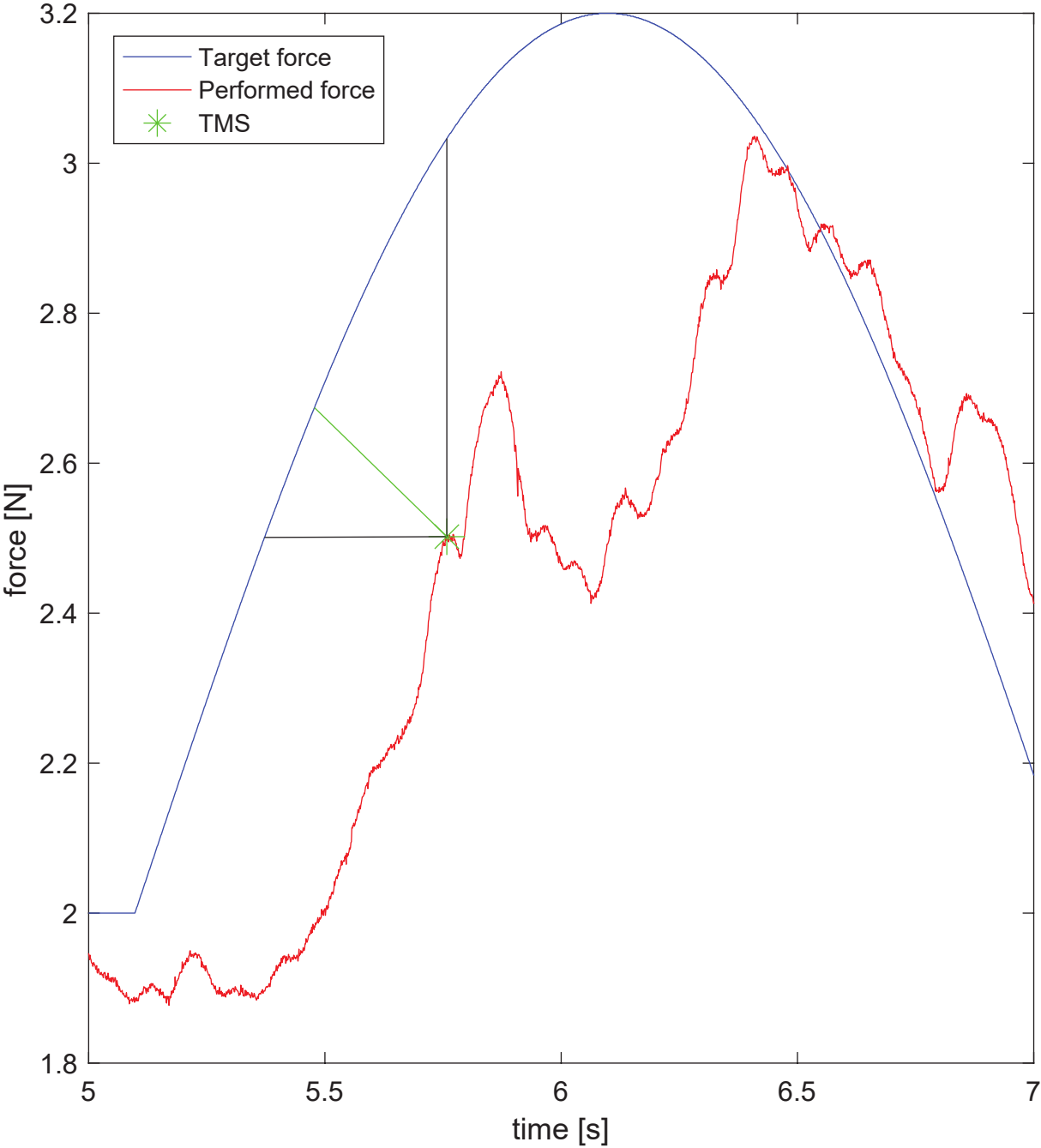
Target force
Performed force
TMS
force [N]
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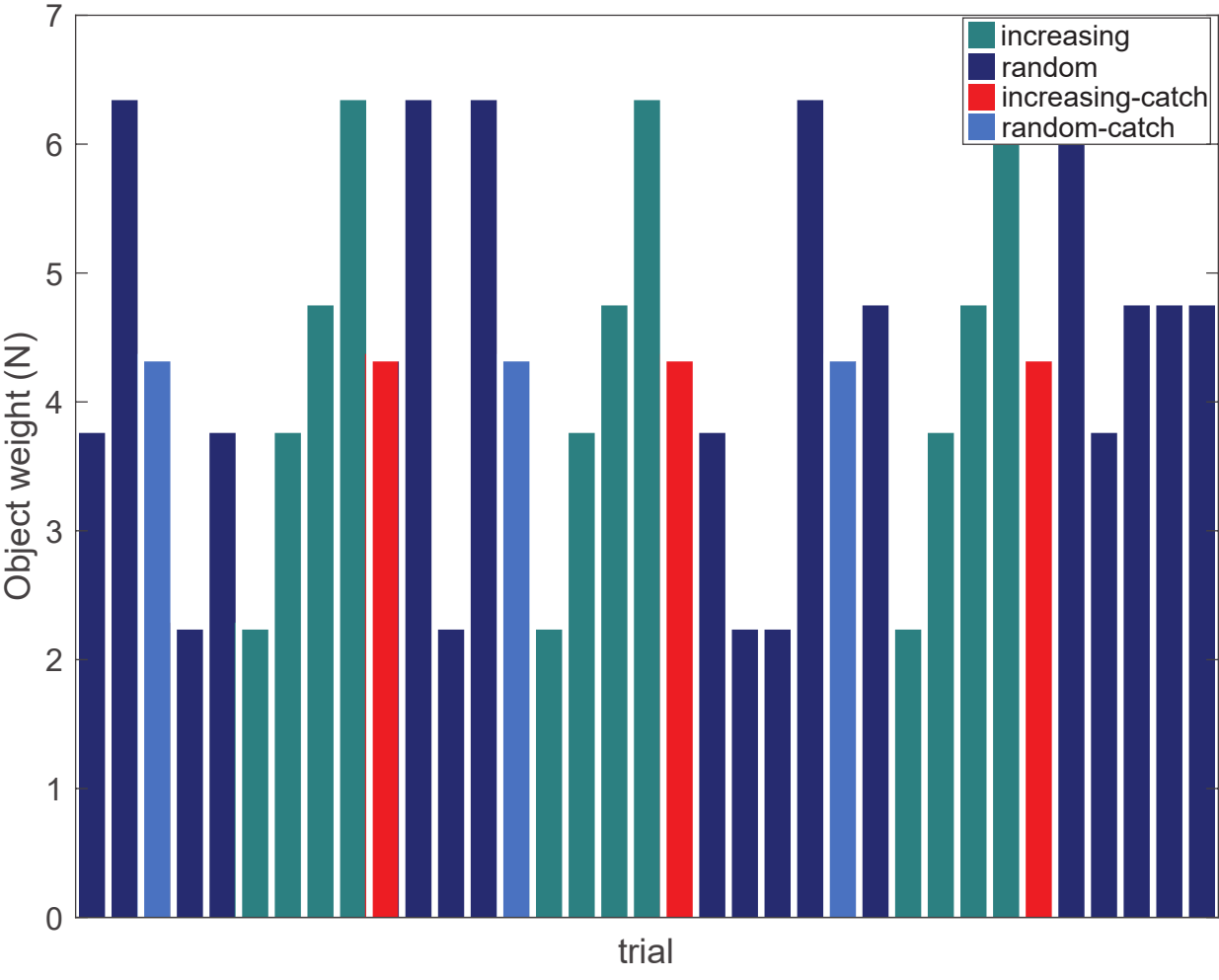
6
6.5
7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random-catch
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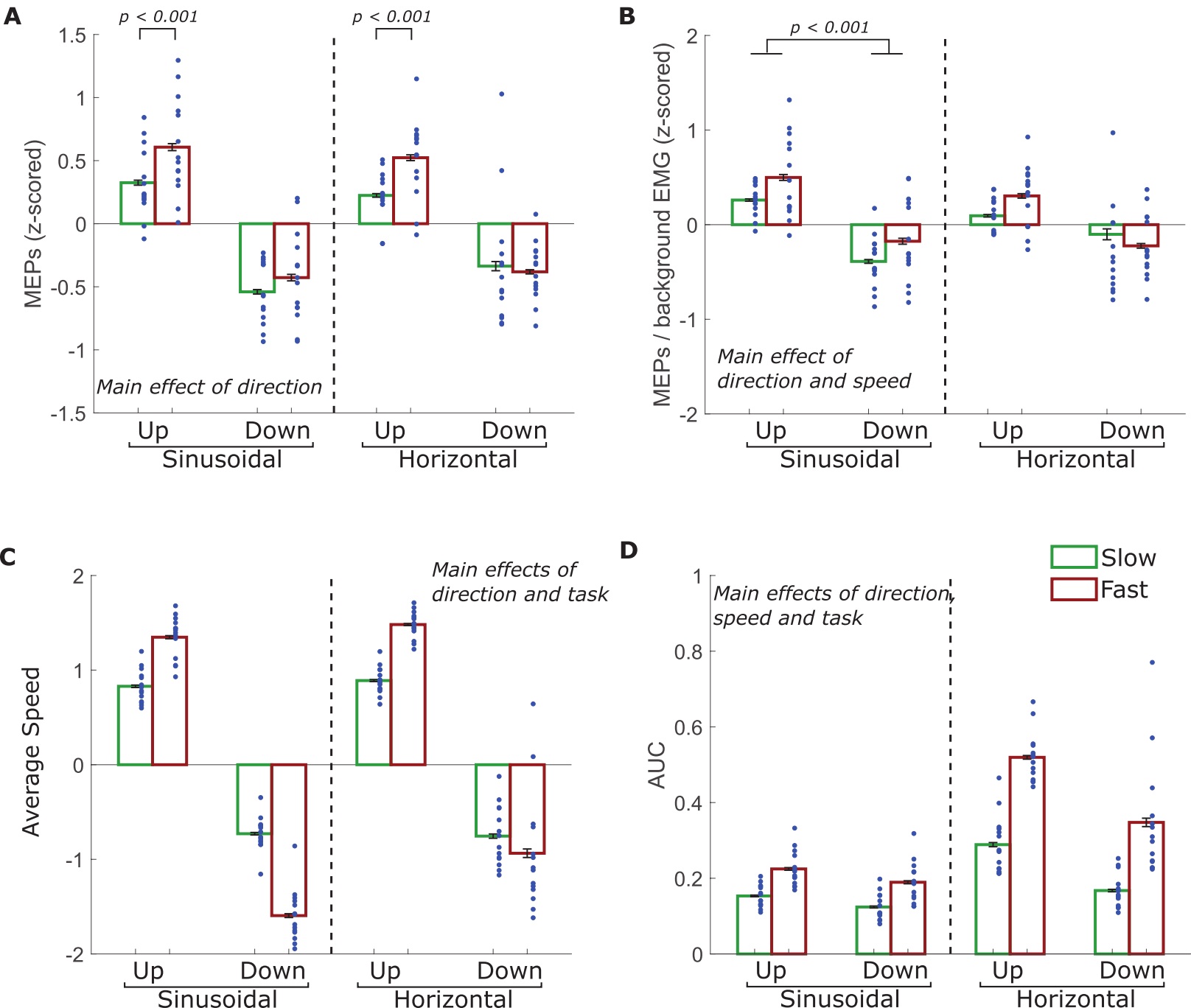
trial
0
1
2
3
4
5
6
7


A
p < 0.001
p < 0.001
MEPs (z-scored)
1.5
1
0.5
0
-0.5
-1
-1.5
Main effect of direction
Up
Down
Up
Down
Sinusoidal
Horizontal
B
p < 0.001
MEPs / background EMG (z-scored)
2
1
0
-1
-2
Main effect of direction and speed
Up
Down
Up
Down
Sinusoidal
Horizontal
C
Main effects of direction and task
Average Speed
2
1
0
-1
-2
Up
Down
Up
Down
Sinusoidal
Horizontal
D
Slow
Fast
Main effects of direction, speed and task
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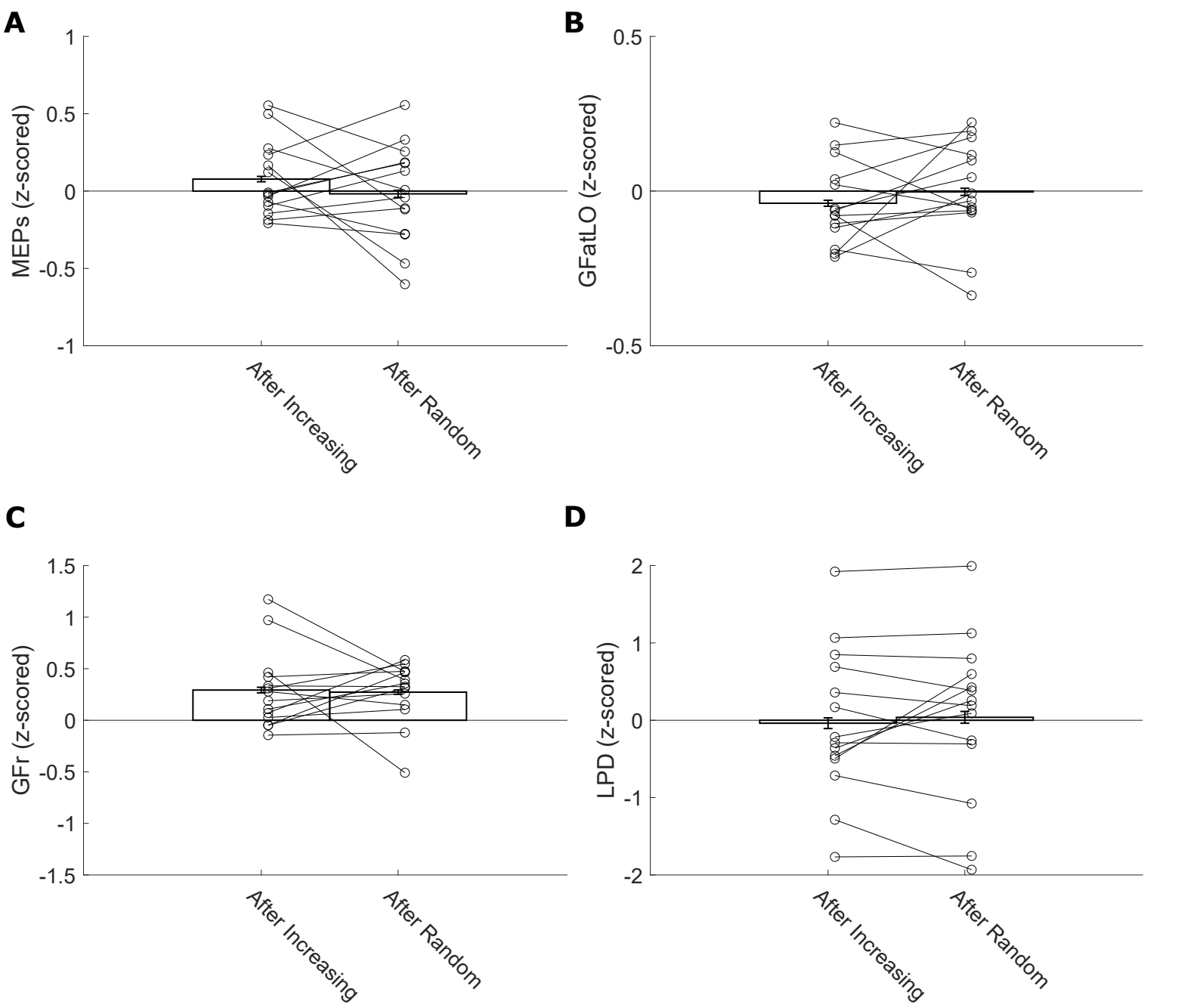
0.4
0.2
0
Up
Down
Up
Down
Sinusoidal
Horizontal


A
MEPs (z-scored)
1
0.5
0
-0.5
-1
After Increasing
After Random
B
GFatLO (z-scored)
0.5
0
-0.5
After Increasing
After Random
C
GFr (z-scored)
1.5
1
0.5
0
-0.5
-1
-1.5
After Increasing
After Random
D
LPD (z-scored)
2
1
0
-1
-2
After Increasing
After Random