

# Contextual expectations shape the motor coding of movement kinematics during the prediction of observed actions: A TMS study

Valentina Bianco<sup>a,b,\*</sup>, Alessandra Finisguerra<sup>c</sup>, Giulia D'Argenio<sup>b,d</sup>, Sara Boscarol<sup>c,e</sup>, Cosimo Urgesi<sup>b,c</sup>

<sup>a</sup> Department of Brain and Behavioral Sciences, University of Pavia, 27100 Pavia, Italy

<sup>b</sup> Laboratory of Cognitive Neuroscience, Department of Languages and Literatures, Communication, Education and Society, University of Udine, Udine, Italy

<sup>c</sup> Scientific Institute, IRCCS E. Medea, Piasan di Prato, Udine, Italy

<sup>d</sup> Fondazione Progettoautismo FVG Onlus, Feletto Umberto, Udine, Italy

<sup>e</sup> University of Camerino, Center for Neuroscience, Camerino, Italy

## ARTICLE INFO

### Keywords:

Action observation  
Social behavior  
Predictive coding  
Transcranial magnetic stimulation  
Corticospinal excitability  
Context

## ABSTRACT

Contextual information may shape motor resonance and support intention understanding during observation of incomplete, ambiguous actions. It is unclear, however, whether this effect is contingent upon kinematics ambiguity or contextual information is continuously integrated with kinematics to predict the overarching action intention. Moreover, a differentiation between the motor mapping of the intention suggested by context or kinematics has not been clearly demonstrated. In a first action execution phase, 29 participants were asked to perform reaching-to-grasp movements towards big or small food objects with the intention to eat or to move; electromyography from the First Dorsal Interosseous (FDI) and Abductor Digiti Minimi (ADM) was recorded. Depending on object size, the intentions to eat or to move were differently implemented by a whole-hand or a precision grip kinematics, thus qualifying an action-muscle dissociation. Then, in a following action prediction task, the same participants were asked to observe an actor performing the same actions and to predict his/her intention while motor resonance was assessed for the same muscles. Of note, videos were interrupted at early or late action phases, and actions were embedded in contexts pointing toward an eating or a moving intention, congruently or incongruently with kinematics. We found greater involvement of the FDI or ADM in the execution of precision or whole-hand grips, respectively. Crucially, this pattern of activation was mirrored during observation of the same actions in congruent contexts, but it was cancelled out or reversed in the incongruent ones, either when videos were interrupted at either early or long phases of action deployment. Our results extend previous evidence by showing that contextual information shapes motor resonance not only under conditions of perceptual uncertainty but also when more informative kinematics is available.

## 1. Introduction

A basic prerequisite allowing the synergy with other people during social interactions is the possibility to anticipate their behavior and to react accordingly. Crucial cues to anticipate others' likely behavior come from the observation and the understanding of the intention behind their actions. Accordingly, the observation of others' action has been found to trigger the activation of a matching motor representation in the observer's motor system, a process referred to as motor resonance (Fadiga et al., 1995) and likely implemented by the action observation network (AON), which includes both visual and motor areas (see

Rizzolatti and Craighero, 2004 for review).

Motor resonance was initially considered within feedforward recognition model according to which the visual information of the action is directly mapped onto its motor representation (Rizzolatti et al., 2001). More recently, it has been further embedded within predictive coding accounts of action understanding (Kilner et al., 2007). This account is based on the concept of a hierarchical organization of action representations, starting from the lowest level depicting the action in terms of muscle involvement and then in terms of kinematics, up to the highest levels depicting the action in terms of goal and, lastly, in terms of overarching intention (Grafton and Hamilton, 2007; Hamilton et al.,

\* Corresponding author at: Department of Brain and Behavioral Sciences, University of Pavia, 27100 Pavia, Italy.

E-mail address: [valentina.bianco@unipv.it](mailto:valentina.bianco@unipv.it) (V. Bianco).

2007). To understand others' behavior, the predicting coding account suggests that the most likely cause of an observed action can be inferred by reducing prediction errors through interactions occurring among different levels of this hierarchy. Crucially, beside the sensorial information retained in the observed action, our system may earlier exploit expectations of the most likely cause of the behavior based on the context where action takes place (Kilner, 2011; Amoruso et al., 2020). Thus, the ability to recognize others' action might be based on the integration between bottom-up sensory input retained in movement kinematics with the top-down expectations that stem from past experience in similar contexts.

Motor resonance can be effectively probed by measuring the change of corticospinal excitability during action observation (Fadiga et al., 1995), as indexed by changes in the amplitude of Motor Evoked Potentials (MEPs; Hallett, 2007) recorded in peripheral muscles after single-pulse transcranial magnetic stimulation (spTMS) over the primary motor cortex. There is indeed large consensus in considering the change of MEPs amplitude during action observation a consequence of the cortico-cortical connections from the AON to M1, which generates motor resonance of the observed movement (Strafella and Paus, 2000; see Fadiga et al., 2005 for review). The direction of the modulation, namely facilitation of MEP amplitude, its timing, showing temporal coupling between the observed kinematics and motor resonance, and muscle-specificity, consisting in the selective modulation of the MEPs that are recorded from the muscles involved in the execution of the observed action (Fadiga et al., 1995; Romani et al., 2005; Strafella and Paus, 2000; Urgesi et al., 2010), are considered as core properties of motor resonance responses (Naish et al., 2014; Amoruso and Finisguerra, 2019).

It is unclear, however, to what extent motor resonance is influenced by low-level sensory aspects (i.e., the observed kinematics) and/or by top-down modulation (i.e., context and previous experience) of action representation (Amoruso and Finisguerra, 2019). On one hand, it has been consistently shown that changes in kinematics modulate cortico-spinal excitability (CSE, e.g., Soriano et al., 2018; Urgesi et al., 2006) and play a crucial role for intention attribution (Cavallo et al., 2016). On the other hand, in keeping with the predictive coding approach, Gangitano et al. (2004) provided pioneering evidence that, while keeping muscle specificity, motor resonance would also reflect the prediction of the movement about to occur rather than the mere transformation of visual (i.e., perceptual) information into motor knowledge (see also Urgesi et al., 2010). In a similar vein, motor resonance was shown to be differently modulated by kinematics adaptations due to movement errors or to deceptive intention (Tidoni et al., 2013; Finisguerra et al., 2018) suggesting that both low- and high-level features of an observed action can be represented in the observer's motor system. Notably, Cavallo and co-authors (2013) showed that, when observing the initial stage of action unfolding, motor resonance reflects the muscle facilitation pattern necessary to achieve the goal of the action (Lago and Fernandez-del-Olmo, 2011). Then, with the progression of action unfolding, motor resonance becomes tuned to the specific kinematic features of the observed movements. Thus, the fine tuning of the motor cortex to goal or movement during action observation may relate to different processing stages. Under this vein, it is crucial to elucidate the critical role played by low- and high-level modulations of motor resonance at different phases of action deployment.

In a series of previous studies (Amoruso and Urgesi, 2016; Amoruso et al., 2016; Amoruso et al., 2018a, 2020) investigating the contextual modulation of motor resonance, participants observed videos of everyday-life actions embedded in congruent (i.e., reaching-to-grasp a mug full of coffee with a precision grip) or incongruent contexts (reaching-to-grasp an empty mug with a precision grip). Action videos were interrupted before action ending (thus showing ambiguous kinematics) and participants were asked to predict action unfolding while MEPs were recorded. Behavioral results pointed at a superior performance in the prediction of actions embedded in congruent than

incongruent contexts. MEPs results showed a facilitation or an inhibition in motor resonance for congruent or incongruent contexts, respectively. Furthermore, while the contextual facilitation occurred at earlier stages of action processing, the inhibition exerted by incongruent contexts only occurred at later stages (Amoruso et al., 2016, 2018a). Although pointing to striking contextual modulation of motor resonance, the stimuli of these studies were not suited to systematically control for muscle specificity, since the involvement of the recorded muscles (i.e., first dorsal interosseous, FDI, and extensor carpi radialis, ECR) did not dissociate between the two alternative action intentions. Thus, it could not be tested whether motor resonance was tuned toward the intention suggested by context or kinematics.

In a subsequent study (Betti et al., 2022), the authors recorded the activation of the muscle specifically involved during the execution of two alternative actions. Namely, the activation of the abductor digit minimi (ADM) was measured during the execution of whole-hand grasping actions toward an apple or a glass; the actions could be performed with the individual intention to eat the apple or to drink from the glass or with the interpersonal intention to offer the object to another peer. In this case, it was found that the ADM differentiated between the two whole-hand reaching-to-grasping actions performed on the same object, but with different intentions, being more activated in performing an individual than an interpersonal action. Then, participants underwent an implicit-learning phase during which the associations between an arbitrary contextual cue (i.e., color of a plate) and a specific action were manipulated, to promote contextual expectations of an action given a specific contextual cue. Finally, the authors assessed motor resonance during observation of the early phases of action deployment embedded in a context that pointed to the same or the opposite intention with respect to the one suggested by the kinematics. Interestingly, the results showed that motor resonance reflected the activation of the most probable action suggested by the contextual information, even when the (ambiguous) kinematics pointed to the opponent intention.

Crucially, in Betti et al. (2022), the contextual modulations were formed ex novo, thus not representing pre-existing ecological condition. Furthermore, kinematics was ambiguous, thus leaving the possibility that context may drive motor resonance only when kinematics cues are scanty (Cavallo et al., 2013). More importantly, the differentiation between the two opposite action intentions was limited to a single action-muscle dissociation, since the ADM was more involved in individual (i.e., to eat) than interpersonal (i.e., to offer) actions, but they did not test an opposite pattern for a muscle that was more involved in the interpersonal than in the individual action. Since a double action-muscle dissociation could not be documented, the possibility that the modulation of ADM MEPS partially reflected general arousal effects, and not specific motor representations, could not be fully excluded.

Considering these observations, the main aims of the present study were to explore the interaction between kinematics and ecological contextual information during the prediction of observed actions at different levels of sensorial ambiguity (i.e., more ambiguous or more reliable kinematics) and to probe the effects of this interaction on both behavioral prediction and motor resonance.

We used videos representing everyday-life actions during breakfast time and showing an actor reaching and grasping sweet objects of different sizes (big, small) or their containers. According to object size, the two actions differently required a whole-hand or a precision grip to implement the intention to eat the piece of food or to move its container. For instance, grasping a big piece of food (i.e., a krapfen) placed on a plate with the intention to eat required a whole hand grip, while grasping its container to move required a precision grip (i.e., with thumb-index opponency). The opposite hold true for a small piece of food (i.e., cream puff) placed in a bowl, where a precision grip was required to eat the food object and a whole hand grip to move its container. In this way, there was a double dissociation of muscle-specificity prompted by different object sizes but with the same over-arched intention. Moreover, actions could be embedded in contextual

scenarios that characterized the plausibility of one action and could be congruent or incongruent with movement kinematics. The context of a set table was congruent with the action of grasping the food object with an eating intention and it was incongruent with the action of grasping the food container with a moving intention. Conversely, the context of a cleared table was congruent with a moving intention and incongruent with an eating intention. Further, action videos were interrupted at early and late interruption points, thus manipulating the amount of available kinematics information between conditions.

The study comprised the following phases. Before the action observation session, we performed Electromyography (EMG) recordings during the execution of eating and moving actions directed to the same objects used in the videos to qualify muscle specificity. Beyond the FDI and ADM, which were expected to be differently involved in precision vs. whole-hand grips, respectively, [Cretu et al. \(2019\)](#), we also recorded EMG from a forearm muscle (i.e., extensor carpi radialis, ECR) as a control muscle. We hypothesized that the FDI should be more involved in precision grips, namely in grasping the small sweet with the intention to eat or the plate containing the big sweet with the intention to move. Instead, the ADM should be more involved in whole-hand grips, namely in grasping the big sweet with the intention to eat or the bowl containing the small sweet with the intention to move. The control forearm ECR muscle was expected to show no grip-specific modulation. We deliberately chose not to include any contextual items during action execution to isolate the muscular involvement in the different actions without any contextual modulation. Indeed, it has been recently shown that contextual modulation can affect the kinematics of executed movements ([Ciceri et al., 2023](#)).

Afterwards, to test the effects of the interaction between kinematic and contextual information on motor resonance, we combined spTMS with recording of MEPs from the same muscles during observation and prediction of the reaching-to-grasp actions in congruent and incongruent contexts. We hypothesized that CSE should be differentially modulated by the observation of whole-hand vs. precision grips, but that top-down contextual expectations might influence these motor resonance processes related to the actual sensorial information, especially at the early interruption points. More specifically, three different hypothetical scenarios were foreseen. If *kinematics prevails* (i), CSE should reflect the differential muscular involvement for the two object-directed movements in both congruent and incongruent contexts. Thus, the FDI should be more activated when observing an unfolding precision grip (i.e., to eat the small objects or to move the container of big objects), while the ADM should be more activated when observing an unfolding whole-hand grasp (i.e., to eat big objects or to move the container of small objects), independently from contextual congruency and interruption time. Alternatively (ii), if *contextual information is integrated with the processing of unfolding kinematics* ([Amoruso et al., 2016, 2018b](#); [Amoruso and Urgesi, 2016](#); [Cretu et al., 2019](#)), motor resonance should be affected by the intention suggested by the contextual scenario, with reduced muscle-specific motor-resonance for incongruent vs. congruent contexts, especially at early interruption times. Finally (iii), if *contextual information drives motor resonance* effects ([Betti et al., 2022](#)), the pattern of action-muscle specificity should follow the action suggested by the context independently from the observed kinematics and the interruption point. Thus, greater cortico-spinal facilitation of the FDI should be observed whenever small objects are embedded in a set table (i.e., pointing to an eating action) or big objects in a cleared table (i.e., pointing to a moving action), while greater ADM facilitation should be observed whenever small objects are embedded in a cleared table and big objects in a set table.

Importantly, different studies showed an alteration deficit in integrating kinematics and contextual information both in individuals with autism spectrum disorder (ASD, [Sinha et al., 2014](#); [Amoruso et al., 2019](#)) and in individuals with high autistic traits, either at a behavioral ([Bianco et al., 2020, 2024](#)) or at the physiological level of motor resonance ([Amoruso et al., 2018b, 2020](#); [Betti et al., 2022](#)). Based on this premise,

an additional exploratory aim of the study was to investigate at what extent the predictions based on contextual cues are related to the presence of autistic traits (measured with the Autism Quotient, AQ, [Baron-Cohen et al., 2001](#)) in neuro-typical populations. We hypothesized that the impact of contextual modulation on the motor coding of the unfolding intention should negatively correlate with the individual levels of autistic traits.

## 2. Materials and methods

### 2.1. Participants

A total of 31 participants (17 F; mean age = 23.58 years; SD = 4.22) were recruited among students at the University of Udine. Participants were all right-handed according to the Standard Handedness Inventory ([Briggs and Nebes, 1975](#)), had normal or corrected-to-normal visual acuity, reported no history of neurological, psychiatric, or other major medical problems and were free from any contraindication to TMS ([Rossi et al., 2009](#)). They gave written informed consent before experimentation and received course credits for their participation in the study. We did not complete the testing of one participant to avoid discomfort because his resting motor threshold was too high (64 % of the stimulator output). Further, data from one participant was excluded due to technical problems during the recordings (lacking > 50 % MEPs for the ADM muscle). Accordingly, data analysis was performed on 29 participants (16 F; mean age = 23.79 years; SD = 4.28). The experimental procedures were approved by the local Ethics Committee (Comitato Etico Unico Regionale, Friuli Venezia Giulia, Italy, *Parere CEUR-2021-Sper-65*) and were carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki. No discomfort or adverse effects during TMS and MEP acquisitions were reported or noticed. Please refer to the data handling session for power analysis and sample size determination.

### 2.2. Stimuli

Experimental videos were recorded in color with a Canon EOS 550D camera at 30 frames per second. Video stimuli depicted a male (43 yo) or a female (36 yo) model performing everyday-life actions during breakfast time. The view angle included the table where the objects were placed and the actor right upper arm, while the face and remaining actor's body parts were not visible. Using their right hand, the actors could reach and grasp a krapfen (big object) or one of two cream puffs (small objects) placed on a container. A white plate served as container for the big object, while a transparent bowl served as container for the small object. Two possible actions were recorded: reaching and directly grasping the food object with the intention to eat or reaching and grasping the food container with the intention to move. Of note, the reach-to-grasp movement patterns were different according to the size of the food object and the shape of the container. For what concerns the action to eat, grasping the big food object required a whole-hand grip, while grasping the small object required a precision grip; for what concerns the action to move, grasping the white plate, where the big food object was placed, required a precision grip, while grasping the transparent bowl, where the small food object was placed, required a whole-hand grip. In this way, we created opposite intentions (eating vs. moving) with equal prehension grips according to object size, thus allowing us to test for a double dissociation between action intention and its kinematics profile. To ensure the spontaneity of the actions, in the original videos the actors were asked to perform the full movement: for the action to eat, they grabbed and brought the food till the mouth; for the action to move, they grabbed and moved the container onto a white tray placed on the table on their right. Actors were further instructed to perform the actions at their own pace so that the movements were fully natural.

Crucially, the actions were embedded in the context of a breakfast

table set with crockery pointing at i) a meal that had yet to be consumed, which provided contextual cues to an eating intent, ii) a meal that had already been consumed, which provided contextual cues to a moving intent. In the set table scenario, the items consisted of a teacup full of tea, a closed teapot with a teabag inside, an empty saucer and a tray; in the cleared table scenario, the items consisted of an empty teacup, an open empty teapot, a teabag placed on the saucer and a tray. Accordingly, the intentions suggested by the two different contextual scenarios could be congruent or incongruent with the intentions behind the actual action kinematics. For instance, the context of the set table was congruent with the action of grasping the food object with the intention to eat, but it was incongruent with the action of grasping the food container with the intention to move. Conversely, the context of the cleared table was congruent with the action of grasping the food container with the intention to move, but it was incongruent with the action of grasping the food object with the intention to eat (Fig. 1). A total of 32 different videos were used, resulting from the factorial combination of 2 Object sizes (big, small)  $\times$  2 Action intentions (to eat, to move)  $\times$  2 Contexts (congruent, incongruent)  $\times$  2 Actors (male, female)  $\times$  2 repetitions of the same condition. The choices of selecting two different actors for action performance and of recording two repetitions of the same condition were made for increasing the variability and avoiding any specific bias in action execution. Videos were edited using Avidemux 2.7.6 - Release Software (<https://avidemux.org/>) to match the duration across the videos (30 frames), where the 18th frame showed the maximal aperture of the hand (pre-shaping) during the reaching phase of the movement and the 30th frame the contact of the hand with the target object. To avoid altering the temporal profile of the movements, we first verified that the duration of the longest video (i.e., slowest movement) was within the 30-frame duration; then, we aligned all the videos at the frame with maximal grip aperture and presented 17 frames before and 12 frames after it. If a video did not contain enough frames before the maximal-aperture frame, we repeated the initial static hand frame to reach the same video duration before maximal grip aperture. Since the latest interruption point was largely ahead the hand-object contact, no manipulation was required at the end of shorter videos. The stimuli were selected based on a pilot experiment in which we validated the stimuli in terms of the plausibility of the contextual manipulation (see Supplementary Fig. 2) and the dissociation between the kinematic parameters of the two action intentions directed to the small or big objects (see Supplementary Fig. 3). In the pilot experiment, original videos also included fruits objects (an apple for the big and strawberries for the small object) and neutral contexts (i.e. a table without any contextual cues). Crucially, fruit objects were not strongly associated with the congruent vs. incongruent context and were excluded from the main experiment (see Supplementary Fig. 4). Further, neutral contexts were removed to simplify the experimental design.

### 2.3. Procedure

The whole experimental design consisted of two parts: an action execution session followed by an action observation session, during which MEPs were recorded. Both sessions were conducted in the same day.

### 2.4. Action execution session

During the action execution session, EMG activity was recorded from the right FDI, ADM and ECR using surface Ag/AgCl disc electrodes (1 cm diameter) placed in a belly-tendon montage. The active electrode positions were determined by palpation during maximum voluntary contraction separately for each muscle; reference electrodes were positioned over the proximal interphalangeal joint of the index, the proximal interphalangeal joint of the little finger and the radial styloid process for the FDI, ADM and ECR, respectively. The ground electrode was positioned on the right arm close to the shoulder. Electrodes and cables were organised to avoid restrictions in participants' movements. All electrodes were connected to a Biopac MP-160 system (BIOPAC System, Inc., Goleta, CA) for amplification, digitalization (sampling rate 6250 Hz) and band-pass filtering (5–2000 Hz) of the EMG signal.

During the action execution session, participants sat in a chair in front of a table with the right hand relaxed. After positioning the electrodes, they were asked to wait for an auditory instruction (“*mangiare*” or “*spostare*”, i.e., in English “to eat” or “to move”) and to wait for a later auditory tone (Go signal) prompting the start of the movement. Two different clay reproductions of a krapfen or cream puff objects were placed, respectively, on a white plate or on a transparent bowl. The container was positioned on a digital platform that triggered the EMG recording when released by object lifting. As in the video stimuli, four different actions were implemented: eating the krapfen by grasping the food using a whole-hand grip, moving the krapfen by grasping the white plate using a precision grip, eating the cream puff by grasping the food using a precision grip and moving the cream puff by grasping the transparent bowl using a whole-hand grip. For the eating actions they were also asked to complete the action by bringing the food towards the mouth (avoiding contact), while for the moving actions they were asked to complete the action by placing the plate/bowl on a tray positioned to their right. Actions were performed in blocks of 10 trials for each condition and the order of blocks was counterbalanced between participants. For each trial, a marker on the EMG trace was obtained concomitantly with the release of the food/container from the digital platform. The action execution session lasted around 40 min.

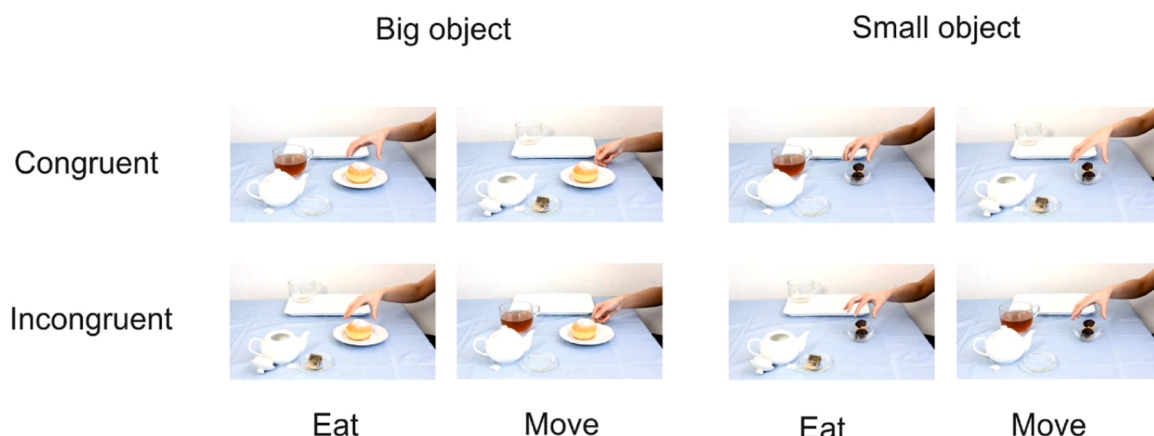


Fig. 1. Overview of the 23rd frame of the action videos embedded in congruent and incongruent contexts.

## 2.5. Action observation session and MEP recording

Following a break of approximately 20 min for set-up arrangement and for allowing cortical excitability to return to baseline levels (Classen et al., 1998), participants underwent the action observation session. The participant sat on a comfortable armchair in a dimly lit room, with the monitor placed 1 m away from the eyes. Participants performed a two-alternative forced choice (2AFC) task in which they were instructed to observe the videos and predict which one of the two possible intentions (i.e., to eat or to move) was behind the actor's movements. Experimental videos were displayed at the centre of a 24-inch LCD monitor (resolution, 1920 × 1080 pixels; refresh frequency, 120 Hz) on a black background and subtended 11.42° × 6.29° of visual angle. For video presentation, each frame was presented for 4 refresh cycles (i.e., 33.33 ms). Video presentation could be interrupted at an early (frame 13) or late (frame 23) action phase. As shown in the kinematics analysis of the videos (see Supplementary Material), at frame 13, the actor was at the very beginning of the reaching movement, providing ambiguous kinematic information; at frame 23, the videos showed the actor's hand approaching the object (7 frames before the hand-object contact), making the pre-shaping of the hand configuration highly informative about the two action intentions. To match the duration of the videos at 766.67 ms for both interruption points, the duration of first frame of the videos, showing a still hand, was lengthened to 366.67 ms for the early interruption time. This way, contextual information was available for the same amount of time for all interruption points so that any effect on task performance reflected the amount of kinematic information of the video and not the different duration of the videos, thus making the comparisons among conditions more reliable. The choice of the interruption frames was dictated by the results of the behavioral task of the pilot study, which originally also included an interruption point at an intermediate frame (frame 18, see Supplementary Fig. 4). Since contextual modulation was similar for both middle (frame 18) and late (frame 23) interruption points, the former was not used in the main experiment.

Participants were informed that videos were interrupted before action completion and were encouraged to predict the action intention by the available information in the videos. Task instructions encouraged the use of kinematic information to make predictions, but also included the presentation of the possible contextual settings and relative objects. Participants were instructed that they were going to observe an actor performing reach-to grasp movements towards different objects, and they were informed that the actor could grasp the object and bring it to the mouth with the intention to eat it or grasp the object to put it on a white tray placed on the table with the intention to move it. Crucially, they were also informed that some items in the scene (i.e., a teapot, a teacup, and a tea bag) were presented in different scenarios: a set or a cleared table. The association between contextual cues and action intentions was not explicitly encouraged, thus remaining implicit.

Each trial started with a white fixation point lasting 1000 ms followed by the presentation of the experimental video. Afterwards, a black screen was presented for 200 ms and, in this interval, the TMS pulse was randomly delivered at 16.67, 50, 83.33, or 116.67 ms after video offset. This variability was implemented to avoid any priming effect that could affect MEP size. Subsequently, a response prompt frame was presented with the verbal descriptors of the two possible options (“*mangiare*” or “*spostare*”, in English “to eat” or “to move”) written in white ink on a black background. The response prompt frame remained until a response was recorded. Since the options “to eat” or “to move” were presented above or below the center of the screen, the participant was asked to verbalize the response by saying “*su*” or “*giù*” (in English “up” or “down”) and the researcher recorded the answer with a computer mouse. To prevent response preparation, the spatial location of the two options was randomized across trials. The rationale of obtaining verbal instead of button press responses was that this procedure would ensure MEPs not to be contaminated by muscular contraction artifacts

associated to hand-response preparation (Meister et al., 2003). Following participant's response, a black screen appeared for 4000 ms. This way, we ensured an intertrial interval of at least 6500 ms, to prevent cumulative effects of TMS (Chen et al., 1997) across trials. A schematic representation of the trial structure is presented in Fig. 2.

Each of the 32 videos was presented four times with an early interruption and four times with a late interruption time, resulting in 256 stimuli randomly presented in four blocks of 64 trials each. Prior to and following the observation task, baseline corticospinal excitability was measured by acquiring 16 MEPs while participants passively watched a fixation cross and 16 MEPs while they watched a static hand image, both presented for 1250 ms. During baseline recordings, the fixation cross or the static hand images were presented in two distinct blocks. The choice of including both a fixation cross and a static hand ensured us to obtain a low-level and a high-level baseline condition (Naish et al., 2014). The order of the two blocks before and after the observation task was the same within each participant, but it was counterbalanced across participants.

During the action observation session, spTMS was applied to the left M1 using a Magstim 200 stimulator (maximum output, 2 T at coil surface; pulse duration, 250  $\mu$ s; risetime, 60  $\mu$ s) connected to a 70 mm figure-of-eight coil (Magstim polyurethane-coated coil). MEPs were recorded simultaneously from the FDI, ADM and ECR of the right hand. EMG recording was as in the action execution session. The TMS coil was placed tangentially to the scalp with the handle pointing backwards and laterally at about a 45° angle away from the midline, approximately perpendicular to the central sulcus (Di Lazzaro et al., 1998). The TMS intensity during the observation session was adjusted to 130 % of the individual resting motor threshold (rMT), which was determined as the minimum intensity able to elicit MEPs with around 50  $\mu$ V peak-to-peak amplitude in the muscle with the lowest threshold in 5 of 10 consecutive pulses (Rossini et al., 1994). In keeping with previous studies (e.g., Finisguerra et al., 2018), using the lower threshold muscle for determining rMT allowed us to avoid saturation of cortico-spinal excitability modulation (Devanne et al., 1997) and possible loss of motor resonance effects (Loporto et al., 2013) during recording MEPs from multiple muscles, while ensuring reliable responses from all muscles with a stimulation intensity of 130 % rMT. The rMT ranged from 29 to 56 % (mean = 45.96 %; SD = 6.59 %) of the maximum stimulator output.

The entire action observation session, including baseline measures collection, lasted around 100 min. The timing of stimuli presentation, EMG recording and TMS trigger and the randomization of stimuli and TMS pulses were controlled with E-Prime 3.0 software (Psychology Software Tools Inc., Pittsburgh, PA) running on a PC.

## 2.6. Psychological measures

Following the action observation session, participants completed the Italian versions of the Autism-Spectrum Quotient (AQ, Baron-Cohen et al., 2001). The AQ has been largely used to evaluate the distribution of autistic traits in the general population and is made of up 50 items classified into five subscales (i.e., Attention switching, Attention to Detail, Communication, Imagination, Social Skills). Responses are provided on a four-point rating scale ranging from definitely agree to slightly agree, slightly disagree and definitely disagree responses. Slightly and definitely agree or slightly and definitely disagree responses are collapsed together in a score of 0 or 1, depending on the absence/presence of the autistic trait. The scoring is reversed for the items in which an “agree” response indicates an autistic trait. Summed scores for each subscale can range from 0 to 10. Higher scores reflect higher autistic traits and in particular greater attention to details and lower attention switching, communication, imagination, and social skills abilities.

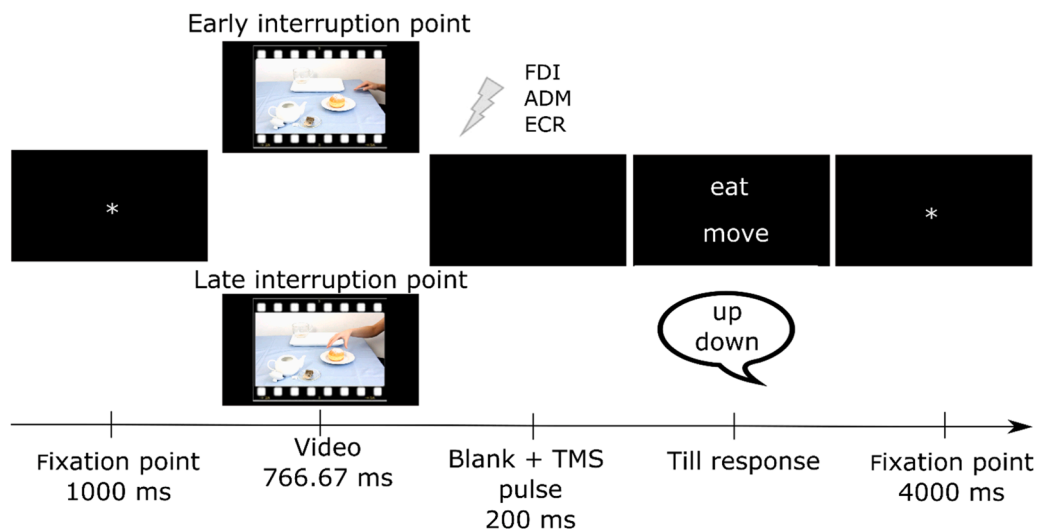


Fig. 2. Schematic representation of the action prediction task used during the TMS session.

## 2.7. Data handling

The required sample size ( $N > 29$ ) for our  $3 \times 2 \times 2 \times 2$  (Muscle  $\times$  Food size  $\times$  Context  $\times$  Time) RM-ANOVA design was determined based on a previous TMS study investigating the effects of kinematics and contextual information on motor resonance during action observation ( $\eta_p^2 = 0.157$ ; Betti et al., 2022). Using the G\*power software (Faul et al., 2009) with the “as in SPSS option”, we set the effect size at 0.43, the alpha level at 0.05 and the desired power at 80 %. For all analyses,  $\eta_p^2$  was used to measure the effect size and the Duncan’s test was used for post-hoc analysis.

## 2.8. Electromyography data during action execution

The EMG data collected during action execution were analysed off-line using the AcqKnowledge 5.0 software (BIOPAC Systems, Inc., Goleta, CA). The EMG signal was rectified using a 30-ms epoch for the windowed mean. The mean rectified EMG signal (in  $\mu\text{V}$ ) was then measured in 12 bins of 200 ms starting from 1400 ms prior to the release of the object from the platform (hand-object contact, 8th bin) and ending 1000 ms after it, for a total of 2400 ms, covering both the reach-to-grasp phase and the lifting phase of the motor act. For each trial, the mean EMG signal of the second bin (200–400 ms) acquired at the beginning of the EMG segment was used as baseline. We did not select the first bin as baseline to avoid any contaminations concomitant with the start of the segment recording. Then, following the procedure proposed by Fridlund and Cacioppo (1986), we subtracted the EMG signal at baseline from that at each experimental bin. The baseline-referenced EMG activity was then averaged within experimental conditions (10 trials for each condition). Separately for each muscle (FDI, ADM, ECR), we conducted a RM-ANOVA with 2 (Object size: Big vs. Small)  $\times$  2 (Action: Eat vs. Move)  $\times$  12 (Time Bin: 1–12) as within-subject variables.

## 2.9. Behavioral data during action observation

Participants’ responses for each experimental condition of the main action-prediction experiment were analysed using a Signal detection theory approach (Stanislaw and Todorov, 1999). The two categories were the “eat” and “move” actions and were based on the actual action kinematics: videos showing “eat” actions correctly identified as “eat” were considered hits; videos showing “move” actions wrongly detected as “eat” were considered false alarms. A bias-corrected measures of sensitivity in discriminating between two categories ( $d'$ ) were obtained

by transforming the response proportion to z-scores, and then subtracting the z-score that corresponds to the false alarm rate from the z-score that corresponds to the hit rate (Stanislaw and Todorov, 1999). Also, we calculated a measure of response criterion ( $c$ ) for each experimental condition, an index of bias in delivering specific response. The  $c$  values were calculated by averaging the z-score corresponding to the hit rate and the z-score corresponding to the false alarm rate, and then multiplying the result by  $-1$  (Stanislaw and Todorov, 1999).

After using Kolmogorov–Smirnov for checking normality in the distribution of the data,  $d'$  and criterion scores for the action prediction task were entered into a RM-ANOVA with 2 Object size (Big vs. Small)  $\times$  2 Context (Congruent vs. Incongruent)  $\times$  2 Interruption point (Early vs. Late) as within-subject variables. Further we calculated the degree of contextual modulation (i.e., difference between congruent and incongruent contexts) for early and late interruption points, which were compared with two-tailed, dependent-sample  $t$ -test analysis.

## 2.10. MEPs data during action observation

MEP amplitudes were measured peak-to-peak (in  $\mu\text{V}$ ) for each experimental trial. Since background EMG activity is known to affect motor excitability (Devanne et al., 1997), MEPs with preceding background EMG activity in the 60 ms window before the TMS pulse deviating from the mean by more than 2 SD were removed from further analysis. Further, we excluded trials in which MEP amplitudes were lower or higher than 2 SD from the participant’s mean in each experimental condition. A total of  $8.9 \pm 4.0\%$ ,  $9.5 \pm 3.9\%$  and  $7.8 \pm 1.9\%$  of MEPs were excluded, respectively, for the FDI, ADM and ECR recordings. Individual mean MEP amplitudes were then calculated for each experimental condition.

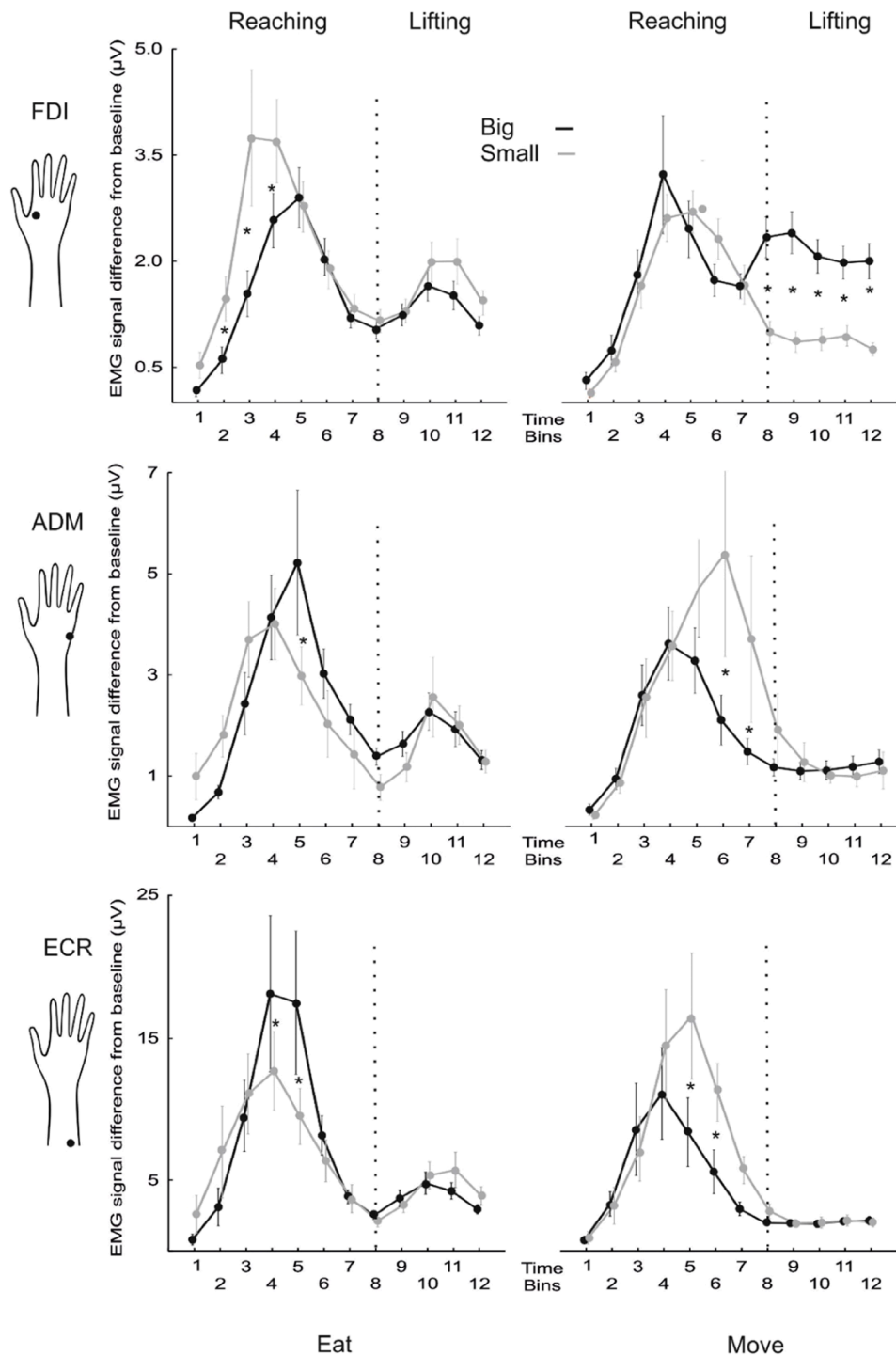
For the baseline recordings, after performing the same procedures of trials exclusion done for the experimental session, we conducted a RM-ANOVA with 2 (Time: Pre vs. Post)  $\times$  2 (Type: Fixation cross vs. Static hand) as within-subject factors, separately for each muscle. After verifying that baseline MEPs did not differ among conditions (see the Results session), they were averaged and used as reference for the data analysis of the MEPs obtained during the task. Indeed, to reduce inter-individual variability, we subtracted the averaged MEP amplitude obtained during baseline recordings from the MEP data obtained during each condition of the action observation task, separately for each muscle. After using Kolmogorov–Smirnov for checking normality in the distribution of the data, the baseline-referenced MEPs data of the action prediction task were entered into an RM-ANOVA with 3 (Muscle: FDI vs. ADM vs. ECR)  $\times$  2 (Object size: Big vs. Small)  $\times$  2 (Context: Congruent vs. Incongruent)  $\times$

2 (Interruption point: Early vs. Late) × 2 (Action: Eat vs. Move) as within-subject variables. Further, peak-to-peak values of background EMG activity (in  $\mu\text{V}$ ) were extracted and submitted to the same RM-ANOVA to verify that this did not affect the main analysis.

2.11. Correlation analysis

Spearman correlation analyses were performed to test whether the

contextual modulation occurring at behavioral and motor levels was associated to individual differences in autistic traits. Based on the results of the RM-ANOVA, we calculated a differential index ( $\Delta d'$  or  $\Delta\text{MEP}$ ) obtained by subtracting, respectively, the  $d'$  scores or the amplitude of MEPs (separately for each muscle) obtained for incongruent contexts from those obtained for congruent contexts.



**Fig. 3.** EMG results. Mean values of the EMG signal (expressed as  $\mu\text{V}$  difference from baseline) during execution of actions (eat, move) directed to a big (black line) and a small (grey line) food object, for the FDI, ADM and ECR muscles. The vertical dashed line at time bin 8 corresponds to the time of the release of the object/container from the digital platform (i.e. the grasping time). Time bins 1–7 refer to the object reaching phase while time bins 9–12 refer to the object lifting phase. Asterisks indicate significant differences ( $p < 0.05$ ). Error bars represent SEM.

### 3. Results

#### 3.1. Action execution

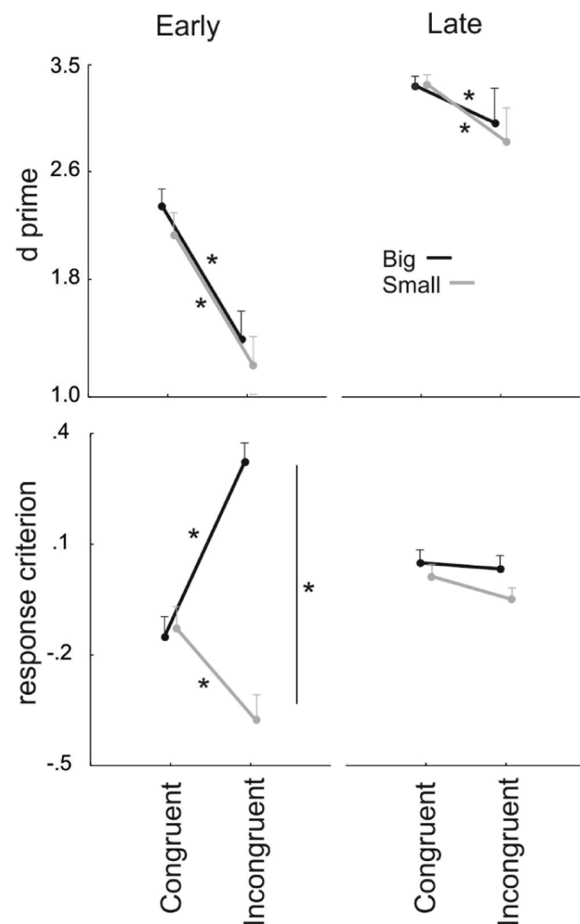
The RM-ANOVA on the EMG data for the FDI muscle (Fig. 3) showed a main effect of Time Bin ( $F_{11,308} = 15.62, p < 0.001, \eta_p^2 = 0.36$ ) and Object size  $\times$  Action ( $F_{1,28} = 18.31, p < 0.001, \eta_p^2 = 0.39$ ), Object size  $\times$  Time Bin ( $F_{11,308} = 5.26, p < 0.001, \eta_p^2 = 0.16$ ), and Action  $\times$  Time Bin ( $F_{11,308} = 6.45, p < 0.001, \eta_p^2 = 0.19$ ) two-way interactions, all qualified by a three-way Object size  $\times$  Action  $\times$  Time Bin interaction ( $F_{11,308} = 4.48, p < 0.001, \eta_p^2 = 0.14$ ). Post-hoc Duncan test on the three-way interaction revealed that the FDI was significantly more engaged for eating the small food object (i.e., involving a precision grip) than for eating the big one (i.e., involving a whole-hand grip) from bin 2 to bin 4 (bin 2:  $p = 0.024$ ; bin 3:  $p < 0.001$ ; bin 4:  $p = 0.001$ ). Conversely, the same muscle was more engaged for moving the big object container (i.e., involving a precision grip of the plate) than for moving the small object container (i.e., involving a whole-hand grip of the bowl) at bins 8–12 (bin 8:  $p < 0.001$ ; bin 9:  $p < 0.001$ ; bin 10:  $p = 0.002$ ; bin 11:  $p = 0.007$ ; bin 12:  $p < 0.001$ ). Collectively, this pattern of results suggests that the FDI was more engaged during precision (i.e., for the eating action directed to the small object and for the moving action directed to the plate containing the big object) than whole-hand grips (i.e., for the moving action directed to the bowl containing the small object and for the eating action directed to the big object). More precisely, the FDI was more activated for the eating action directed to the small object particularly during the reaching phase and for the moving action directed to the big object particularly during the lifting phase.

The RM-ANOVA on the EMG data for the ADM muscle (Fig. 3) showed a main effect of Time Bin ( $F_{11,308} = 12.78, p < 0.001, \eta_p^2 = 0.31$ ) and an Action  $\times$  Time Bin interaction ( $F_{11,308} = 2.31, p = 0.009, \eta_p^2 = 0.08$ ), which were qualified by a three-way Object size  $\times$  Action  $\times$  Time Bin interaction ( $F_{11,308} = 4.47, p < 0.001, \eta_p^2 = 0.14$ ). Post-hoc Duncan test on the three-way interaction revealed that, in the eating action, the ADM was significantly more engaged for the big than the small object at bin 5 ( $p = 0.002$ ); in the moving action, the ADM was significantly more engaged for the small than the big object at bins 6 ( $p < 0.001$ ) and 7 ( $p = 0.003$ ). Collectively, this pattern of results revealed that the ADM, particularly during the reaching phase, was more engaged during whole-hand (i.e., for the eating action directed to the big object and for the moving action directed to the bowl containing the small object) than precision grips (i.e., for the eating action directed to the small object and for the moving action directed to the plate containing the big object).

The RM-ANOVA on the EMG data for the ECR muscle (Fig. 3) showed main effects of Action ( $F_{1,28} = 10.87, p = 0.002, \eta_p^2 = 0.28$ ) and Time Bin ( $F_{11,308} = 10.49, p < 0.001, \eta_p^2 = 0.27$ ) and an Action  $\times$  Time Bin interaction ( $F_{11,308} = 1.83, p = 0.048, \eta_p^2 = 0.06$ ), all qualified by a three-way Object size  $\times$  Action  $\times$  Time Bin interaction ( $F_{11,308} = 3.86, p < 0.001, \eta_p^2 = 0.12$ ). Post-hoc Duncan test revealed that, in the eating action, the ECR was significantly more engaged for the big than the small object at bins 4 ( $p = 0.019$ ) and 5 ( $p < 0.001$ ); in the moving action, this muscle was significantly more engaged for the small than the big object at bin 5 ( $p < 0.001$ ) and 6 ( $p = 0.029$ ). Similar to the ADM, the ECR was more engaged during actions with whole-hand than precision grips and was more activated for the eating action directed to the big object and for the moving action directed to the small object, mostly during the reaching phase.

#### 3.2. Action observation: behavioral data

The RM-ANOVA on  $d'$  (Intercept:  $F_{1,28} = 539.63, p < 0.001, \eta_p^2 = 0.96$ , Fig. 4) yielded significant main effect of Object size ( $F_{1,28} = 4.20, p = 0.049, \eta_p^2 = 0.13$ ), with better performance for big ( $2.573 \pm 0.107$ ) than small ( $2.437 \pm 0.118$ ) objects. Furthermore, the main effects of Context ( $F_{1,28} = 8.41, p = 0.007, \eta_p^2 = 0.23$ ) and Interruption point ( $F_{1,28} = 175.29, p < 0.001, \eta_p^2 = 0.86$ ) and their two-way interaction ( $F_{1,28} =$



**Fig. 4.** Behavioral results during action observation. Upper panel: participants' sensitivity ( $d'$ ) in predicting the action towards the big (black line) or the small object (grey line) for the two contexts (congruent, incongruent) at the two interruption points (early, late). Lower panel: participant's response criterion for the same conditions. Data points represent group averages. Asterisks indicate significant comparisons ( $p < 0.05$ ). Error bars represent SEM.

$16.69, p < 0.001, \eta_p^2 = 0.37$ ) were significant. Duncan post-hoc comparisons showed that  $d'$  scores were higher for congruent than incongruent contexts for both early (congruent:  $2.339 \pm 0.110$ , incongruent:  $1.339 \pm 0.200, p < 0.001$ ) and late (congruent:  $3.349 \pm 0.048$ , incongruent:  $2.992 \pm 0.251, p = 0.003$ ) interruption points. However, the contextual modulation (i.e., difference between congruent and incongruent contexts) was greater for the early ( $1 \pm 1.245$ ) than the late ( $0.357 \pm 1.408, t_{28} = 4.085, p < 0.001$ ) interruption point.

The RM-ANOVA on response criterion (Fig. 4) yielded significant main effects of Object size ( $F_{1,28} = 36.10, p < 0.001, \eta_p^2 = 0.56$ ) and Interruption point ( $F_{1,28} = 5.27, p = 0.029, \eta_p^2 = 0.16$ ), as well as significant two-way interactions between Object size and Context ( $F_{1,28} = 57.37, p < 0.001, \eta_p^2 = 0.67$ ), Object size and Interruption point ( $F_{1,28} = 8.38, p = 0.007, \eta_p^2 = 0.23$ ), Context and Interruption point ( $F_{1,28} = 5.84, p = 0.022, \eta_p^2 = 0.17$ ), all qualified by a significant three-way interaction between Object size, Context and Interruption point ( $F_{1,28} = 72.85, p < 0.001, \eta_p^2 = 0.72$ ). Duncan post-hoc comparisons showed that, in the case of congruent contexts, no differences emerged between objects, either for the early (big:  $-0.150 \pm 0.054$ , small:  $-0.128 \pm 0.059, p = 0.584$ ) or for the late interruption point (big:  $0.050 \pm 0.035$ , small:  $0.013 \pm 0.032, p = 0.387$ ). In the case of incongruent contexts, the response criterion was higher for the big ( $0.324 \pm 0.052$ ) than for the small object at the early interruption point ( $-0.379 \pm 0.071, p < 0.001$ ), while the difference between objects was only marginally significant at the late interruption point (big:  $0.033 \pm 0.037$ , small:  $-0.049 \pm 0.031, p = 0.058$ ).

This means that, at early interruption points and for incongruent contexts, participants had a bias in reporting a moving action for the big objects and an eating action for the small objects, suggesting that response bias was independent from the affordance provided by the size of the food object. Indeed, independently from the container, one could expect that, in the absence of informative context and kinematics, the cream puffy afforded a precision grip, while the krapfen a whole-hand one, reflecting into a bias to report an eating action, which should lead to a negative criterion for both objects. Conversely, for both objects, we found a bias to report an action associated to a precision grip, required to eat the small object and to move the big object. In keeping with previous findings of higher accuracy for predicting a precision than a whole-hand grip (Amoruso et al., 2016), this bias for reporting a precision-grip action might reflect its easier detection, since it deviates more and earlier from the hand pre-shaping with a maximal finger aperture compared to a whole-hand grip.

3.3. MEPs data during action observation

The RM-ANOVA on baseline measures showed no significant effects

for any muscles (FDI: all  $F < 2.3$ ,  $p > 0.14$ ,  $\eta_p^2 < 0.07$ ; ADM: all  $F < 0.1$ ,  $p > 0.79$ ,  $\eta_p^2 < 0.01$ ; ECR: all  $F < 0.2$ ,  $p > 0.78$ ,  $\eta_p^2 < 0.01$ ). This suggested that baseline CSE was comparable while viewing a fixation cross and a static hand and remained stable across the experimental session.

The RM-ANOVA on baseline-referenced MEPs during the action prediction task (Intercept:  $F_{1,28} = 11.02$ ,  $p = 0.002$ ,  $\eta_p^2 = 0.28$ , Fig. 5) yielded a significant Muscle  $\times$  Object size interaction ( $F_{2,56} = 4.38$ ,  $p = 0.017$ ,  $\eta_p^2 = 0.13$ ), qualified by a four-way Muscle  $\times$  Object size  $\times$  Context  $\times$  Action interaction ( $F_{2,56} = 6.29$ ,  $p = 0.003$ ,  $\eta_p^2 = 0.18$ ).

Duncan post-hoc test of the modulation of the FDI across observation conditions revealed that, when eating actions were shown in congruent contexts (i.e., a set table), FDI CSE was higher for the small ( $268.557 \pm 56.535 \mu\text{V}$ ) than the big object ( $214.293 \pm 63.465 \mu\text{V}$ ;  $p = 0.046$ ), in keeping with the pattern of EMG activation of this muscle during the reaching phase of eating action execution. Relatedly, observing the precision grip required to reach the cream puff activated more the FDI than the whole-hand grip required to reach the krapfen. This between-object difference did not emerge for the moving action (small:  $247.698 \pm 59.553 \mu\text{V}$ ; big:  $268.427 \pm 73.418 \mu\text{V}$ ,  $p = 0.382$ ), namely between the reaching of the plate containing the krapfen and of the bowl

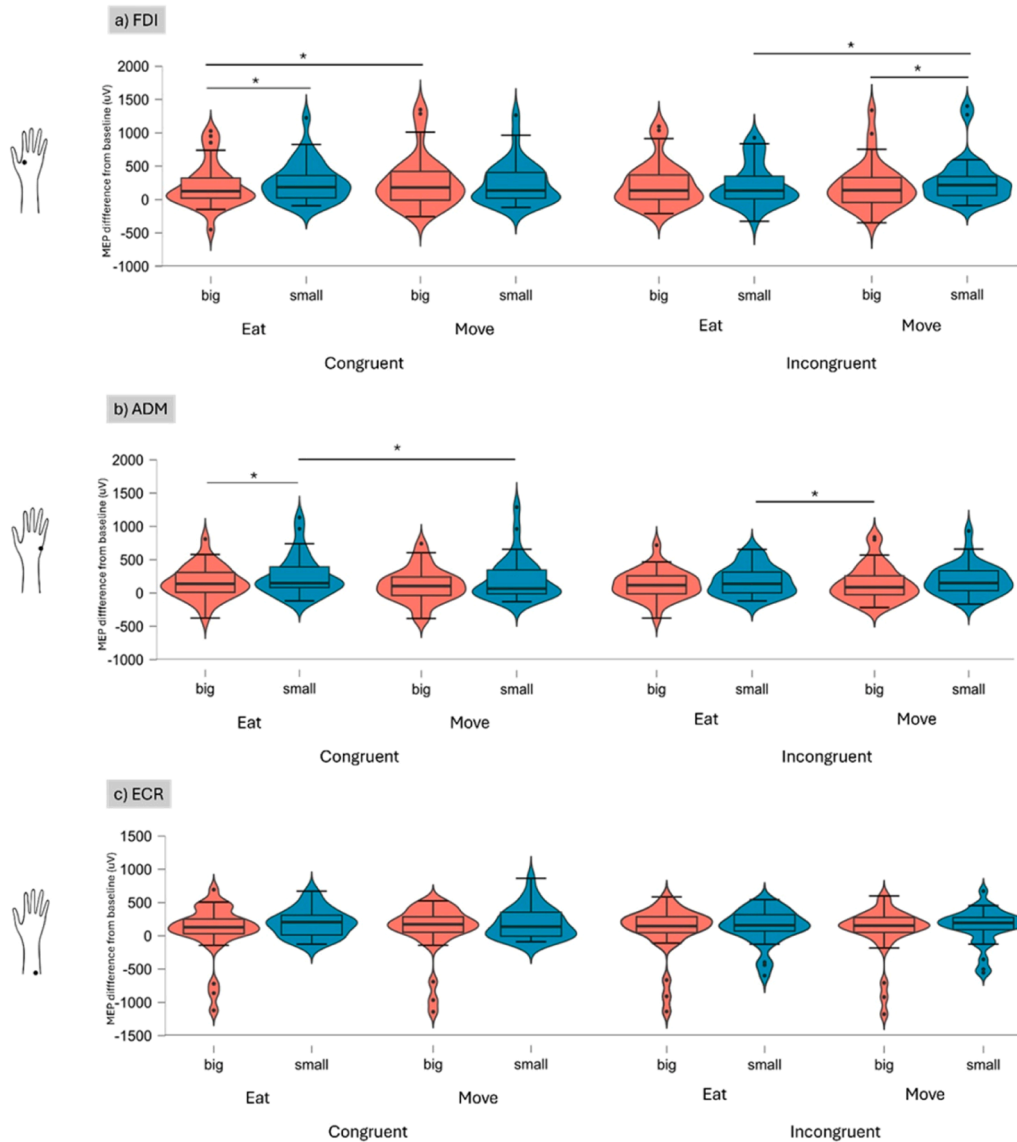


Fig. 5. MEP results (expressed as  $\mu\text{V}$  difference between each condition and baseline) during the action prediction task for the FDI, ADM and ECR muscles for big (black bar) and small (grey bar) objects for eating and moving actions embedded in congruent and incongruent contexts. Asterisks indicate statistically significant differences ( $p < 0.05$ ); error bars indicate SEM.

containing the cream puffs. Furthermore, for congruent contexts, the FDI MEPs were higher while observing the actor grasping the plate containing the big object to move (precision grip) than when grasping the big object to eat (whole-hand grip,  $p = 0.042$ ). This pattern reversed in the case of incongruent contexts, when the FDI CSE was higher for moving the small ( $276.495 \pm 64.936 \mu\text{V}$ ) than the big object ( $203.392 \pm 66.172 \mu\text{V}$ ;  $p = 0.008$ ), while no between-object difference was observed for the eating actions ( $p = 0.324$ ). Therefore, for the moving action, the FDI activation reflected the pattern of the kinematics suggested by the context (i.e. incongruently pointing at a whole-hand grip for eating the krapfen and at a precision grip for eating the cream puff). Additionally, for the small objects embedded in incongruent contexts, FDI MEPs were higher for the moving (when context pointed at eating the cream puff with a precision grip) than the eating action (when context pointed at moving the bowl with a whole-hand grip) ( $215.917 \pm 58.574 \mu\text{V}$ ,  $p = 0.025$ ). Thus, independently from kinematics and the interruption time, the facilitation of FDI CSE during observation of actions directed to small objects was maximal when the objects were embedded in a set table, which pointed to an eating action (i.e., eat-congruent and move-incongruent conditions). Its facilitation during observation of actions directed to big objects was greater when the context and kinematics congruently pointed to a moving action, while this action-specific modulation was suppressed for incongruent kinematic-contextual information.

For congruent contexts, the ADM showed an opposite pattern as compared to the FDI. Indeed, when eating actions were shown in congruent contexts (i.e., a set table), the ADM CSE was higher for the big ( $159.421 \pm 45.948 \mu\text{V}$ ) than the small object ( $76.839 \pm 45.704 \mu\text{V}$ ;  $p = 0.004$ ), in keeping with the pattern of EMG activation of this muscle during the reaching phase of eating action execution. Relatedly, observing the whole-hand grip required to reach the krapfen activated more the ADM than observing the precision grip required to eat the cream puff. This between-object difference did not emerge for the moving action (small:  $134.059 \pm 46.821 \mu\text{V}$ ; big:  $127.094 \pm 47.57 \mu\text{V}$ ,  $p = 0.783$ ), namely between the precision grip required for reaching the plate containing the krapfen and the whole-hand grip required for reaching the bowl containing the cream puffs. Further, for congruent contexts, the ADM MEPs were higher while observing the actor grasping the bowl containing the small object to move compared to grasping the small object to eat ( $p = 0.045$ ). In the case of incongruent contexts, the ADM MEPs were higher for moving the plate containing the big object ( $155.559 \pm 50.784 \mu\text{V}$ ) than for eating the small object ( $82.318 \pm 50.445 \mu\text{V}$ ;  $p = 0.007$ ). However, all the other comparisons were not significant all  $ps > 0.09$ . Overall, this suggests that the incongruence between the kinematic and contextual information suppressed the action-muscle specific modulation of ADM that was observed in congruent contexts.

For the ECR, Duncan post-hoc revealed no significant differences between any conditions (all  $ps > 0.636$ ), confirming that the facilitation of the CSE of this muscle was not modulated by the observation of different types of reaching-to-grasp actions.

Further, an Object size  $\times$  Interruption point  $\times$  Action three-way interaction emerged ( $F_{2,56} = 4.74$ ,  $p = 0.038$ ,  $\eta_p^2 = 0.14$ ). Post-hoc Duncan test on this three-way interaction revealed that, when the interruption point was late, MEPs were higher for the moving ( $172.17 \pm 46.267 \mu\text{V}$ ) than the eating actions ( $116.883 \pm 45.982 \mu\text{V}$ ;  $p = 0.003$ ) directed to the small object. No other significant differences emerged for any comparison (all  $ps > 0.070$ ). All other effects of the RM-ANOVA were not significant (all  $F_s < 2.98$ , all  $ps > 0.059$ , all  $\eta_p^2 < 0.09$ ).

The RM-ANOVA on the raw background EMG activity only yielded a main effect of Muscle ( $F_{2,56} = 9.26$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.25$ ), with the ECR ( $66.67 \pm 5.09 \mu\text{V}$ ) showing higher background EMG activity than the FDI ( $44.5 \pm 6.18 \mu\text{V}$ ;  $p = 0.003$ ) and ADM ( $37.08 \pm 4.8 \mu\text{V}$ ;  $p < 0.001$ ), which did not differ each other ( $p = 0.3$ ). The generally high background EMG activity before the TMS pulse across muscles, and particularly that of the ECR, is likely to reflect postural adjustments during the long

action observation session or to signal recording noise that could not be attenuated. All other effects of the RM-ANOVA were not significant (all  $F_s < 3.89$ , all  $ps > 0.056$ , all  $\eta_p^2 < 0.09$ ), suggesting that our effects on MEP modulation were not driven by alterations of background EMG activity during action observation.

### 3.4. Correlation analysis

Spearman correlations between  $\Delta d'$  and the AQ scores were not significant for any domain. For what concerns the ADM, we found significant negative correlations between  $\Delta\text{MEP}$  and the communication ( $r_s = -0.41$ ,  $p = 0.023$ ) and the imagination ( $r_s = -0.38$ ,  $p = 0.04$ ) subscales (Fig. 6). Collectively these findings indicate that, for the ADM, higher levels of autistic traits reflecting communication and imagination deficits were associated with a reduced contextual modulation of motor resonance.

## 4. Discussion

In the present study, we aimed at testing the effects of the interaction between kinematics and contextual information on behavioral performance and motor resonance during an action prediction task. We used videos showing everyday-life actions in which we manipulated the kinematics of the observed actions, by using actions directed to small or big food objects placed in a container and performed with different intentions to eat the food object or to move its container. Crucially, we preliminarily recorded EMG during the execution of eating or moving actions directed to the objects or to their container to define which muscles were differentially involved in the two motor acts. Afterwards, we measured MEPs from these muscles while the same participants were administered an action prediction task involving the observation of these actions performed by an actor in the context of a breakfast scenario that could be congruent or incongruent with the intention suggested by the kinematics of the action.

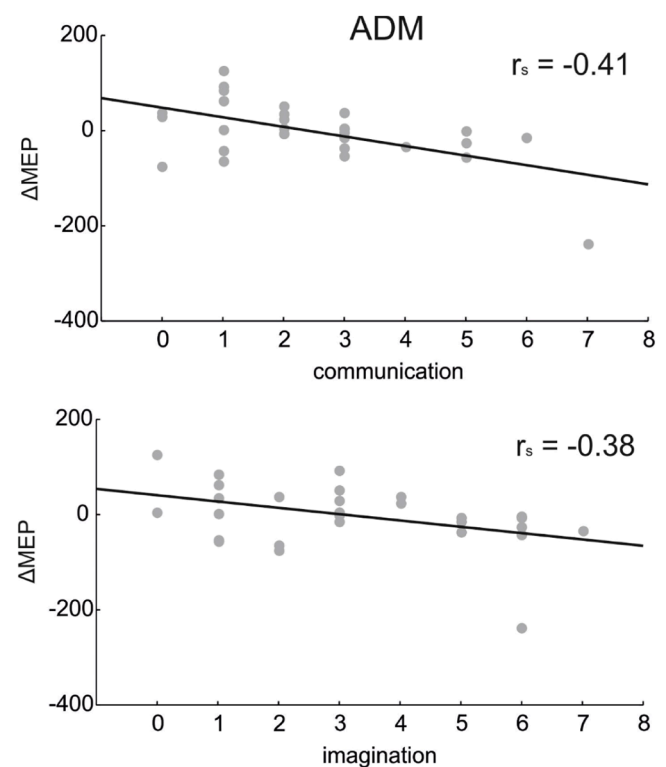


Fig. 6. Correlational results for the MEP differential index ( $\Delta\text{MEP}$ ) of the ADM and the communication (up) and imagination (bottom) subscales. Significant negative correlation emerged.

#### 4.1. Contextual modulation affects action discrimination performance

The behavioral findings showed that sensitivity, which was defined based on kinematics, increased as a function of action deployment from the early to the late interruption point, independently from object type and context. Thus, action prediction performance was dependent on the availability of the kinematics cues, which were increasingly more visible with the progression of the observed action (Ansuini et al., 2014; Becchio et al., 2018) also in the case of contextualized actions (Bianco et al., 2024). Importantly, at both early and late interruption points, the two action intentions led to small difference in terms of kinematic parameters (i.e., thumb-index finger, thumb-little finger, and wrist-table distances; see Supplementary Fig. 3) of the movements directed to the two object sizes. Participants were able to detect these differences, since their sensitivity to action discrimination was nevertheless good ( $d' > 1$ ) at the earliest interruption point and when context provided incongruent information. This is in keeping with previous evidence that even limited kinematics information can be used by the observers to discriminate between alternative action intentions (Cavallo et al., 2016). Previous studies demonstrated that differences in the kinematics profile of observed actions does not necessarily imply that the onlooker can spot this information (Becchio et al., 2018) and that the informativeness of kinematics does not necessarily increase over time (Ansuini et al., 2015). However, the behavioral results clearly demonstrated that the informativeness of the kinematics was higher for later than earlier interruption points both in the main and in the pilot experiments (see Supplementary Fig. 4). Furthermore, while the behavioral results of the main experiment, where actions were embedded in congruent or incongruent contexts, might be inflated by contextual information, the pilot experiment (see Supplementary material) took a pure measure of kinematic informativeness, void of contextual information, by presenting actions embedded in neutral-context scenarios. The results showed that, even in the absence of contextual information, participants were able to discriminate the two action intentions from their kinematic profile, with this ability increasing at later interruption points. However, since kinematic informativeness seemed to plateau at the intermediate interruption point (i.e. 18th frame), we decided to use only early and late interruption points in the main experiment.

Crucially, results also confirmed that the congruency/incongruency between sensorial and contextual information did have an impact on the perception of action intentions (Amoruso and Urgesi, 2016; Amoruso et al., 2016, 2019, 2020; Bianco et al., 2020; Betti et al., 2022, 2024). Indeed, when the contextual setting (i.e., as an effect of top-down expectations) pointed at the opposite intention compared to the one suggested by kinematics (i.e., the actual sensory information), prediction performance was impaired (Friston, 2010; Knill and Pouget, 2004; Dunovan et al., 2014). This occurred not only at early phases of action unfolding, when kinematics was ambiguous, but also at later phases, when more kinematics cues were available. Thus, contextual effects are not only contingent on the ambiguity of kinematic information, but contextual information is iteratively integrated with kinematics to better explain others' behavior (Amoruso and Finisguerra, 2019). This evidence fits well with a recent behavioral study (Bianco et al., 2022) in which the authors investigated the interaction between implicit contextual priors and explicit learning using an action prediction task. Crucially, this study demonstrated that, even after providing a trial-by-trial performance feedback that reinforced the use of kinematic information, the advantage of predicting ambiguous actions embedded in high-probability compared to low-probability contexts persisted. This, together with our results, supports the view that the top-down expectations are continuously integrated with the actual sensory input, independently from its degree of reliability, to make the best predictions of upcoming actions.

#### 4.2. Muscular activity patterns of action execution

For what concerns the EMG measurements during action execution, we found that performing reaching-to-grasp actions towards big or small objects did produce a differential involvement of specific finger muscles, namely the FDI and the ADM. Indeed, the FDI was more activated for precision grip actions, thus for the eating action directed to the small object, mostly during the initial reaching phase, and for the moving action directed to the container of the big objects, mostly during the lifting phase. Conversely, the ADM was more activated for whole-hand grasping actions, thus for eating actions directed to the big object and for the moving actions directed to the container of the small object, mostly during the late reaching phase in either condition. The presence of a double dissociation between the involvement of different finger muscles in movements directed to different intentions represented a key strength of the present study, in that it allowed us to further explore if the muscle-specific activation was mirrored by motor resonance during the observation of the same movements. Further, we expected that the lifting phase induced a higher activation of all muscles compared to the reaching phase, in line with previous studies (e.g. Betti et al., 2022; Finisguerra et al., 2018; Lemon et al., 1995). The evidence that this did not hold true for the present study was presumably related to the specific experimental setting. Indeed, in our case the lifting of the object was not limited to the maintenance of the contraction to counteract gravity, but it also included horizontal displacement to bring the object to the mouth, for the eating action, or to move it onto the tray, for the moving action. The displacement might have reduced the load on the required force for the muscular contraction related to the lifting. This finding further highlights the importance of registering EMG activity to understand the actual patterns of muscular activation during specific actions.

#### 4.3. Cortico-spinal excitability during action observation

The muscle-specific activations observed during action execution were broadly mirrored at motor level during the observation of the same actions in congruent contexts. Indeed, when reaching-to-grasp movements were embedded in congruent contexts, namely in contextual scenarios pointing at the same intention subtended by the kinematics profile, CSE during action observation followed the pattern of muscle-specific activations observed during action execution. Specifically, FDI MEPs were higher for the eating action directed towards the small object, which prompted a precision grip, than for the same action intention but directed towards the big object, which prompted a whole-hand grip. Additionally, FDI MEPs for the eating action directed to the big object were lower than those obtained for the moving action directed to the same big object, which prompted a precision grip. Conversely, ADM MEPs were higher for the eating action directed towards the big object, which prompted a whole-hand grip, than for the same action intention but directed towards the small object, which prompted a precision grip. Further, ADM MEPs for the eating action directed to the small object were lower than those observed for the moving action directed to the same small object, which prompted a whole-hand grip.

Crucially, when the reaching-to-grasp movements were embedded in incongruent contexts, namely in contextual scenarios pointing at the opposite intention compared to that subtended by the kinematics profile, the mirroring of muscle-specific activations was cancelled out or even reversed. Indeed, in the incongruent condition, in which the context suggested an eating intention (i.e., ideally performed with a precision grip for the small object and with a whole-hand grip for the big object), the FDI MEPs for moving the bowl of the small objects (requiring a whole-hand grasping and mainly involving the ADM) were higher compared to those for moving the plate on which the big objects was placed (requiring a precision grip and mainly involving the FDI). Furthermore, the FDI MEPs for moving the small object when the context pointed to an eating intention were also higher than the FDI MEPs for eating the small object when the context pointed to a moving

intention. For the ADM, the differences between actions obtained for congruent contexts disappeared when actions were embedded in congruent contexts.

In sum, in keeping with the results obtained by [Betti et al. \(2022\)](#) for the ADM CSE during the observation of whole-hand grasping of objects, the FDI CSE was maximally facilitated whenever the context pointed to a precision grip to implement the intention to either eat a small piece of food or move the container of a big piece of food. Conversely, the ADM CSE was facilitated during observation of actions implying a whole-grasp actions to implement the intention to either eat a big piece of food or move the container of small pieces of food, but only when contextual cues converged in suggesting the same intention. Importantly, this contextual modulation of motor resonance could not be ascribed to a general emotional reaction to stimuli embedded in incongruent compared to congruent contexts, since the preliminary validation of the stimuli revealed that contextual congruence modulated the evaluation of the stimuli in terms of action plausibility, but not in terms of emotional valence (see Supplementary Fig. 2).

That the double action-muscle dissociation during action prediction was more specific for the FDI than for the ADM muscle might relate to the timing at which the two muscles were more involved in performing precision or whole-hand actions. Indeed, the FDI showed selective modulation of EMG activation according to object size at both reaching and lifting phases, while the ADM only at the reaching phase. It is also worth noting that thumb-opponent movements of the index finger (contributed by the FDI) are required, even if at different strength, in both whole-hand and precision grips, while little-finger opponency (contributed by the ADM) is only involved for whole-hand grips. Therefore, although previous studies have shown different modulation of FDI and ADM CSE for precision and whole-hand grasping ([Cretu et al., 2019](#)), the level of selectivity of the two muscles may differ for different actions. Indeed, the contextual modulation of object-directed actions found by [Betti and co-authors \(2022\)](#) did acknowledge the modulation of the ADM CSE, but the discrimination concerned only whole-hand grips that led to different object lifting according to the underlying intention.

Furthermore, the different modulation of FDI and ADM CSE could also be related to how the stimuli were processed to perform the task. When actions were interrupted very early, no evidence of response bias was found for actions embedded in congruent contexts, while, in incongruent contexts, responses were biased toward the intention to move (i.e., positive response criterion) for big objects and toward the intention to eat (i.e., negative response criterion) for small objects. Since in both cases this response bias pointed to a greater involvement of the FDI, it may have boosted the selective modulation of FDI MEPs and hindered that of the ADM. In a similar vein, we found that MEPs for the ECR did not follow the kinematics profile suggested by action execution, neither were affected by contextual modulation. Therefore, although the involvement of this muscle during action execution was like the ADM, muscle-specific activations were not mirrored at motor level. This might be related to the fact that the ECR was not clearly visible in the videos or because this muscle was greatly involved in the execution of both actions directed to either object (with peak differences always  $> 10 \mu\text{V}$ ), which might have saturated any specific modulation during action observation.

Last, a crucial aspect that deserves further consideration is related to the between the correspondence between the action execution and the action observation results, considering the consistently reported similarity of mechanisms underlying both execution and observation (e.g. [Cesari et al., 2011](#)). For instance, the evidence that no differences emerged for the FDI during execution of the reaching-to-move actions directed to the small and big objects could be due to the coding of not only of the size (and hence grip type) of the object but also of its weight, which was comparable for the two object-container combinations and has been shown to affect motor activation ([Alaerts et al., 2010a,b, 2012](#); [Finisguerra et al., 2018](#); [Runnalls et al., 2014](#)), especially for the FDI

muscle ([Valchev et al., 2015](#)). Importantly, in our study no differences emerged for the moving action between big and small objects also for the observation results, at least when actions deployed in a congruent context (please refer to the congruent condition in [Fig. 5](#)), pointing to the correspondence between muscular activation during action observation and execution.

Collectively, our findings provide further evidence that the observation of others' actions prompts the activation of the corresponding motor representations in the onlooker's motor system ([Rizzolatti and Craighero, 2004](#)) in a muscle specific manner. However, in keeping with our hypothesis of a continuous integration between contextual expectations and kinematics, these motor representations are strongly modulated by top-down contextual expectations ([Amoruso and Finisguerra, 2019](#)). Further, extending the results of [Betti and co-authors \(2022\)](#), where arbitrary contextual cues were associated to a given action after an intensive learning phase, here we showed that contextual modulation shapes motor resonance also for what concerns every-day life actions which are embedded in ecological contexts, as in the case of a typical breakfast table.

Notably, the finding that contextual information is actively shaping the motor processing of observed actions has been previously acknowledged when contextual cues anticipated kinematic information or in case of ambiguous sensorial information ([Amoruso and Urgesi, 2016](#); [Amoruso et al., 2016, 2018a,b, 2020](#); [Betti et al., 2022](#); [Cretu et al., 2019](#); [Koul et al., 2019](#)). According to sensorimotor views of action understanding, representing the intention underlying an action is directly related to the unfolding parameters of the viewed movement (see [Becchio et al., 2018](#) for review). In this view, only at initial stages of action deployment does motor resonance mirror "expected" action; conversely, it codes the ongoing kinematics whenever sensorial information is available at later stages of action observation ([Cavallo et al., 2013](#)). The decoding of an action goal is, therefore, related to the linking of kinematics cue of an observed action to the motor chain to which it belongs. However, previous studies have often showed action kinematics in an empty surrounding, providing only verbal cues about the expected movements, a condition that strongly differs from the complexity of contextual information in ecological situations. By using ecological contextual scenarios, here we support predictive coding accounts of action understanding ([Friston, 2010](#); [Knill and Pouget, 2004](#)), by showing that motor resonance is modulated by contextual expectations not only when kinematics information is ambiguous (i.e., under conditions of perceptual uncertainty), but even when it can clearly differentiate between the opposite intentions. Indeed, it is relevant that, even if at behavioral level we observed an improved performance for late than early occlusions (i.e., with increased kinematics information, in line with [Bianco et al. \(2024\)](#)), this was not mirrored at motor level, independently from the contextual modulation. This might suggest that our measure of motor resonance with MEP recording was not sensitive enough to reflect more subtle action prediction processes that may occur later and/or at a different level of motor coding ([Finisguerra et al., 2015](#); [Soriano et al., 2019](#)). Further, our findings that motor resonance is susceptible to top-down processes are in keeping with evidence highlighting the crucial role of goals in action processing ([Cattaneo et al., 2013](#); [Decroix et al., 2020](#); [Barchiesi et al., 2022](#)).

#### 4.4. Contextual modulation and autistic traits

The presence of a relation between individual autistic traits and the contextual effects on corticospinal excitability during the prediction of observed actions for the ADM might point at an association between autistic traits and an impaired sensitivity of motor resonance to contextual modulation ([Amoruso et al., 2018b](#); [Betti et al., 2022](#)). Therefore, the impairments in context-based prediction of actions largely observed in clinical ASD ([Sinha et al., 2014](#); [Schuwerk et al., 2016](#); [Amoruso et al., 2019](#)) might extend to the individual levels of subclinical autistic traits. Our results corroborate a previous study

(Puzzo et al., 2009) showing that participants with higher autistic traits showed reduced motor resonance when observing dynamic compared to static displays of actions. Of note, we did not find a correlation between individual autistic traits and contextual modulation at behavioral level, in keeping with previous studies (Amoruso et al., 2018a,b; Betti et al., 2022; Bianco et al., 2020; Bianco et al., 2024). Altogether, this would point at a deficit in the motor coding of context-based prediction in subclinical ASD, but at the same time, at the existence of compensatory processes for action prediction performance. Even if linked to subclinical and not to a clinical sample of individuals with ASD, these findings might be of clinical interest. This result can indeed increase the understanding of the deficits in the clinical sample of ASD individuals. Furthermore, given the possibility to improve the use of contextual prior information for action prediction through non-invasive brain stimulation (Oldrati et al., 2021) and/or Virtual Reality cognitive training (Butti et al., 2020; Urgesi et al., 2021), it can encourage studies aiming at boosting the use of contextual information for social prediction in a rehabilitation setting.

#### 4.5. Limitations and future directions

The conclusions that can be drawn from our results must be considered in the light of the study limitations. First, differently than in previous studies (Amoruso and Urgesi, 2016; Amoruso et al., 2016, 2018a, 2020), we used only a single type of food-directed actions. Therefore, we cannot infer how the contextual modulation of motor resonance may similarly extend to other types of object-directed actions. Testing different types of object-directed actions would contribute to disentangling if the contextual modulation of motor resonance is affected by the strength of the association between selected object-directed actions and the specific context. Second, the sampling of the temporal dynamics of contextual modulation of behavioral and cortico-motor responses was limited to the initial stages of action processing. Testing the modulation of motor resonance at intermediate and later phases of action deployment might have allowed a better description of the time course of context modulation on action prediction and motor resonance. However, we tested intermediate interruption times in the pilot behavioral experiment (see Supplementary Fig. 4), and we did not find any difference with performance at later interruption times. Relatedly, we recorded MEPs after the conclusion of the video, which lasted the same for the two different interruption points. Therefore, any effect on motor resonance response could reflect the integration of increasing kinematic information available in the video with the contextual information that was available since the very beginning of the video. This effect could have masked the time course of context processing in the motor system, as revealed by Amoruso et al. (2016). Thus, future studies should aim to dissociate the availability of kinematic information and the time of context processing to better clarify the integration of context and kinematic processing in an observer's motor system. A further limitation of our study is that we did not measure EMG activity while recording action execution performed by the actors of our video stimuli as done in other studies (e.g., Soriano et al., 2018). However, we prioritized preserving the naturalness of the movement, which could have been hindered by the actor wearing the electrodes, both for the actor and the observer. Relatedly, future investigations should consider comparing the action observation of the participants with their own action execution sessions to reduce the inter-individual variability in motor control strategies and better shape the one-to-one mapping between observed kinematics and underlying motor commands. (e.g., Hilt et al., 2020). Last, we must acknowledge that performing an action rather than pretending to perform an action can lead to different kinematic profiles (Ansuini et al., 2016) and observers can detect these kinematic differences at behavioral (Podda et al., 2017; Quarona et al., 2020) and neural levels (Królczak et al., 2007). We tried to keep as more natural as possible the movements by asking the actors to bring the object to the mouth or to place it on the

tray, but it was not possible to repeatedly record real eating actions, during either video or EMG recording, for feasibility reasons.

#### 4.6. Conclusions

The present findings clearly point at an integration of contextual and kinematic information (e.g., Koul et al., 2019), in the context of motor chains (e.g., Soriano et al., 2018), at behavioral and motor levels during action observation. Leveraging a double-muscle dissociation we extended previous studies showing that this integration occurs independently from kinematics information ambiguity. Thus, contextual information does not only compensate for missing kinematics information, but it qualifies kinematic mapping at levels of action prediction.

#### Funding

This work was supported by grants from the Italian Ministry of University and Research (PRIN 2017, Prot. 2017N7WCLP; to C.U.; PRIN 2020 Prot. 20203LT7H3) and the Italian Ministry of Health (Bando Ricerca Finalizzata, Prot. GR-2016-02363640; to C.U.; Ricerca Corrente 2023–2024, Scientific Institute, IRCCS E. Medea; to A.F.).

#### CRediT authorship contribution statement

**Valentina Bianco:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Alessandra Finisguerra:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Giulia D'Argenio:** Writing – review & editing, Investigation. **Sara Boscarol:** Writing – review & editing, Investigation. **Cosimo Urgesi:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

#### Declaration of competing interest

The authors declare that they have no conflict of interest.

#### Data availability

All data are available at <https://osf.io/2kta9/files/osfstorage/65c5fc0235be200d5ca50754>.

#### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2024.120702](https://doi.org/10.1016/j.neuroimage.2024.120702).

#### References

- Alaerts, K., Swinnen, S.P., Wenderoth, N., 2010a. Observing how others lift light or heavy objects: which visual cues mediate the encoding of muscular force in the primary motor cortex? *Neuropsychologia* 48 (7), 2082–2090.
- Alaerts, K., Senot, P., Swinnen, S.P., Craighero, L., Wenderoth, N., Fadiga, L., 2010b. Force requirements of observed object lifting are encoded by the observer's motor system: a TMS study. *Eur. J. Neurosci.* 31 (6), 1144–1153.
- Alaerts, K., de Beukelaar, T.T., Swinnen, S.P., Wenderoth, N., 2012. Observing how others lift light or heavy objects: time-dependent encoding of grip force in the primary motor cortex. *Psychol. Res.* 76, 503–513.
- Amoruso, L., Urgesi, C., 2016. Contextual modulation of motor resonance during the observation of everyday actions. *Neuroimage* 134, 74–84.
- Amoruso, L., Finisguerra, A., Urgesi, C., 2016. Tracking the time course of top-down contextual effects on motor responses during action comprehension. *J. Neurosci.* 36 (46), 11590–11600.
- Amoruso, L., Finisguerra, A., Urgesi, C., 2018a. Contextualizing action observation in the predictive brain: causal contributions of prefrontal and middle temporal areas. *Neuroimage* 177, 68–78.
- Amoruso, L., Finisguerra, A., Urgesi, C., 2018b. Autistic traits predict poor integration between top-down contextual expectations and movement kinematics during action observation. *Sci. Rep.* 8 (1), 16208.

- Amoruso, L., Finisguerra, A., 2019. Low or high-level motor coding? The role of stimulus complexity. *Front. Hum. Neurosci.* 13, 332.
- Amoruso, L., Narzisi, A., Pinzino, M., Finisguerra, A., Billeci, L., Calderoni, S., Urgesi, C., 2019. Contextual priors do not modulate action prediction in children with autism. *Proc. R. Soc. B* 286 (1908), 20191319.
- Amoruso, L., Finisguerra, A., Urgesi, C., 2020. Spatial frequency tuning of motor responses reveals differential contribution of dorsal and ventral systems to action comprehension. *Proc. Natl. Acad. Sci.* 117 (23), 13151–13161.
- Ansuini, C., Cavallo, A., Bertone, C., Becchio, C., 2014. The visible face of intention: why kinematics matters. *Front. Psychol.* 5, 815.
- Ansuini, C., Cavallo, A., Koul, A., Jacono, M., Yang, Y., Becchio, C., 2015. Predicting object size from hand kinematics: a temporal perspective. *PLoS One* 10 (3), e0120432.
- Ansuini, C., Cavallo, A., Campus, C., Quarona, D., Koul, A., Becchio, C., 2016. Are we real when we fake? Attunement to object weight in natural and pantomimed grasping movements. *Front. Hum. Neurosci.* 10, 471.
- Barchiesi, G., Zazio, A., Marcantoni, E., Bulgari, M., di San Pietro, C.B., Sinigaglia, C., Bortoletto, M., 2022. Sharing motor plans while acting jointly: a TMS study. *Cortex* 151, 224–239.
- Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., Clubley, E., 2001. The autism-spectrum quotient (AQ): evidence from asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *J. Autism. Dev. Disord.* 31 (1), 5–17.
- Becchio, C., Koul, A., Ansuini, C., Bertone, C., Cavallo, A., 2018. Seeing mental states: an experimental strategy for measuring the observability of other minds. *Phys. Life Rev.* 24, 67–80.
- Betti, S., Finisguerra, A., Amoruso, L., Urgesi, C., 2022. Contextual priors guide perception and motor responses to observed actions. *Cereb. Cortex* 32 (3), 608–625.
- Bianco, V., Finisguerra, A., Betti, S., D'Argenio, G., Urgesi, C., 2020. Autistic traits differently account for context-based predictions of physical and social events. *Brain Sci.* 10 (7), 418.
- Bianco, V., Finisguerra, A., Urgesi, C., 2022. Updating implicit contextual priors with explicit learning for the prediction of social and physical events. *Brain Cogn.* 160, 105876.
- Bianco, V., Finisguerra, A., Urgesi, C., 2024. Contextual priors shape action understanding before and beyond the unfolding of movement kinematics. *Brain Sci.* 14 (2), 164.
- Briggs, G.G., Nebes, R.D., 1975. Patterns of hand preference in a student population. *Cortex* 11 (3), 230–238.
- Butti, N., Corti, C., Finisguerra, A., Bardoni, A., Borgatti, R., Poggi, G., Urgesi, C., 2020. Cerebellar damage affects contextual priors for action prediction in patients with childhood brain tumor. *Cerebellum* 19 (6), 799–811.
- Cattaneo, L., Maule, F., Barchiesi, G., Rizzolatti, G., 2013. The motor system resonates to the distal goal of observed actions: testing the inverse pliers paradigm in an ecological setting. *Exp. Brain Res.* 231, 37–49.
- Cavallo, A., Bucchioni, G., Castiello, U., Becchio, C., 2013. Goal or movement? Action representation within the primary motor cortex. *Eur. J. Neurosci.* 38 (10), 3507–3512.
- Cavallo, A., Koul, A., Ansuini, C., Capozzi, F., Becchio, C., 2016. Decoding intentions from movement kinematics. *Sci. Rep.* 6 (1), 1–8.
- Cesari, P., Pizzolato, F., Fiorio, M., 2011. Grip-dependent cortico-spinal excitability during grasping imagination and execution. *Neuropsychologia* 49 (7), 2121–2130.
- Chen, R., Gerloff, C., Classen, J., Wassermann, E.M., Hallett, M., Cohen, L.G., 1997. Safety of different inter-train intervals for repetitive transcranial magnetic stimulation and recommendations for safe ranges of stimulation parameters. *Electroencephalogr. Clin. Neurophysiol./Electromyogr. Motor Control* 105 (6), 415–421.
- Ciceri, T., Malerba, G., Gatti, A., Diella, E., Peruzzo, D., Biffi, E., Casartelli, L., 2023. Context expectation influences the gait pattern biomechanics. *Sci. Rep.* 13 (1), 5644.
- Classen, J., Liepert, J., Wise, S.P., Hallett, M., Cohen, L.G., 1998. Rapid plasticity of human cortical movement representation induced by practice. *J. Neurophysiol.* 79 (2), 1117–1123.
- Cretu, A.L., Ruddy, K., Germann, M., Wenderoth, N., 2019. Uncertainty in contextual and kinematic cues jointly modulates motor resonance in primary motor cortex. *J. Neurophysiol.* 121 (4), 1451–1464.
- Decroix, J., Borgomaneri, S., Kalénine, S., Avenanti, A., 2020. State-dependent TMS of inferior frontal and parietal cortices highlights integration of grip configuration and functional goals during action recognition. *Cortex* 132, 51–62.
- Devanne, H., Lavoie, B.A., Capaday, C., 1997. Input-output properties and gain changes in the human corticospinal pathway. *Exp. Brain Res.* 114, 329–338.
- Di Lazzaro, V., Oliviero, A., Profice, P., Saturno, E., Pilato, F., Insola, A., Rothwell, J.C., 1998. Comparison of descending volleys evoked by transcranial magnetic and electric stimulation in conscious humans. *Electroencephalogr. Clin. Neurophysiol.* 109 (5), 397–401.
- Fadiga, L., Fogassi, L., Pavesi, G., Rizzolatti, G., 1995. Motor facilitation during action observation: a magnetic stimulation study. *J. Neurophysiol.* 73 (6), 2608–2611.
- Dunovan, K.E., Tremel, J.J., Wheeler, M.E., 2014. Prior probability and feature predictability interactively bias perceptual decisions. *Neuropsychologia* 61, 210–221.
- Fadiga, L., Craighero, L., Olivier, E., 2005. Human motor cortex excitability during the perception of others' action. *Curr. Opin. Neurobiol.* 15 (2), 213–218.
- Faul, F., Erdfelder, E., Buchner, A., Lang, A.G., 2009. Statistical power analyses using G\* power 3.1: tests for correlation and regression analyses. *Behav. Res. Methods* 41 (4), 1149–1160.
- Finisguerra, A., Maffongelli, L., Bassolino, M., Jacono, M., Pozzo, T., d'Ausilio, A., 2015. Generalization of motor resonance during the observation of hand, mouth, and eye movements. *J. Neurophysiol.* 114 (4), 2295–2304.
- Finisguerra, A., Amoruso, L., Makris, S., Urgesi, C., 2018. Dissociated representations of deceptive intentions and kinematic adaptations in the observer's motor system. *Cereb. Cortex* 28 (1), 33–47.
- Fridlund, A.J., Cacioppo, J.T., 1986. Guidelines for human electromyographic research. *Psychophysiology* 23 (5), 567–589.
- Friston, K., 2010. The free-energy principle: a unified brain theory? *Nat. Rev. Neurosci.* 11 (2), 127–138.
- Gangitano, M., Mottaghy, F.M., Pascual-Leone, A., 2004. Modulation of premotor mirror neuron activity during observation of unpredictable grasping movements. *Eur. J. Neurosci.* 20 (8), 2193–2202.
- Grafton, S.T., Hamilton, A.F.D.C., 2007. Evidence for a distributed hierarchy of action representation in the brain. *Hum. Mov. Sci.* 26 (4), 590–616.
- Hallett, M., 2007. Transcranial magnetic stimulation: a primer. *Neuron* 55 (2), 187–199.
- Hamilton, A.F., Grafton, S.T., Hamilton, A., 2007. The motor hierarchy: from kinematics to goals and intentions. *Sensorimotor Found. High. Cogn.* 22, 381–408.
- Hilt, P.M., Cardellicchio, P., Dolfini, E., Pozzo, T., Fadiga, L., D'Ausilio, A., 2020. Motor recruitment during action observation: effect of interindividual differences in action strategy. *Cereb. Cortex* 30 (7), 3910–3920.
- Kilner, J.M., 2011. More than one pathway to action understanding. *Trends Cogn. Sci.* 15 (8), 352–357.
- Kilner, J.M., Friston, K.J., Frith, C.D., 2007. Predictive coding: an account of the mirror neuron system. *Cogn. Process.* 8 (3), 159–166.
- Knill, D.C., Pouget, A., 2004. The Bayesian brain: the role of uncertainty in neural coding and computation. *Trends Neurosci.* 27 (12), 712–719.
- Koul, A., Soriano, M., Tversky, B., Becchio, C., Cavallo, A., 2019. The kinematics that you do not expect: integrating prior information and kinematics to understand intentions. *Cognition* 182, 213–219.
- Kroliczak, G., Cavina-Pratesi, C., Goodman, D.A., Culham, J., 2007. What does the brain do when you fake it? An fMRI study of pantomimed and real grasping. *J. Neurophysiol.* 97 (3), 2410–2422.
- Lago, A., Fernandez-del-Olmo, M., 2011. Movement observation specifies motor programs activated by the action observed objective. *Neurosci. Lett.* 493 (3), 102–106.
- Lemon, R.N., Johansson, R.S., Westling, G., 1995. Corticospinal control during reach, grasp, and precision lift in man. *J. Neurosci.* 15 (9), 6145–6156.
- Loporto, M., Holmes, P.S., Wright, D.J., McAllister, C.J., 2013. Reflecting on mirror mechanisms: motor resonance effects during action observation only present with low-intensity transcranial magnetic stimulation. *PLoS One* 8 (5), e64911.
- Meister, I.G., Boroojerdi, B., Foltys, H., Sparing, R., Huber, W., Töpper, R., 2003. Motor cortex hand area and speech: implications for the development of language. *Neuropsychologia* 41 (4), 401–406.
- Naish, K.R., Houston-Price, C., Bremner, A.J., Holmes, N.P., 2014. Effects of action observation on corticospinal excitability: muscle specificity, direction, and timing of the mirror response. *Neuropsychologia* 64, 331–348.
- Oldrati, V., Ferrari, E., Butti, N., Cattaneo, Z., Borgatti, R., Urgesi, C., Finisguerra, A., 2021. How social is the cerebellum? Exploring the effects of cerebellar transcranial direct current stimulation on the prediction of social and physical events. *Brain Struct. Funct.* 226 (3), 671–684.
- Podda, J., Ansuini, C., Vastano, R., Cavallo, A., Becchio, C., 2017. The heaviness of invisible objects: predictive weight judgments from observed real and pantomimed grasps. *Cognition* 168, 140–145.
- Puzzo, I., Cooper, N.R., Vetter, P., Russo, R., Fitzgerald, P.B., 2009. Reduced corticospinal facilitation in a normal sample with high traits of autism. *Neurosci. Lett.* 467 (2), 173–177.
- Quarona, D., Koul, A., Ansuini, C., Pascolini, L., Cavallo, A., Becchio, C., 2020. A kind of magic: enhanced detection of pantomimed grasps in professional magicians. *Q. J. Exp. Psychol.* 73 (7), 1092–1100.
- Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2 (9), 661–670.
- Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. *Annu. Rev. Neurosci.* 27, 169–192.
- Romani, M., Cesari, P., Urgesi, C., Facchini, S., Aglioti, S.M., 2005. Motor facilitation of the human cortico-spinal system during observation of bio-mechanically impossible movements. *Neuroimage* 26 (3), 755–763.
- Rossi, S., Hallett, M., Rossini, P.M., Pascual-Leone, A., Safety of TMS Consensus Group, 2009. Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clin. Neurophysiol.* 120 (12), 2008–2039.
- Rossini, P.M., Barker, A.T., Berardelli, A., Caramia, M.D., Caruso, G., Cracco, R.Q., Dimitrijević, M.R., Hallett, M., Katayama, Y., Lücking, C.H., Maertens de Noordhout, A.L., Marsden, C.D., Murray, N.M.F., Rothwell, J.C., Swash, M., Tomberg, C., 1994. Non-invasive electrical and magnetic stimulation of the brain, spinal cord and roots: basic principles and procedures for routine clinical application. Report of an IFCN committee. *Electroencephalogr. Clin. Neurophysiol.* 91 (2), 79–92.
- Runnalls, K.D., Anson, G., Wolf, S.L., Byblow, W.D., 2014. Partial weight support differentially affects corticospinal excitability across muscles of the upper limb. *Physiol. Rep.* 2 (12), e12183.
- Schuwerk, T., Sodian, B., Paulus, M., 2016. Cognitive mechanisms underlying action prediction in children and adults with autism spectrum condition. *J. Autism. Dev. Disord.* 46 (12), 3623–3639.

- Sinha, P., Kjelgaard, M.M., Gandhi, T.K., Tsourides, K., Cardinaux, A.L., Pantazis, D., Held, R.M., 2014. Autism as a disorder of prediction. *Proc. Natl. Acad. Sci.* 111 (42), 15220–15225.
- Soriano, M., Cavallo, A., D'Ausilio, A., Becchio, C., Fadiga, L., 2018. Movement kinematics drive chain selection toward intention detection. *Proc. Natl. Acad. Sci.* 115 (41), 10452–10457.
- Soriano, M., Koul, A., Becchio, C., Cavallo, A., 2019. Modulation of corticospinal output during goal-directed actions: evidence for a contingent coding hypothesis. *Neuropsychologia* 134, 107205.
- Stanislaw, H., Todorov, N., 1999. Calculation of signal detection theory measures. *Behav. Res. Methods, Instrum., Comput.* 31 (1), 137–149.
- Strafella, A.P., Paus, T., 2000. Modulation of cortical excitability during action observation: a transcranial magnetic stimulation study. *Neuroreport* 11 (10), 2289–2292.
- Tidoni, E., Borgomaneri, S., Di Pellegrino, G., Avenanti, A., 2013. Action simulation plays a critical role in deceptive action recognition. *J. Neurosci.* 33 (2), 611–623.
- Urgesi, C., Butti, N., Finisguerra, A., Biffi, E., Valente, E.M., Romaniello, R., Borgatti, R., 2021. Social prediction in pediatric patients with congenital, non-progressive malformations of the cerebellum: From deficits in predicting movements to rehabilitation in virtual reality. *Cortex* 144, 82–98.
- Urgesi, C., Candidi, M., Fabbro, F., Romani, M., Aglioti, S.M., 2006. Motor facilitation during action observation: topographic mapping of the target muscle and influence of the onlooker's posture. *Eur. J. Neurosci.* 23 (9), 2522–2530.
- Urgesi, C., Maieron, M., Avenanti, A., Tidoni, E., Fabbro, F., Aglioti, S.M., 2010. Simulating the future of actions in the human corticospinal system. *Cereb. Cortex* 20 (11), 2511–2521.
- Valchev, N., Zijdwind, I., Keysers, C., Gazzola, V., Avenanti, A., Maurits, N.M., 2015. Weight dependent modulation of motor resonance induced by weight estimation during observation of partially occluded lifting actions. *Neuropsychologia* 66, 237–245.