Contextual priors guide perception and motor responses to observed actions

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Running title: Context drives motor resonance during action prediction

Abstract

In everyday-life scenarios, prior expectations provided by the context in which actions are embedded support action prediction. However, it is still unclear how newly learned action-context associations can drive our perception and motor responses. To fill this gap, we measured behavioral (Experiment 1) and motor responses (Experiment 2) during two tasks requiring the prediction of occluded actions or geometrical shapes. Each task consisted of an implicit probabilistic learning and a test phase. During learning, we exposed participants to videos showing specific associations between a contextual cue and a particular action or shape. During the test phase, videos were earlier occluded to reduce the amount of sensorial information and induce participants to use the implicitly learned action/shape-context associations for disambiguation. Results showed that reliable contextual cues made participants more accurate in identifying the unfolding action or shape. Importantly, motor responses were modulated by contextual probability during action, but not shape prediction. Particularly, in condition of perceptual uncertainty the motor system coded for the most probable action based on contextual informativeness, regardless from action kinematics. These findings suggest that contextual priors can shape motor responses to action observation beyond mere kinematics mapping.

Keywords: action prediction, context, motor resonance, priors, top-down modulations.

1. Introduction

A vast body of evidence suggests that our brain is constantly involved in actively interpreting the outside world in a predictive manner (e.g., Bubic et al., 2010). This is particularly relevant in social situations, where we need to not only interpret what others have done, but also anticipate what they are going to do next to successfully interact with them in a timely manner. In this vein, our ability to read others' intentions from observing their actions plays a crucial role in everyday life experiences, where others' movement kinematics provide key information that allows intention decoding (e.g., Bisio et al. 2010; Sartori et al. 2011; Stapel et al. 2012; D'Ausilio et al. 2015; Cavallo et al. 2016; De Marco et al. 2020). Crucially, observing others' actions activates matching motor representations in the onlooker's motor system (Fadiga et al. 1995), in a mechanism referred to as 'motor resonance'. This motor resonant mechanism tends to map the observed movement kinematics, but it is also modulated by higher-level aspects of the observed action (Betti et al. 2015; Finisguerra et al. 2018).

According to Grafton and Hamilton (2007), an action can be described at different levels in a hierarchical way, from lower levels, in which muscle activation pattern and kinematic profile of the action are represented, to the highest ones, representing the goal and the intention underlying a particular movement. Even if motor resonance is sensitive to the low-level features of an observed action, when the stimulus complexity increases going from the presentation of the sole movement kinematics to the presentation of the same movement embedded in a more complex, ecological scenario, motor resonance also appears to be modulated by high-level information (see Amoruso and Finisguerra 2019 for a review). Given that we usually observe others' actions in contexts, high-level information (i.e., the action intention) can be triggered also by contextual cues, which then constitute an important source of information for top-down predictions (e.g., Bar 2003; Fenske et al. 2006; Trapp and Bar 2015). According to the hierarchical feedback model of social perception proposed by Kilner and colleagues (2007), the predictive involvement of the motor system during action observation combines information provided by the observed action (likelihood) and the observer's knowledge (prior), trying to minimize the mismatch between the observed and the expected movements (prediction error). In this Bayesian framework, the ability to recognize someone's action and underlying intention appears then to rely on the combination of bottom-up sensory inputs provided by the observed movement kinematics and of top-down predictions on the likely cause of the behavior, thus reflecting previous experiences (e.g., Brown and Brüne 2012; Amoruso and Urgesi 2016; Amoruso et al. 2016, 2018a).

An increasing number of studies have attempted to investigate how action prediction is influenced by both prior beliefs and sensory information (e.g., Chambon et al. 2011, 2017; Hudson et al. 2016; Amoruso et al. 2019; Koul et al. 2019). For example, in a psychophysics study, Koul and colleagues (2019) showed that decoding others' intention is achieved through evidence accumulation, with explicit priors affecting more strongly the intentional attribution for an ambiguous and poorly informative movement kinematics as compared to a highly informative one. Similarly, by manipulating both the informativeness of a cue provided before the observation of an action and the availability of its kinematic information, Cretu et al. (2019) assessed the combined effect of priors and kinematics on motor resonance. To do so, motor-evoked potentials (MEPs) induced by single-pulse Transcranial Magnetic Stimulation (spTMS) over the hand motor cortex (M1) were measured as a proxy for corticospinal excitability (CSE) during the observation of either full or occluded whole hand or precision grasping movements. Importantly, movement presentation was preceded by an informative or uninformative contextual cue (i.e., a square) that, based on its color, strongly suggested (as per arbitrary experimental instructions) a specific grasp or equally suggested a whole hand or a precision grasp. The authors demonstrated that providing informative cues boosted the muscle-specific CSE facilitation for the expected type of grasp, particularly when the actual kinematics was spatially occluded and even in an initial phase of the action before presentation of the grasp-typing kinematics (see also, de Beukelaar et al. 2016). Overall, these studies suggest that the perception of an action and the motor responses to it are shaped by the integration of prior knowledge and sensory evidence, showing that informative cues can assist action prediction and motor resonance, especially for poorly informative kinematics.

However, these previous studies have mainly adopted explicit informative cues (explicitly indicating for example the probability to subsequently encounter an action with a given intention), which hardly reflect how we usually learn and refine in a flexible manner our expectations in everyday life experience (i.e., ‘contextual expectations’; Series & Seitz, 2013). Indeed, we rarely receive explicit information on what others are going to do and why they do so, but we have to extract this information from implicit learning of behavioral regularities (e.g., Jacquet et al., 2016). In addition, the role of implicitly-learned informative cues embedded in naturalistic contexts (Trapp and Bar 2015; Amoruso and Urgesi 2016) has been mostly neglected.

Recently, Amoruso et al. (2019) developed an experimental paradigm that allowed investigating how implicitly-learned associations between contextual cues and movement kinematics biased intention prediction in ambiguous social situations. In particular, a probabilistic learning phase (Learning) was followed by a prediction task (Test). In the Learning phase, the color of an object in the visual scene (contextual cue) was arbitrarily and implicitly associated with actions guided by the intention to interact or not with another individual. During the test phase, the same actions were presented, but their presentation was earlier occluded, so that the amount of kinematic information was reduced. Participants were able to decently predict actions unfolding independently from the context in which they were embedded, pointing to a readability of the initial kinematics. However, the performance of children (Amoruso et al. 2019) and adults (Bianco et al. 2020) with typical development notably improved when actions were embedded in the same context to which they were consistently associated in the learning phase. Conversely, individuals with autism spectrum disorders (ASD) were not able to capitalize on priors for predicting action unfolding (Amoruso et al. 2019), thus bringing out the difficulty characterizing ASD in integrating kinematic information and contextual representations in social contexts (Sinha et al., 2014). In a following study, Bianco and colleagues (2020) tested the generalizability of these context-based predictions to non-social domains by using, along with the above-mentioned action prediction task, a control task that implemented the same probabilistic learning structure, but required the prediction of moving geometrical shapes. Furthermore, they extended the findings of a deficit of context-based predictions associated to subclinical autistic traits in the general population, as measured by the Autistic Quotient (AQ) questionnaire (Baron-Cohen et al. 2001).

In sum, these previous studies showed that the implicit learning of new contextual priors may aid action understanding by complementing information provided by movement kinematics, and that a weak relying on these contextual priors is associated with ASD and with subclinical autistic-like traits. It remains unclear, however, whether and how these effects are mediated by modulation of activity in the observer's motor cortex. In other words, does the observer's motor cortex keep coding for the observed (reduced, but not obscure) kinematics or does it rely on the most likely action given a (reliable) contextual prior? Furthermore, is the motor coding of contextual priors specific for the social domain, or does it also extend to the mapping of non-social event likelihood (Schubotz and von Cramon 2004)? Finally, are individual differences in the motor coding of contextual priors associated to the distribution of autistic traits in the general population?

To address these issues, we combined the tasks of context-based predictions of actions and shapes with spTMS and electromyography (EMG) recording techniques to test CSE facilitation during action observation. In Experiment 1, we probed a replication of the effect of contextual priors on the prediction of both social and non-social events (Amoruso et al., 2019; Bianco et al., 2020) and of its association with autistic traits at a behavioral level. We also probed whether the observers' predictions were influence by the strength of the association between a contextual cue and a particular event. Indeed, in our probabilistic learning, we implicitly manipulated the co-occurrence of contextual cues (color) and a given event presentation (action/shape) by setting different probabilities (10%, 40%, 60% and 90% of the trials), so that an event was more or less probable in a particular context. Critically, it could also be more or less strongly expected in that context based on the strength of the association (i.e., 10-90% and 40-60%, respectively). Therefore, in the high expectancy condition, a contextual cue was associated with an action/shape in 10% of the trials (low probability) and to a different action/shape in the remaining 90% (high probability). Conversely, in the low expectancy condition, the association between a contextual cue and a given event was weaker, having the 40% of the trials for the low probable condition and 60% for the high probable one. In this way, through the probabilistic manipulation, a contextual prior could more or less strongly suggest the incoming presentation of a given event. In Experiment 2, we probed motor resonance during observers' predictions. We first used EMG recording during execution of interpersonal and individual actions to identify which muscle activation differentiate them at a motor level. Then, we recorded MEPs from these muscles during observation of interpersonal and individual action kinematics embedded in contexts that pointed to the same or a different action, as implicitly learned in the initial learning phase. Finally, we correlated the strength of these context-driven CSE modulations to individual autistic traits.

Behaviorally, in line with previous findings (Amoruso et al. 2019; Bianco et al. 2020), we expected participants to be biased towards the implicitly-learned contextual priors in order to facilitate predictions of both unfolding actions and shapes, especially in the high expectancy condition, in which the learned association was stronger. In motor terms, given the specific role played by the motor cortex in action but not shape prediction (Paracampo et al. 2018), a CSE modulation was expected to be confined to the action task, whereas no specific modulation was expected for the shape control task. Regarding the respective role of the contextual prior versus the action kinematics, if the latter is predominant in shaping observers' motor responses during action prediction, then motor resonance should mimic in a muscle-specific way the action predicted on the basis of the observed kinematics, regardless of or moderated by contextual information (Amoruso and Urgesi 2016; Amoruso et al. 2016, 2018b; Cretu et al. 2019). Conversely, if information derived from contextual priors guides motor responses, at least at the initial stages of action perception when the visual input is more ambiguous, then muscle responses should reflect the most probable action suggested by the context, in particular for the high expectancy condition, independently from the observed kinematics. Based on the findings of a lower reliance on contextual prior to predict event unfolding in individuals with higher autistic traits (Amoruso et al. 2018b; Bianco et al. 2020) or with ASD (Amoruso et al. 2019), we expected lower contextual modulation of perceptual and motor responses in individuals with higher autistic traits.

2. Experiment 1

2.1. Materials and methods

2.1.1. Participants

A total of 32 healthy participants (9 men and 23 women, age range 19-36 years, mean age 22.8 years) took part in this experiment. We determined the required sample size of this repeated measure ANOVA design (numerator df = 1) through the G*Power software (Faul et al., 2007) with the “as in Cohen (1988)” option by setting the expected effect size at f (V) = 0.6, the significance level at 0.05, and the desired power (1- β) at 0.85. The expected effect size was estimated on the basis of previous behavioral studies adopting the same prediction tasks (Amoruso et al. 2019; Bianco et al. 2020; Butti et al. 2020) and addressing the effect of context congruency in action perception (Amoruso et al. 2018a). The value of the partial eta squared obtained in these studies was then averaged resulting in an estimate of partial eta squared (η^2_p) = 0.265. The study was approved by the local Ethics Committee (Comitato Etico Unico Regionale, Friuli Venezia Giulia, Italy) and was carried out in accordance with the ethical standards of the Declaration of Helsinki. All participants were naïve to the purposes of the experiment and gave their written informed consent for their participation.

2.1.2. Stimuli

Two main types of video clips were adopted as experimental stimuli in two different tasks:

a) *Action videos* (see Fig. 1A) depicted the right arm of a male child actor (10 years old) sitting at a table in front of a peer during execution of reach-to-grasp movements on one of two objects, namely an apple or a glass. These objects could be grasped to perform either an individual or an interpersonal action (i.e., grasping-to-eat/drink vs. grasping-to-offer, respectively). The kinematic profile of the individual and interpersonal actions differed in how a power grip was executed to pursue the two aims: the object was grasped on the side for the individual intentions to eat or drink, whereas it was grasped from the top when it was offered to the other child (i.e., interpersonal action). Importantly, each action was performed in presence of a specific contextual cue: for the actions performed with the apple, these cues were a violet colored dish or an orange one, while for the actions performed with the glass, these cues were a white or a blue tablecloth. Thus, a total of eight action-context association videos were created. In stimulus preparation, we ensured that the kinematics of the actor's movements for the same action was matched between the two different contexts and that the contextual scenario was matched between the two actions. Other aspects of the videos (e.g., peer's arm position or actor's resting limb posture) could vary across different contextual scenarios, but they were always the same for the same action, ruling out that they could provide cues in contrast with the plate color (see Amoruso et al., 2019 for validation and further details).

b) *Shape videos* (see Fig. 1B) depicted a geometrical shape moving from the left side of the screen towards a central receptor shape. The shape could be either a right-angle polygon (i.e., a square or a rectangle) or an acute-angle polygon (i.e., a parallelogram or a trapezoid). For each video, one of two possible receptors was presented, which could have on its left side a concavity to host alternatively a right-angle polygon or an acute-angle polygon. While the nature (i.e., right- or acute-angle polygon) of the moving shape was immediately visible at the beginning of the videos, what specific polygon was presented could be detected only when the horizontal segment appeared to be longer (unequal-length sided: rectangle or trapezoid) or of the same length (equal-length sided: square or trapezoid) compared to the vertical one. Similar to what was done in the Action videos, within the two couples of polygons, each shape could be presented in two different colors, namely in orange or violet, for the right-angle polygons, and in white or blue, for the acute-angle polygons. Thus, a total of eight shape-context association videos were created (see Bianco et al., 2020 for more details).

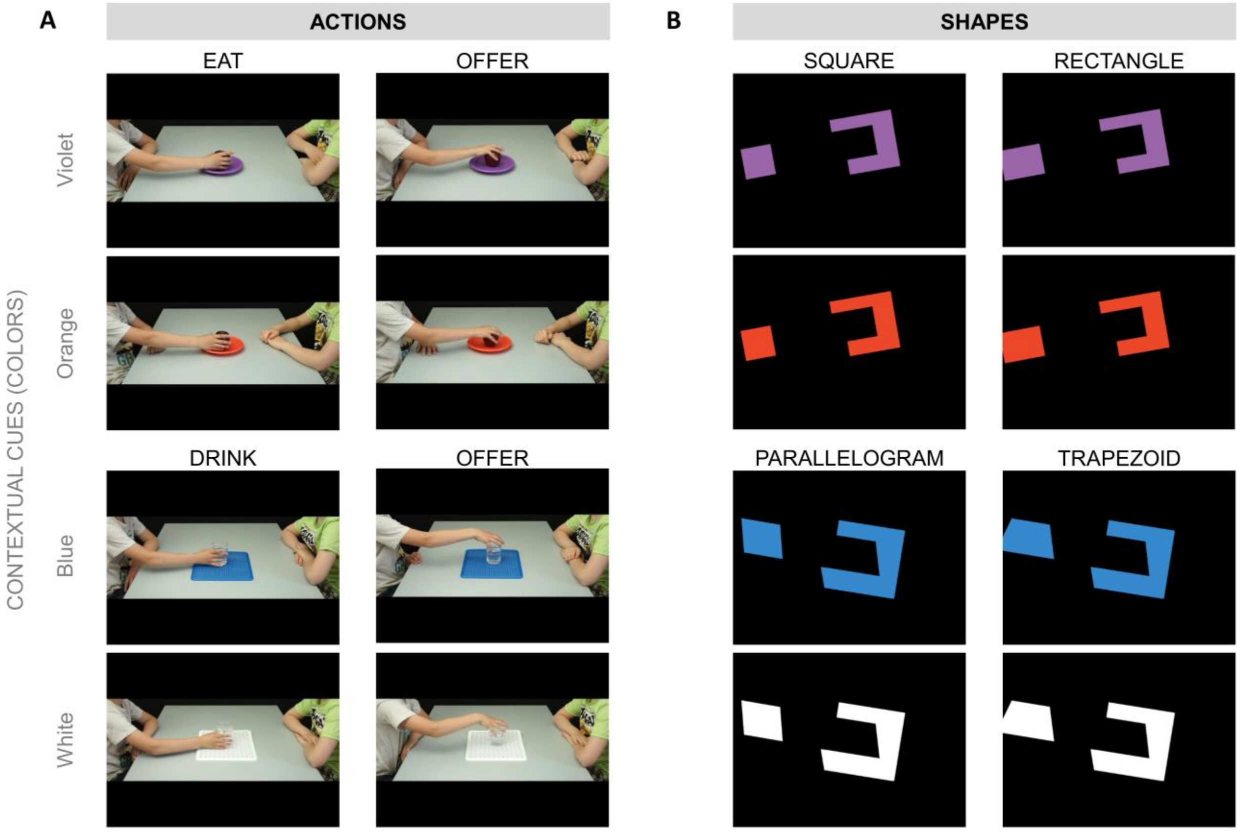

Figure 1. Experimental stimuli. In the Action videos (A), participants observed a child performing an individual (eat or drink; left) or interpersonal (offer; right) action toward an apple (top) or a glass (bottom) object. In the Shape videos (B), participants observed a shape, which could be equal-length sided (i.e., square, parallelogram; left) or unequal-length sided (i.e., rectangle, trapezoid; right), moving towards a right- (top) or acute-angle receptor (bottom). The color of the contextual cues associated with the actions or the shapes could be violet/orange and blue/white.

2.1.3. Kinematic analysis of the action video stimuli

To detect kinematic differences and similarities between the observed Action videos, we extracted a series of kinematic parameters from the actor's right hand by using a dedicated software for motion analysis (Kinovea 0.8.15). For data reduction, after careful visual inspection of the action sequence from the start of the action to the hand-object contact, all videos were divided in five moments (i.e., T1, T2, T3, T4, and T5) at which the kinematics parameters were measured. At T1 the child was completely still, eventually the reaching movement started (T2), with his hand moving toward the object, progressively unveiling distinctive action kinematics based on the hand preshaping and wrist trajectory (T3-T4) till the hand-object contact occurred (T5). Specifically, at these time points we extracted: i) the "wrist angle", which was defined as the joint angle obtained by connecting the lateral epicondyle of the humerus, the ulnar styloid process and the metacarpophalangeal joint of the little finger (Fig. 2A); ii) the "little finger angle", defined as the joint angle obtained by connecting the ulnar styloid process, the metacarpophalangeal and the proximal interphalangeal joint of the little finger (Fig. 2B); iii) the "index finger angle", defined as the joint angle obtained by connecting the radial styloid process, the metacarpophalangeal and the proximal interphalangeal joint of the index finger (Fig. 2C). These three parameters were extracted for each video. Differences between types of action (Individual, Interpersonal) within the same time-frame (from T1 to T5) were tested through nonparametric Mann–Whitney U tests. Four repetitions of each type of action (Individual, Interpersonal) were considered, based on the two colors of the contextual cues for the two objects. Results revealed that a significant difference between individual and interpersonal actions for the wrist angle occurred only at T5, at the time of hand-object contact ($p = 0.03$; Fig. 2A). Conversely, the little finger angle was significantly wider for individual than interpersonal actions from T4, when the hand was approaching the object ($p_s = 0.03$; Fig. 2B), while the index finger angle already differentiated between action types since T2, when the hand was starting to move toward the object ($p_s \leq 0.04$; Fig. 2C). Overall, this pattern of results suggests that the considered kinematic parameters differently contributed over time to differentiate between action types, with some indexes providing differential information from an early phase of the actions, and others showing a dissimilar pattern for individual and interpersonal actions only when the hand approached the object. Crucially, only in the last part of the movement (i.e., at T5, approximately two frames before the hand contact with the object as shown during the learning phase) all parameters clearly differentiated the individual from the interpersonal action. Differently, in the first part of the movement, the two actions could be only partially differentiated. This allows the observers to decode the observed intentional actions through evidence accumulation over time.

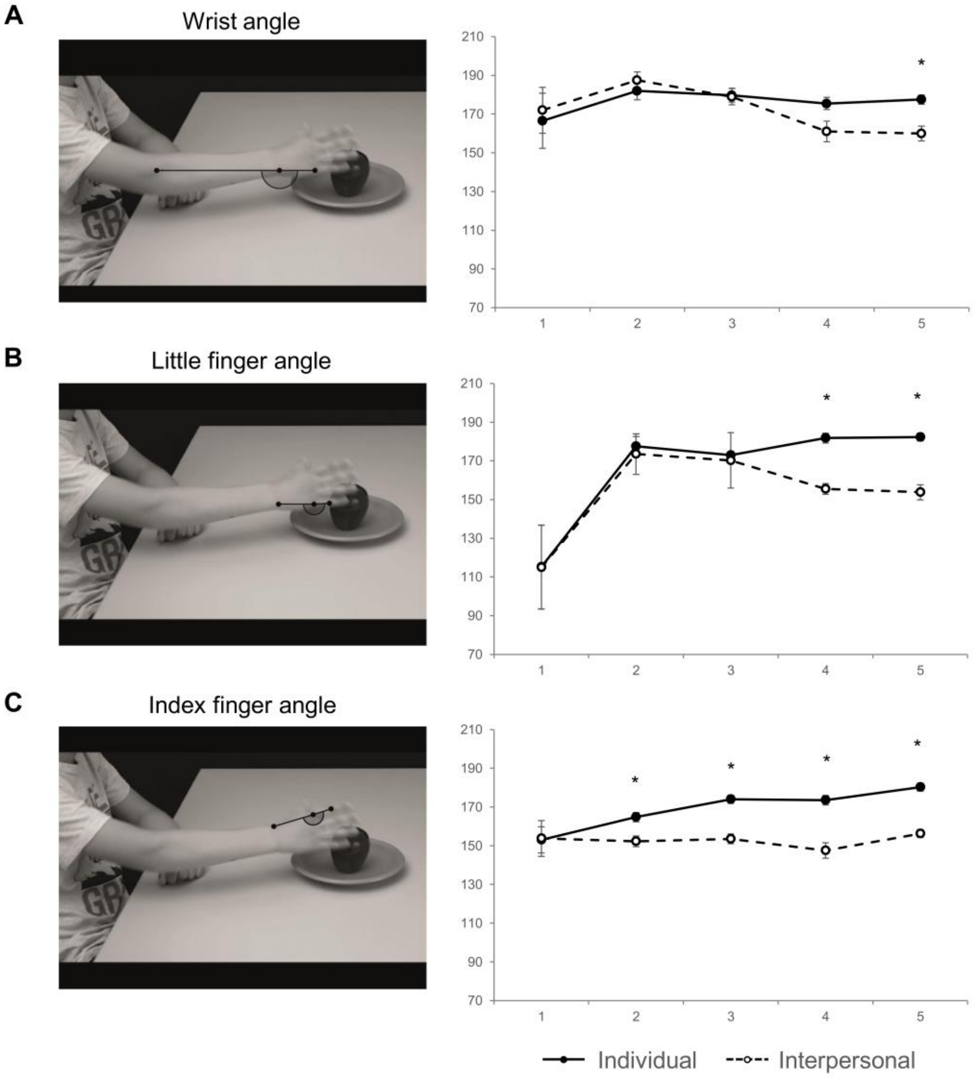

Figure 2. Kinematic parameters (left) and corresponding results (mean ± SEM; right) extracted for the wrist angle (A), the little finger angle (B), and the index finger angle (C) for the reach-to-grasp individual (solid

line) and interpersonal (dashed line) actions performed by the actor at five moments (T1-T5). Asterisks indicate statistically significant differences ($p < 0.05$) between types of action within each time frame.

2.1.4. Procedure

A within-subject design was used. It consisted in two sessions lasting approximately 20 minutes each, during which participants were asked to perform either an Action Prediction Task or a Shape Prediction Task (Amoruso et al. 2019; Bianco et al. 2020). Action and Shape videos were presented during Action and Shape prediction tasks, respectively. The order of the two sessions was counterbalanced between participants. Participants were asked to sit in front of a computer screen located about 60 cm from their faces. Before each session, instructions about the tasks and the experimental structure were given to the participants. Plus, they were introduced to the two objects of the action videos and to paper made reproductions of the four shapes, and received a demonstration of the different manipulations to grasp the objects or of the differences between the shapes in their form and length. Each task comprised a probabilistic learning phase followed by a test phase, each repeated twice, for a total of four blocks. Learning and Test phases were repeated and alternated to maintain the implicitly learned association and prevent any possible attenuation of the effect over time due to the equiprobable video presentation characterizing the Test phase.

In both phases, participants were requested to respond in a two-alternative forced choice (2AFC) task, indicating which type of action (eat vs. offer; drink vs. offer) or shape (square vs. rectangle; parallelogram vs. trapezoid) was shown.

During the two learning blocks (80 trials each), participants implicitly learned the association between contextual cues and events. In this phase, videos were stopped shortly before the target event realization, namely two frames before the hand made full contact with the object for the Action session, or when the geometrical shape was almost completely visible while getting closer to the receptor for the Shape session (25 frames, see Fig. 3). Critically, the eight videos for each task were presented for an unequal number of trials, thus the presentation of the action/shape context associations was manipulated to bias the predictability of each action/shape depending on the contextual cue. Specifically, prior expectations were implicitly manipulated by setting different expectancy and probabilities (i.e., 10%, 40%, 60% or 90%) for the co-occurrence of contextual cues (color) and actions/shapes presentation (4, 16, 24 and 36 trials in total, respectively). For example, in the Action session, we could have biased 10-90% the action-cue association for the apple videos, having the motor intention ‘to offer’ combined with the presence of the violet plate in 90% of the trials (high expectancy, high probability), while in the other 10% of the trials the same action was associated to the orange plate (high expectancy, low probability). Accordingly, the ‘to eat’ action was associated with the orange plate in 90% of the trials (high expectancy, high probability), whereas in only 10% of the trials it was associated with the violet plate (high expectancy, low probability). Differently, for the glass videos, we biased at 40-60% the action-cue association, having the motor intention ‘to offer’ combined with the presence of the white tablecloth in 60% of the trials (low expectancy, high probability), while in the other 40% it was combined with the blue tablecloth (low expectancy, low probability). The opposite color association was true for the ‘to drink’ intention. As such, we manipulated the expectancy of an event given the context, having strongly or moderately informative context-based expectation associated to a specific object or pair of polygons: high expectancy for 90-10% versus low expectancy for 60%-40%. At the same time, within each level of expectancy, we manipulated the probability of an event given the context, which could be either low (i.e., 10% or 40%) or high (i.e., 90% or 60%). It is noteworthy that this probabilistic structure was kept identical throughout each session for each participant, but the association between a given color and each action/shape was fully counterbalanced between participants. For each block, videos were randomly presented.

In the subsequent Test phase blocks (40 trials each), the same task was administered, but the amount of visual information was reduced by shortening the videos so that they stopped much earlier (i.e., only the first 15 frames were shown from the original 25 frames; see Fig. 3). With respect to the Action Prediction task, even if the initial reaching of the action could still contain kinematic information to distinguish the two actions, the later hand pre-shaping that could clearly differentiate between the two grasping movements was occluded (see par. 2.1.3). Regarding the Shape Prediction task, the left half of the longer moving shapes was partially occluded, even if minimal information about the respective length of the horizontal axes was still available, thus hindering the detection of the vertical/horizontal segment ratio and the discrimination within each couple of polygons. This way, we aimed to induce participants to rely on the previously learned action/shape – context associations to predict the target events under perceptual uncertainty. In the Test phase, differently from the Learning phase, all possible action/shape-context associations were equally presented. Each association was then presented five times per block, for a total of 10 trials across the two blocks (i.e., 20 trials for each probability). To summarize, for each experimental session, participants performed 160 Learning and 80 Test trials, for a total of 240 trials.

At the end of the experiment, participants filled out the Italian version of the Autism Spectrum Quotient (AQ) questionnaire (Baron-Cohen et al. 2001; Ruta et al. 2012) to quantify the amount of autistic-like traits across five domains – social skills, attention switching, attention to detail, communication, and imagination. This self-report questionnaire comprises 50 questions and higher scores are associated with higher traits related to the autism spectrum.

2.1.5. Trial structure

Stimuli were presented using the E-Prime V2 software (Psychology Software Tools, Inc., Pittsburgh, PA, United States) on a 24’’ monitor (resolution 1920 x 1080 pixels, refresh rate 60 Hz). The trial structure is represented in Figure 3. Each trial started with a two-second presentation of a fixation cross at the center of the screen to ensure all participants started observing the videos from the same spatial position. The overall trial structure was the same in the Learning and Test phases but videos lasted 833.33 ms (25 frames) in Learning blocks and 500 ms (15 frames) in Test blocks. Two verbal descriptors (in Italian) of the response alternatives were shown at the bottom of the screen; they referred to the possible overarching intentions underlying the grasping action for the

Action session (e.g., to eat vs. to offer) or to the type of shape presented (e.g., square vs. rectangle). Participants were requested to respond by pressing with their left or right index fingers the “Z” and “M” keys on a QWERTY keyboard, to report the left- or the right-sided descriptor, respectively. The descriptors were presented at the end of video presentation in the learning phase, to ensure participants were exposed to whole video presentation before responding, while they were shown since the beginning of video presentation in the Test phase, to ensure participants could respond as soon as they figured out the outcome of the action or the moving shape using both sensorial and contextual cues. The keys were covered with stickers to make them easily recognizable. The location of the two descriptors was fixed during the task for a participant, but it was counterbalanced between participants.

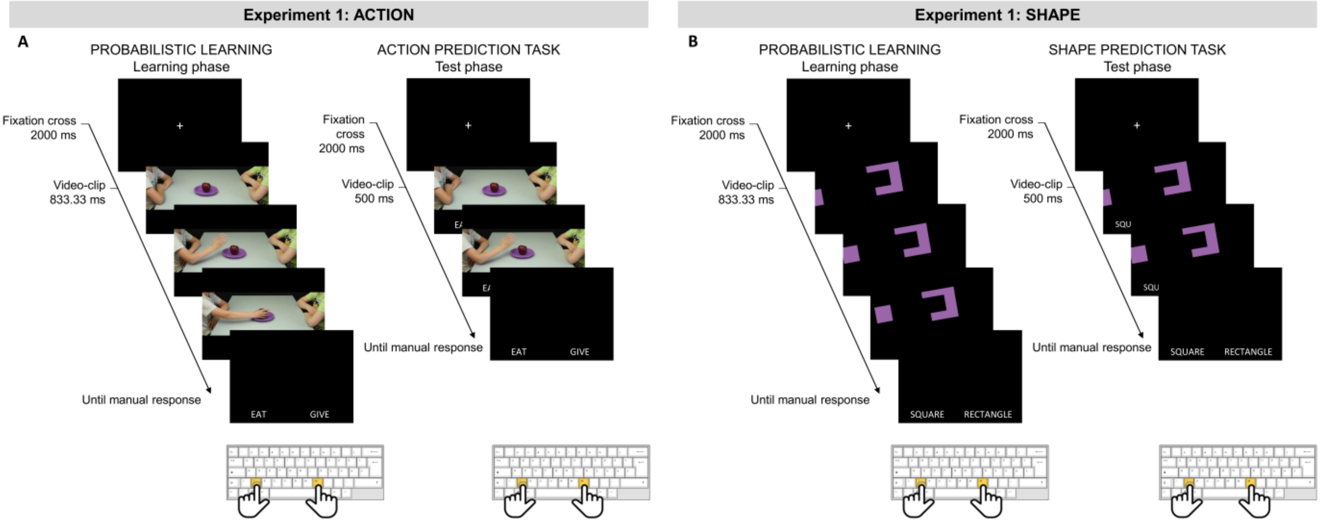

Figure 3. Example of trial structure used in Experiment 1 for the Action (A) and Shape (B) videos. Each trial began with a fixation cross presentation (2,000 ms), followed by the video clip lasting 833.33 ms for the Learning and 500 ms for the Test phase. Participants were requested to respond with their index fingers when the verbal descriptors of the two possible intentions or shapes were presented at the bottom of the screen.

2.1.6. Data handling

All the analyses were performed using the STATISTICA software (StatSoft Inc., version 8, Tulsa, OK, USA). The partial eta squared (η^2_p) value was used as an estimate of effect size. Post hoc analysis was performed using Duncan's test correction. A significance threshold of 0.05 was set for all statistical analyses.

Individual performance in carrying out the two prediction tasks was measured through d prime values (*d'*), a bias-corrected measure of sensitivity in discriminating between two categories, according to the signal detection theory (Macmillan and Kaplan 1985; Stanislaw and Todorov 1999). Higher values of *d'* are indicative of a greater sensitivity to discriminate between the two action outcomes or the two shapes. Response bias was estimated by means of response criterion (*c*), which expresses to what extent one response is more biased towards the other, regardless of sensitivity (Green and Swets 1966). The *d'* was calculated as the difference between the normalized z values of the proportions of Hit (H) and False Alarm (FA) rate (d' = zH- zFA; Stanislaw and Todorov, 1999). For H in the Action task we considered Individual actions (eat the apple, drink the water) identified as "Individual action", whereas FA referred to Interpersonal actions (offer the apple, offer the water) identified as "Individual action". Similarly, for the Shape task, H referred to equal-length sides shapes (square, parallelogram) identified correctly, whereas FA referred to unequal-length sided shapes (rectangle, trapezoid) identified incorrectly. The *c* measure was computed by averaging the normalized *z* values of the H and FA rates, then multiplying the result by -1 [$c = –(z\text{H} + z\text{FA})/2$]. In this context, c values close to 0 suggested no bias, negative c values suggested a tendency in reporting an individual action or an equal-length sided shape, while positive values suggested a tendency to report an interpersonal action or an unequal-length sided shape. To check whether the contextual probabilistic learning affected the speed at which participants made their predictions in the Test phase, we also analyzed reaction times (RTs).

All data were checked for normality distribution using the Kolmogorov–Smirnov test. In case of normal distribution, parametric statistics (repeated-measures ANOVA, Pearson's correlations) were applied; in case of non-normal distribution, non-parametric statistics were used (Friedman ANOVA). As *d'* and *c* values for the Learning phase were non-normally distributed, they were separately entered into Friedman's ANOVAs with Task (Action, Shape) and Block (Block 1, Block 2) as variables. The probability and expectancy levels were collapsed due to their unequal number of trials following the probabilistic manipulation. Differently, for the Test phase, in keeping with previous studies (Oldrati et al. 2021), rmANOVAs on *d'* scores, *c* values and RTs were performed with Task (Action, Shape), Expectancy (Low expectancy, High expectancy) and Probability (Low probability, High probability) as within-subject variables.

We also ran a Pearson's correlation analysis (with Bonferroni correction) to test whether the sensitivity to the contextual priors' manipulation was related to individual differences in autistic-like traits measured through the AQ questionnaire. Based on the results of the rmANOVAs, for each type of task, we calculated a differential index obtained by subtracting the *d'* values of the difference between high and low probability for the high and low expectancy conditions, respectively [$\Delta_{d'}$ = (90% - 10%) - (60% - 40%)]. In this way, we obtained individual measures of the reliance in using contextual priors based on the context-dependent expectancy and the probability of association in predicting the upcoming event. We focused on two AQ subscales – i.e., attention to detail and social skills –, which were specifically related to contextual modulation of motor responses during action observation in a previous study (Amoruso et al. 2018b). Notably, we corrected the AQ scoring of Item 1 according to Baron-Cohen et al.'s (2001) errata. Please see Table 1 for mean sample score, SD and score range for the total AQ questionnaire scores and its subscales.

Table 1. Mean (SD) scores and score range for the total AQ and its subscales of both Experiment 1 (left) and Experiment 2 (right).

	EXPERIMENT 1				EXPERIMENT 2			
	N	Mean	SD	Range	N	Mean	SD	Range
Social skills	32	2.4	2.3	0-9	25	1.6	1.8	0-7
Attention switching	32	4.6	2.1	1-8	25	4.1	1.8	1-7
Attention to detail	32	4.9	2.2	1-9	25	5.0	2.3	1-9
Communication	32	2.1	1.9	0-8	25	1.6	1.3	0-4
Imagination	32	2.7	1.9	0-7	25	2.3	1.4	0-5
AQ Total	32	16.7	6.5	4-36	25	14.6	4.5	5-22

2.2. Results

During Learning, both *d'* and *c* data showed no significant effects ($\chi^2_{(3)} = 6.98$, p= 0.073 and $\chi^2_{(3)} = 1.10$, p= 0.777, respectively). The rmANOVA performed on *d'* scores in the Test phase revealed a main effect of Probability ($F_{1,31} = 8.30$, p = 0.007, $\eta^2_p = 0.211$), as participants performed better for the highly probable actions/shapes (mean = 1.90, SEM = 0.11) than for the low probable ones (mean = 1.43, SEM = 0.17). Plus, a significant interaction of Probability x Expectancy ($F_{1,31} = 6.851$, p = 0.014, $\eta^2_p = 0.18$) emerged. Post-hoc comparisons on this interaction indicated that participants were more susceptible to the probability of the event in the high expectancy context with respect to the low expectancy one. Indeed, for high expectancy, they were better at predicting the type of action/shape when probability was high (90%; mean = 2.03, SEM = 0.13) compared to when it was low (10%; mean = 1.20, SEM = 0.23; p < 0.001); no difference instead emerged between low and high probabilities with low expectancy (40% vs. 60%; p = 0.52; Fig. 4). In addition, participants performed worse when they had to identify a low probable action/shape in a high expectancy situation (10%) compared to either a low- or a high-probable event in a low expectancy situation (40%, $p = 0.025$; 60%, $p = 0.007$, respectively; Fig. 4). The main effect of task or the interactions between probability, expectancy and task were not significant (all $F < 1.47$, $p_s > 0.24$, $\eta^2_p < 0.05$). Thus, comparable effects of the probabilistic manipulation of contextual priors were obtained for the action and shape tasks at a behavioral level.

The rmANOVA on *c* scores (Fig. 4) yielded a main effect of Task ($F_{1,31} = 27.113$, $p < 0.01$, $\eta^2_p = 0.47$), as *c* was significantly lower in the Shape (mean = -0.17, SEM = 0.05) than in the Action (mean = 0.04, SEM = 0.03) task. This suggests that participants tended to report an equal- rather than an unequal-length sided shape; whereas, in the action task they were unbiased. No other main effects nor interactions with either probability or expectancy emerged (all $F < 1.84$, $p_s > 0.18$, $\eta^2_p < 0.06$).

No significant effects nor interactions emerged when considering RTs (all $F < 2.77$, $p_s > 0.11$, $\eta^2_p < 0.08$), overall indicating that our probabilistic manipulation did not affect the speed of the responses provided in the Test phase and ruling out speed accuracy trade-off effects.

When testing the association between the $\Delta_{d'}$ index and the scores at the AQ subscales, no significant correlations emerged both for attention to detail (Action: $r = -0.2933$, $p = 0.206$; Shape: $r = 0.005$, $p = 0.979$) and for social skills (Action: $r = 0.104$, $p = 1$; Shape: $r = -0.144$, $p = 0.864$).

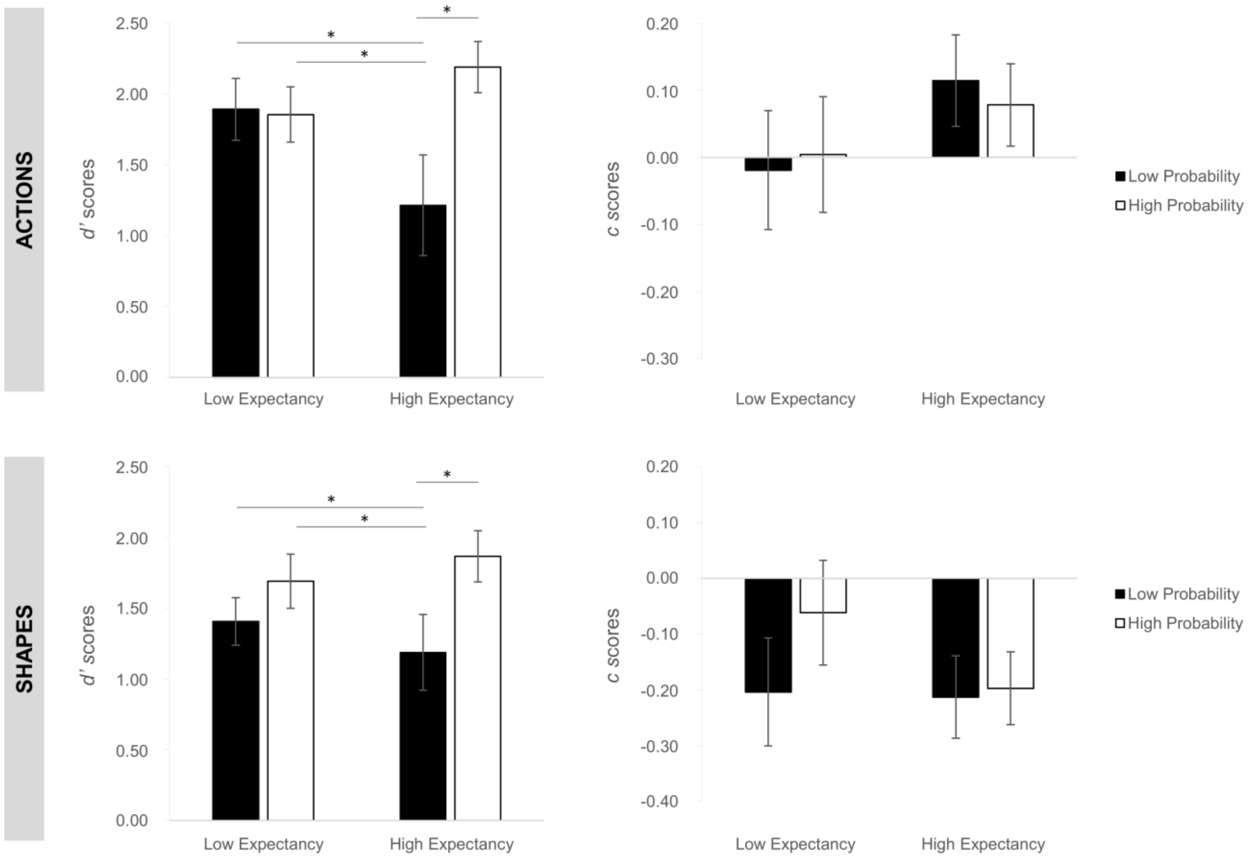

Figure 4. Behavioral results. *d'* (left) and *c* scores (right) results for Actions (top) and Shapes (bottom) in the Test phase of Experiment 1. Error bars represent standard error of the mean (SEM). Asterisks indicate statistically significant differences ($p < 0.05$) for the Probability x Expectancy interaction, for which higher sensitivity was found in the High vs. Low probability condition in the High expectancy condition only, irrespective of the task. The Probability x Expectancy x Task interaction was not significant.

3. Experiment 2

3.1. Materials and methods

3.1.1. Participants

A total of 25 healthy participants (7 men and 18 women, age range 19-42 years, mean age 24.5 years) took part in the experiment. The sample size of this repeated measure ANOVA design (numerator df = 1) was determined a priori through the G*Power software (Faul et al. 2007) with the "as in Cohen (1988)" option by setting the expected effect size at f (V) = 0.685, the significance level at 0.05, and the desired power (1- β) at 0.85. The expected effect size was estimated on the basis of a previous TMS study addressing the muscle-specific effect of context congruency on motor resonance during action perception ($\eta^2_p = 0.32$; Amoruso et al. 2018b). All participants had normal or corrected-to-normal vision and were right-handed, as assessed by a standard Handedness Inventory (Briggs and Nebes 1975). Participants were screened for TMS exclusion criteria and for neurological, psychiatric and medical issues (Rossi et al. 2009) and none of them had contraindication to TMS. None of the participants complained of discomfort or adverse effect during the experimental session. To avoid any learning effect, which could have confounded the probabilistic learning manipulation, no participant who took part in Experiment 1 was recruited for Experiment 2.

3.1.2. Stimuli, Procedure and Trial Structure

Participants were tested individually in a single experimental session lasting approximately two hours and a half, comprising two main sessions (Action, Shape) of about 30-40 minutes each, with a small break between them, and a final session of about 15 minutes in which the AQ questionnaire was filled out. The order of the two main sessions was counterbalanced between participants. Participants were comfortably seated in a recliner chair with their right arm resting on a pillow. Participants were instructed to remain relaxed while watching the video clips presented on a 24’’ monitor (resolution 1920 x 1080 pixels, refresh rate 60 Hz) set at eye level at a distance of about 100 cm. At the beginning and at the end of the experiment, participants’ baseline CSE was acquired in two Baseline blocks. During Baseline, participants observed for 1,250 ms a fixation cross (10 repetitions) or a picture of a static resting hand (10 repetitions) in two respective blocks – counterbalanced between participants – while a single TMS pulse was administered. We decided to include the image of a static hand during baseline to control the possible influence that simply observing a body part – without any action being processed – had on CSE (Naish et al., 2014).

During the action observation sessions, the same Action and Shape stimuli and block structure used in Experiment 1 were employed with the same probabilistic manipulation. However, to adapt the trial structure of the test blocks for the TMS and MEP recording, videos in the Test phase lasted 500 ms (15 frames), but they were followed by further 333.33 ms (10 frames) of black screen presentation. During the black screen presentation, a single TMS pulse was administered in one of five-time delays: 167, 200, 233, 267 and 300 ms after video offset (i.e., 667, 700, 733, 767 and 800 ms after video onset). We opted for a variable TMS-pulse timing to prevent any effect related to the anticipation of the stimulation (e.g., Tran et al. 2021). The timing after occlusion was chosen to match the timing of a muscle-specific response during action observation (>150 ms; Cavallo et al. 2013; Naish et al. 2014). A fixation cross lasting 2,000 ms was presented before the beginning of each video to ensure the observers adopted a central fixation prior to the video presentation. Moreover, a black screen was presented for 1,000 ms between trials after the recording of the participants' responses, so that inter-pulse interval was longer than 5,000 ms, thereby avoiding changes in CSE due to repeated TMS pulses (Chen et al. 1997). Furthermore, in both the Learning and Test phases, participants were required to provide verbal, rather than manual, responses by saying "left" or "right" to report the left- or the right-sided descriptor. The experimenter recorded the response by pressing the left or the right mouse button. A verbal, rather than a motor response as in Experiment 1, was chosen to ensure that hand-response preparation would not affect MEP recordings during the task (Tokimura et al. 1996; Meister et al. 2003). In addition, the location of the two descriptors was counterbalanced and randomized within each block, so that in half of the trials a descriptor was unpredictably on the left and in the other half on the right. This way, we prevented participants from planning the response in advance based on the expected spatial location of the descriptors. At the same time, these adaptations of the task to the TMS setting prevented us from recording, in a reliable way, participants' direct behavioral responses to action/shape unfolding. Furthermore, since it has been shown that TMS can exert non-specific effects on performance (e.g., blinking, alerting by tactile and acoustic sensations, etc.; Amoruso et al. 2016;

see also Duecker et al. 2013 for a discussion on non-neural effect of TMS on task performance), verbal responses were, indeed, merely required to engage the participants in the action/shape prediction task but not to test modulation effects. Thus, we only checked whether the participants were engaged in the task, by comparing overall task performance against chance (i.e., d' = 0), but verbal responses in Experiment 2 were not further considered in the analyses. Nevertheless, behavioral responses were reliably measured and analyzed in Experiment 1 only.

3.1.3. Electromyographic (EMG) recording during action execution

This exploratory investigation aimed to describe the EMG activations characterizing the execution of the actions adopted in the experiment and to identify the finger and forearm muscles whose activity could discriminate between individual and interpersonal motor intentions. Prior to the design of the main TMS experiment, a total of 14 naïve right-handed healthy participants (3 men and 11 women, age range 20-40 years, mean age 26.1 years) were recruited for a 30-min experimental session in which EMG activity during the execution of individual and interpersonal actions was recorded. None of these participants took part in the main TMS experiment to avoid uncontrolled effects of visual or motor experience on motor resonance. They were seated at a table in front of an experimenter (female, 30 years) and were requested to perform a reach-to-grasp action toward an object (i.e., glass or apple) placed in front of them, with either an individual (i.e., to eat, to drink) or an interpersonal (i.e., to offer) intention. The types of grasp to be used were demonstrated by the experimenter at the beginning of the session, in order to ensure that they corresponded to the videos. Further, participants were requested to perform the instructed action as naturally as possible. At the beginning of each trial, participants kept their hands relaxed and resting on the table surface. They wore headphones and, for each trial, they were asked to first listen to a recorded voice indicating (in Italian) the type of action they had to perform toward the object, i.e., 'to eat', 'to drink' or 'to offer'. Then, they had to wait for the Go-signal sound (a high-pitched tone lasting 700 ms) to start the action. Participants performed the actions in blocks of 10 repetitions for each condition; the order of the conditions was counterbalanced between participants. In each trial, an experimenter carefully observed the performed movements to place a marker on the EMG trace in correspondence with the time of hand-object contact. The EMG activity of the First Dorsal Interosseous (FDI) and Abductor Digiti Minimi (ADM) muscles of the right hand, and of the Extensor Carpi Radiali (ECR) and Flexor Carpi Ulnaris (FCU) muscles of the right forearm was recorded. Electrode position was determined by palpation during maximum voluntary contraction for each muscle; electrodes and wires were arranged so as not to restrict the participants' movements. Reference electrodes were placed over the ipsilateral proximal interphalangeal joint for the ADM and FDI hand muscles, over the ulnar styloid process for the ECR and over the radial styloid process for the FCU. The ground electrode was positioned on the right elbow. For each muscle, surface Ag/AgCl electrodes (1 cm diameter) placed in a belly-tendon montage were used and connected to a Biopac MP-36 system (BIOPAC System, Inc., Goleta, CA) for amplification, band-pass filtering (5 to 2,000 Hz) and digitalization of the EMG signal (sampling rate 5,000 Hz). EMG data were analyzed offline using the AcqKnowledge software (BIOPAC Systems, Inc., Goleta, CA). For each trial, the EMG signal was rectified and the data points of the recording were averaged on a sliding mean of 30 ms. The mean rectified EMG signal (in mV) was then measured in bins of 200 ms starting from 1,000 ms before hand-object contact, as marked on the EMG trace, and ending 1,000 ms later (11 bins). This time window encompassed the relevant phases of the actions, starting with the participant's arm laying in a still position and ending when the object was brought toward the mouth or handed to the co-experimenter (Fig. 5C). Even if the marker for hand-object contact was manually positioned – thus potentially introducing some temporal uncertainty in its definition – we believe that it was precise enough not to affect the description of EMG activation during action deployment in 200-ms bins across a two-second time window. For each trial, the mean EMG signal of the second bin (200 ms) after the start of the trial, acquired prior to the Go-signal, was used as baseline. The second bin was used to ensure ruling out any artifact at the beginning of epoch recording. To allow comparisons between conditions and between participants, a comparative index was obtained for each trial and muscle by subtracting the EMG signal at baseline from that at each time point (Fridlund and Cacioppo 1986). We then normalized the EMG comparative indexes for each trial according to the distribution of all trials for each participant and each muscle (z-scores). The z-scores of each participant and muscle were then averaged for each condition (10 trials per cell). Each muscle was analyzed separately with rmANOVAs with Actions (Individual, Interpersonal) x Objects (Apple, Glass) x Muscles (FDI, ADM, ECR, FCU) x 11 Time bins as within-subject variables. Estimates of the effect size were obtained using the partial eta-squared and post-hoc analysis was carried out using the Duncan's test.

The rmANOVA on the EMG signal (z-scores) showed a main effect of Time bins for all muscles: FDI ($F_{10,130} = 99.13$, $p < 0.001$, $\eta^2_p = 0.88$), ADM ($F_{10,130} = 64.19$, $p < 0.001$, $\eta^2_p = 0.83$), ECR ($F_{10,130} = 117.43$, $p < 0.001$, $\eta^2_p = 0.90$) and FCU muscle ($F_{10,130} = 47.35$, $p < 0.001$, $\eta^2_p = 0.79$), indicating, as expected, that the EMG activation increased over time while reaching and grasping the objects. The ECR muscle showed a main effect of Action, with a higher muscle activation for Individual than Interpersonal action ($F_{1,13} = 12.14$, $p = 0.004$, $\eta^2_p = 0.48$). No other significant effects emerged either for the FDI and FCU muscles ($p_s > 0.05$). Conversely, for both the ADM and the ECR muscles a significant interaction of Object x Time bin emerged (F10,130 = 1.91, p = 0.049, $\eta^2_p = 0.13$ and F10,130 = 2.61, p = 0.007, $\eta^2_p = 0.17$, respectively), along with a main effect of Object only for the ADM muscle (F1,13 = 4.75, p = 0.048, $\eta^2_p = 0.27$). In particular, significant differences were found for the ADM and ECR EMG activity between actions directed to the two objects, with higher activation for apple- compared to glass-directed actions starting from 200 ms since hand-object contact for the ADM muscle (ps < 0.042) and from 800 ms until 1,000 ms after it for the ECR muscle (ps < 0.015; Fig. 5A). Only for the ADM muscle we had a significant Action x Time bin interaction ($F_{10,130} = 2.50$, $p = 0.009$, $\eta^2_p = 0.16$; Fig. 5B), with individual actions presenting higher ADM activations compared to interpersonal ones in the late phase of the action, namely 800-1,000 ms after hand contact with the object ($p_s < 0.040$; Fig. 5B).

In summation, the results of this preliminary acquisition showed that, whereas the EMG activity of all recorded muscles changed over time while reaching and grasping the objects, only the ADM muscle activity differentiated between actions performed on the same object, but executed with an individual compared to an interpersonal intention. Therefore, the ADM hand muscle was considered as target muscle for the TMS main experiment; whereas, the ECR forearm muscle was kept as a control.

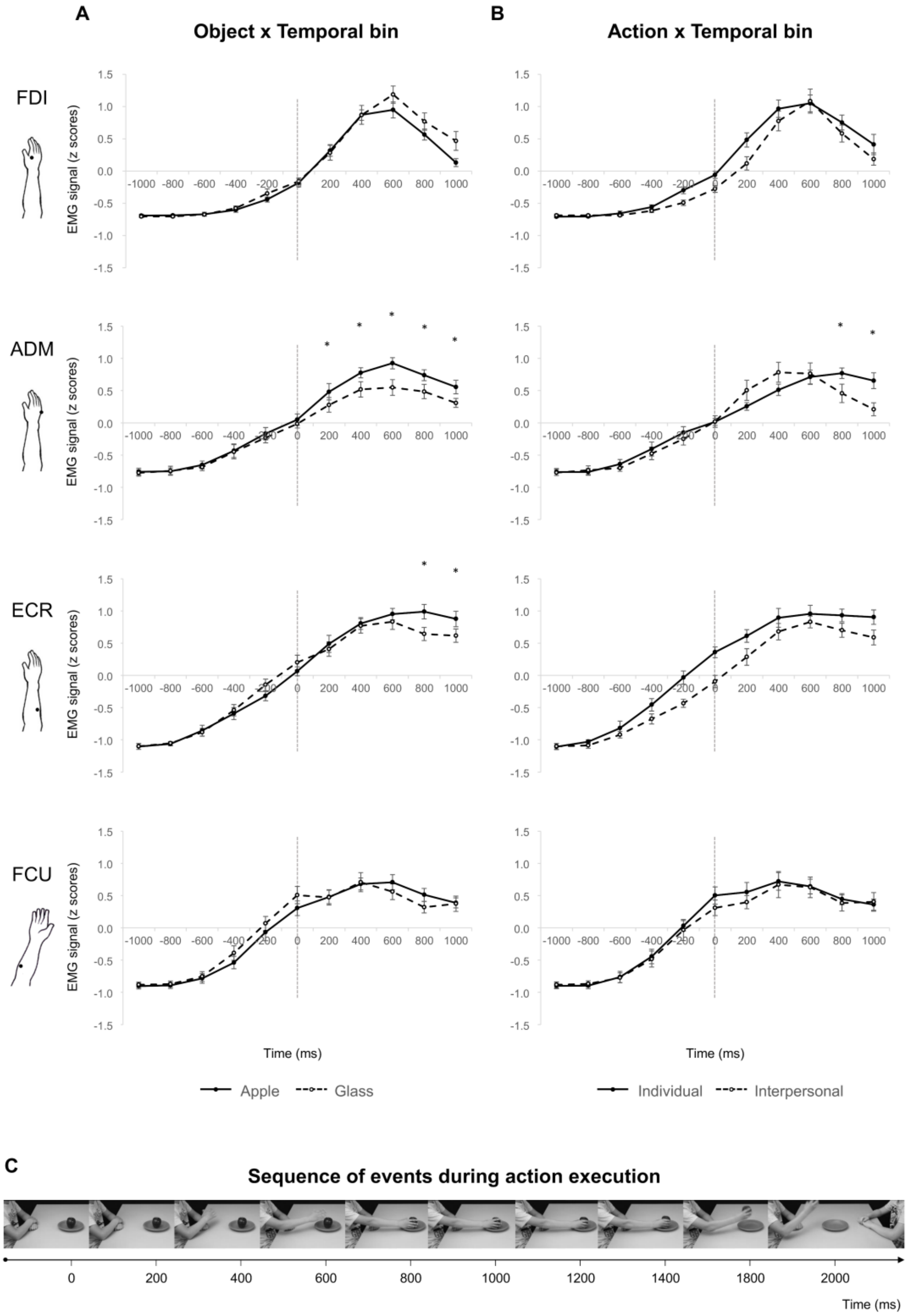

Figure 5. EMG results. Mean (±SEM) values of the EMG rectified signal (expressed as z-scores of the difference to baseline) during execution of actions directed to an apple and a glass (A; solid and dashed lines, respectively) or executed with individual and interpersonal intentions (B; solid and dashed lines, respectively), for the FDI, ADM, ECR and FCU muscles. The vertical grey dashed line corresponds to the time of hand-object contact. Asterisks indicate significant differences ($p < 0.05$) in the EMG activations

between different objects (left) or intentions (right). An example of the timing corresponding to the various action phases during action execution is shown in the bottom panel (C).

3.1.4. TMS and EMG recordings during action observation

In the main experiment, single-pulse TMS was delivered to the hand motor region of the participant's left M1 through a 70 mm figure-of-eight coil connected to a Magstim 200 stimulator (Magstim Co., Whitland, UK). TMS-induced motor-evoked potentials (MEPs), whose amplitude is considered as a measure of motor excitability and being modulated by action observation (see Naish et al., 2014 for a review), were recorded simultaneously from the ADM and ECR muscles. EMG recording was performed as in the action execution exploratory experiment, but digitalization of the EMG signal was set at a 6250-Hz sampling rate to optimize MEP epoch acquisition. For each participant, the optimal scalp position (OSP), where MEPs with maximal amplitude from both target muscles were simultaneously recorded, was identified and marked on a tight-fitting cap wore by participants. During the experiment, the coil was held in correspondence of the OSP by a coil holder with an articulated arm, and continuously checked by the experimenter to correct for potential small head movements. The intensity of TMS stimulation was set at 130% of the individual resting motor threshold (rMT), that is the minimum TMS intensity that allows recording MEPs from the higher threshold muscle with at least 50 µV of amplitude in five out of 10 consecutive pulses (Rossini et al., 1994). The rMT ranged from 28 to 59% (mean = 43.4; SD = 7.2). Timing of stimuli presentation, TMS stimulation and EMG recording was managed by E-Prime V2 software (Psychology Software Tools, Inc., Pittsburgh, PA, USA).

3.1.5. Data analysis

Individual mean peak-to-peak MEP amplitudes (in mV) were calculated separately for each muscle and condition. Trials in which peaks of EMG activity in the 75 ms window preceding the TMS pulse exceeded 2 SD from the mean background activity were discarded to prevent any MEP contamination due to muscle preactivation. In addition, trials in which MEP amplitude was lower than 2 SD from the mean background EMG or exceeded 2 SD from the participant’s mean in each experimental session were excluded from further analysis as outliers. A total (mean ± SD) of 3.9 ± 8.6% and 3.4 ± 5.6% of MEPs were excluded for ADM and ECR, respectively. To check for any basal CSE change during the experiment, pre and post Baseline raw MEPs were compared through paired-sample t-tests (two-tailed). Due to technical problems, the Baseline post of one participant was not recorded. Paired-sample t-tests were also carried out to compare fixation cross and static hand observation conditions during Baseline recording. In addition, to control for interindividual variability in MEP amplitudes, for each participant and each muscle the raw MEP amplitudes were z-transformed. Differently from the behavioral responses in Experiment 1, the two tasks were analyzed separately as the two levels of Action (individual and interpersonal) and Shape type (equal and unequal-length sided) were nested within each task and could not be compared. All data were checked for normality distribution using the Kolmogorov–Smirnov test with no violations noted. For the Action task, we ran an rmANOVA with Muscle (ADM, ECR), Action type (Individual, Interpersonal), Expectancy (Low expectancy, High expectancy) and Probability (Low probability, High probability) as within-subject variables. For the Shape task, we ran an rmANOVA with Muscle (ADM, ECR), Shape type (Equal-, Unequal-length sided), Expectancy (Low expectancy, High expectancy) and Probability (Low probability, High probability) as within-subject variables.

To test the possible associations with motor responses and individual differences in autistic-like traits, we ran Pearson’s correlations between the contextual modulation of CSE and the AQ subscales ‘attention to detail’ and ‘social skills’ (see also Experiment 1). In particular, based on the results of the MEP rmANOVA, separately for the two tasks and muscles, we calculated a MEP differential index (Δ_{MEP}) by subtracting the difference between the high and low probability conditions for the two types of actions/shapes [i.e., Δ_{MEP} Actions = (Individual High Probability – Individual Low Probability) – (Interpersonal High Probability – Interpersonal Low Probability); Δ_{MEP} Shape = (Equal-length sided shape High Probability – Equal-length sided shape Low

Probability) – (Unequal-length sided shape High Probability – Unequal-length sided shape Low Probability)]. This index estimates the amount of the MEP modulation according to the interaction between probability and type of action, thus how much the MEPs were facilitated by a contextual cue pointing to an individual or an equal-length sided shape as compared to a contextual cue pointing to an interpersonal or an unequal-length sided shape. P-values of correlations were Bonferroni corrected. In addition, a Fisher test was performed to compare the two correlation coefficients obtained for each subscale.

3.2. Results

3.2.1. MEP modulation

No differences between MEP amplitudes recorded during baseline sessions at the beginning and at the end of the experiment emerged, either for the ADM ($t_{23} = -0.80$, $p = 0.43$) or the ECR ($t_{23} = 1.35$, $p = 0.19$) muscle. This indicates that TMS per se did not induce general changes in motor excitability during the experiment. Moreover, no difference was found when comparing fixation-cross and resting-hand observation conditions, either for the ADM ($t_{24} = -0.19$, $p = 0.85$) or the ECR ($t_{24} = -0.27$, $p = 0.79$) muscle.

The rmANOVA performed on the normalized MEPs for the Action task (Table 2) revealed a significant interaction Muscle x Action type x Probability ($F_{1,24} = 4.481$, $p = 0.045$, $\eta^2_p = 0.157$); no other main effects nor interactions were significant (all $F < 3.23$, $p_s > 0.09$, $\eta^2_p < 0.12$). Duncan post-hoc comparisons revealed that the ADM MEPs were differently modulated by the probability of action-context associations in the two action conditions (see Fig. 6). For the low probability condition, the ADM MEPs were higher for Interpersonal (mean = 0.20, SEM = 0.07) than for Individual actions (mean = 0.08, SEM = 0.06; p = 0.006); conversely, for the high probability condition, MEPs were higher for Individual (mean = 0.23, SEM = 0.08) than Interpersonal actions (mean = 0.13, SEM = 0.05; p = 0.019). Critically, the ADM MEP amplitudes were higher while observing Individual actions in the high- compared to the low-probability condition (p = 0.001).

This pattern of results suggests, in line with the EMG results, that higher ADM MEPs were measured when the contextual cues suggested for an Individual action, independently from whether the initial kinematics displayed an Individual (i.e., individual actions in the high probability condition) or an Interpersonal action (i.e., interpersonal actions in the low probability condition). Critically, no difference between those two conditions indeed emerged ($p = 0.491$).

Regarding the Shape task (Table 2), the rmANOVA yielded only a main effect of Muscle ($F_{1,24} = 4.69$, $p = 0.041$, $\eta^2_p = 0.16$), with the MEP amplitudes of the ADM muscle being significantly lower than those of the ECR muscle. No other main effects or interaction turned out to be significant (all $F < 4.14$, $p > 0.05$, $\eta^2_p < 0.12$).

It is important to note that participants were actually engaged in the prediction task and correctly responded above chance in both tasks (Actions: Mean = 2.45, SD = 0.53; one-sample t-test against 0: $t_{24} = 23.25$, $p < 0.001$; Shapes: Mean = 1.44, SD = 0.65; one-sample t-test against 0: $t_{24} = 11.05$, $p < 0.001$).

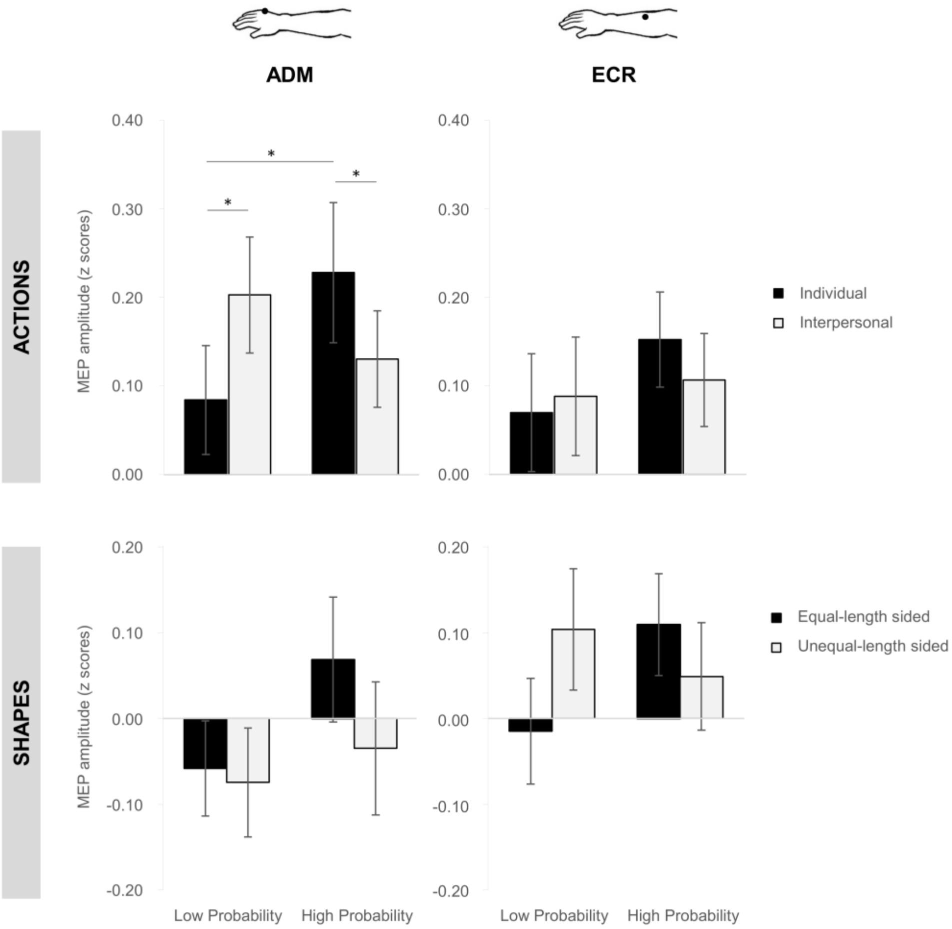

Figure 6. MEP results for the ADM and ECR muscles for the Action (top) and Shape (bottom) Prediction tasks. CSE was probed while participants were predicting occluded stimuli unfolding in situations of Low and High contextual probability and were requested to discriminate between Individual (black) vs. Interpersonal (light gray) actions (top) or between Equal-length sides (black) vs. Unequal-length sided (light grey) shapes (bottom). Asterisks indicate statistically significant differences ($p < 0.05$); error bars indicate SEM.

Table 2. MEP z-score means (±SEM) for the ADM and ECR muscles according to the Expectancy and Probability levels of the Action and Shape prediction tasks.

Muscle	Expectancy	Probability	Individual actions	Interpersonal actions	Equal-length sided shapes	Unequal-length sided shapes
ADM	Low	Low 40%	0.076±0.064	0.190±0.066	-0.073±0.064	-0.011±0.077
		High 60%	0.177±0.096	0.141±0.070	0.032±0.070	-0.049±0.092
	High	Low 10%	0.093±0.077	0.216±0.091	-0.043±0.06	-0.138±0.077
		High 90%	0.279±0.086	0.120±0.065	0.106±0.093	-0.021±0.083
ECR	Low	Low 40%	0.073±0.074	0.085±0.075	0.024±0.070	0.137±0.074
		High 60%	0.073±0.062	0.141±0.075	0.074±0.067	0.035±0.071
	High	Low 10%	0.067±0.078	0.091±0.076	-0.053±0.065	0.071±0.088
		High 90%	0.231±0.074	0.072±0.050	0.145±0.084	0.063±0.077

3.2.2. Correlation results

Probing whether the contextual modulation of the ADM CSE was related to individual differences in autistic traits (Amoruso et al., 2018), a marginally significant negative moderate correlation emerged between the ADM Δ_{MEP} in the Action task and the social skills subscale (r = -0.44, p = 0.05; Fig. 7), whereas no correlation emerged for the attention to detail subscale (r = 0.09, p = 1). This suggests that poorer social skills were associated with lower facilitation of the ADM MEPs for contextual cues pointing to an individual rather than to an interpersonal action. No significant correlations instead emerged in the Shape task for both AQ subscales (r = 0.28, p = 0.336, Fig. 7; r = -0.02, p = 1, respectively). Similarly, for the ECR muscle no correlations emerged for both the attention to detail subscale (r = -0.15, p = 0.98; r = -0.17, p = 0.82) and the social skills subscale (r = -0.21, p = 0.62; r = 0.20, p = 0.70) for both the Action and Shape task, respectively. When contrasting the two correlation coefficients obtained for the ADM and ECR in the social skills subscale in the two tasks, a significant difference emerged for ADM (p = 0.014), with a more negative correlation for the Action than the Shape task; whereas, no difference between the two correlation coefficients emerged for ECR (p = 0.176). This suggests that poorer social skills were selectively associated to weaker contextual modulation of the ADM MEPs in the action, but not in the shape prediction task.

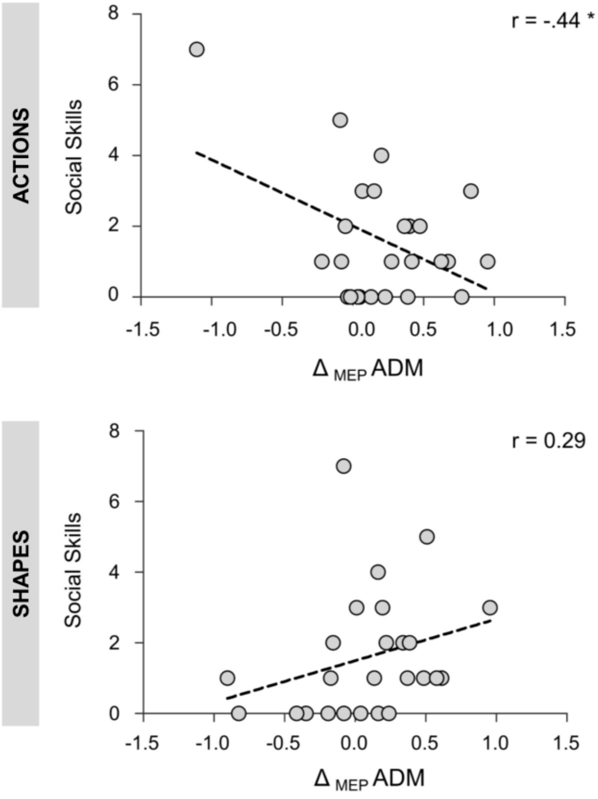

Figure 7. Correlational results for the ADM MEP differential index (Δ_{MEP}) and the social skill subscale of the AQ. A significant negative correlation emerged for the Action task (top), whereas no correlation emerged for the Shape task (bottom). * p = 0.05.

4. Discussion

In the present study, we sought to investigate the impact of implicitly learned associations between contextual cues and a given event in biasing predictions and motor responses when disambiguating unfolding social and non-social inputs. In keeping with a recent behavioral study (Bianco et al., 2020), in Experiment 1 we demonstrated that the implicit learning of event-context associations affected participants' responses during the prediction of both social and physical events. In particular, when poor visual information was available, a reliable contextual cue led to a more accurate identification of the action intention or shape. This was particularly true for high expectancy contexts, where indeed the learnt contextual prior was stronger than for low expectancy contexts. When we tested the motor correlates of these context-based predictions, in Experiment 2 it emerged that contextual priors shaped motor responses during the prediction of intentional actions, but not during the prediction of geometrical shapes. Since we found that contextual priors drove, at a behavioral level, the prediction of unfolding events for both tasks, we can rule out that differences in context-based prediction abilities in the social and non-social domains can per se explain the absence of CSE modulation for non-social events at a neurophysiological level. Our findings rather indicate that the observer's motor cortex selectively codes for contextual priors within the social domain.

A large body of findings has demonstrated that observing others' actions activates corresponding motor representations in the observer's motor system, which are functionally equivalent to those involved in action execution (see Rizzolatti and Craighero 2004; Naish et al. 2014 for reviews). In the Shape control task, where no human motion was shown, no such modulation was observed. This is in line with findings from Paracampo and colleagues (2018) who pointed out the causal role played by M1 in action prediction, but not in the prediction of non-human shape movements. Previous evidence from Schubotz and von Cramon (2004) instead reported the involvement of the premotor cortex for prediction of both biological movements and abstract event sequences, pointing to the idea that anticipatory motor processing reflected a domain-general motor contribution to perception, not limited to action-specific simulation (Press and Cook 2015). Our findings, showing the context-based modulation of motor activity during observation of actions, but not of abstract moving stimuli, instead suggests that it is seemingly confined to the action domain, without reflecting a more general mapping of predictability applying also to non-biological stimuli (see also Urgesi et al., 2006).

Furthermore, the CSE modulation during the action prediction task was specific for the muscle that turned out to differentiate between individual and interpersonal actions during actual execution. Indeed, when we first assessed the muscle activity pattern characterizing the execution of the individual versus interpersonal actions adopted in the Action task, the ADM muscle – compared to the other recorded muscles (i.e., FDI, ECR, FCU) – showed to be specifically sensitive in discriminating actions based on intentions. In particular, the ADM EMG was more active when participants executed individual actions compared to interpersonal ones. Accordingly, when we then probed CSE through MEP recording during action observation, the ADM muscle showed to be modulated by the intention underlying the observed action, thus mimicking its action-specific tuning during action execution. The action and muscle specificity of CSE modulation suggests that it likely reflected motor resonance with the observed actions (Naish et al. 2014).

The CSE modulation that emerged for the Action Prediction task seems to be predictive in nature. Indeed, CSE was probed later than 167 ms after action video offset (i.e., while a black screen was presented). Likewise, the preceding observed action was trunked at an early phase of the action unfolding, namely during the hand pre-shaping and before the hand contact with the object, so that the amount of provided visual information was limited. Contrarily, the EMG data revealed that the differential ADM activation during the execution of actions performed with individual compared to interpersonal intentions emerged after the contact with the object. Thus, since TMS was administered earlier than the expected moment of the hand-object contact in the video, the CSE increase for individual actions as compared to interpersonal ones suggests a predictive coding based on later stages of the action. This is in line with studies demonstrating that CSE is higher during middle action phases than in the final phase (Urgesi et al. 2010) and is affected by the future course of the action (Sartori et al. 2015), suggesting that our motor system is preferentially tuned to anticipatory simulation of the observed action (Kilner et al. 2004).

This is also in accordance with another recent study showing the predictive nature of others' intention mapping into the observer motor system (Soriano et al. 2018). In this study, the authors found that, in absence of any contextual cues hinting toward a particular intention, subtle changes in kinematics drive, in a predictive way, the motor mapping of the inferred intention. Crucially, differently from Soriano et al. (2018), here we found that when contextual cues were available and were informative about the most plausible action intention, as it occurs in most of everyday life situations, the coding of subtle changes in kinematics in the observer's motor system is integrated, and possibly overwritten, by context-based intention coding.

Indeed, the ADM MEPs were higher when individual actions were observed embedded in a context congruently pointing to the same action (i.e., in the individual high probability condition) than in a context pointing to an interpersonal action (i.e., in the individual low probability condition). However, differently from Experiment 1, this effect was unrelated to the strength of the previously learned association (i.e., expectancy), but it was guided by probability. This might point to a great sensitivity of motor resonance to even weak prior signals (i.e., 60% vs. 40%), which was not enough to influence participants' response at a behavioral level. A non-perfect correspondence between behavioral and neurophysiological results could be related to the fact that changes in MEP amplitude during action observation reflect processes not completely overlapping with the response production required in the behavioral task, and potentially related to different stages of stimulus processing (e.g., Bestmann and Krakauer 2015; Soriano et al. 2019). Nonetheless, our differential MEP modulation during intention prediction, based on contextual information, is in line with a series of studies showing that motor resonance is susceptible to top-down information (Amoruso and Finisguerra 2019). In particular, Amoruso et al. measured the effects of contextual information when participants had to disambiguate the intention of an action embedded in congruent or incongruent contexts, namely, when the grasping kinematics and the action setting pointed toward the same or toward different intentions (Amoruso and Urgesi 2016; Amoruso et al. 2016, 2018b). When probing CSE during observation of a reaching action, they found higher CSE facilitation for actions embedded in congruent contexts as compared to actions embedded in incongruent contexts or in ambiguous neutral contexts in which different intentions were equally plausible. Accordingly, our low probability conditions were characterized by a mismatch between kinematic information and the action more frequently associated with the contextual cue in the probabilistic learning phase, leading to lower ADM CSE facilitation for individual actions as compared to the high probability conditions.

Critically, differently from Amoruso et al.'s studies (Amoruso and Urgesi 2016; Amoruso et al. 2016, 2018b, 2020) and moving beyond the mere context-kinematics compatibility, here we could dissociate motor resonance for two types of actions (individual vs. interpersonal) and we had a muscle-specific marker for one of the two actions (i.e., greater ADM activation during execution of individual than interpersonal action). This way, we showed that the ADM CSE was comparably facilitated during the observation of (initial) individual or interpersonal kinematics whenever it was embedded in a context calling for the presentation of an individual action. Indeed, comparable ADM MEPs were recorded in the individual high probability condition and in the interpersonal low probability condition. Thus, not only was motor resonance sensitive to the congruence between contextual and kinematic cues, it also reflected the most probable action based on the contextual prior, even when the actual available motor information provided by kinematics was in contrast with it. Contextual priors therefore appeared to shape motor resonance at the initial stages of action unfolding, a result that is in line with previous literature highlighting the role of priors in guiding motor responses (e.g., de Beukelaar et al. 2016; Amoruso et al. 2018a; Cretu et al. 2019; Koul et al. 2019). Our findings, however, not only support the idea that motor resonance is susceptible to top-down information (Amoruso and Finisguerra 2019), but they also suggest that contextual priors may even override motor representations derived by bottom-up sensory information.

It is worth noting that Amoruso et al. (2016) described a temporal modulation of contextual processing during action observation, with an early facilitatory effect for congruent contexts at ≈ 240 ms after video onset and a later inhibition for incongruent contexts at ≈ 400 ms. Since we recorded MEPs only at a relatively late time window after video onset (i.e., 667-800 ms), we could not establish whether the observer's CSE could reflect different sources of information, namely, kinematic and contextual cues, at early versus late time windows. Thus, future studies, directly exploring the time-course of these effects over a wider time window, will be needed to shed light on the respective role of prior expectancies guided by contextual cues and available kinematic information in shaping motor responses over time.

We also found a relationship between the extent of contextual modulation of observer's CSE during action prediction and the distribution of social aspects of autistic traits in the general population. In particular, the ADM CSE facilitation for contexts calling for an individual action, independently from the observed kinematics, was lower in those individuals that reported poorer social skills at the AQ questionnaire. This finding is in keeping with evidence that the CSE of individuals with lower social and communication abilities is less modulated by the congruence between the kinematics of actions and the context in which they take place (Amoruso et al. 2018b). The association between the social aspects of autistic traits and the contextual modulation of CSE was selective for the action task and for the ADM muscle and was not detected in the shape prediction task or for the ECR muscle. This suggests that the presence of autistic-like traits may be associated with a worse motor coding of observed intentional actions (e.g., Puzzo et al., 2009), without being generalized to the motor processing of visual stimuli in general. Notably, as in previous studies (Amoruso et al. 2018b; Bianco et al. 2020), no relation was detected between the social aspects of autistic traits and the contextual modulation of the action prediction performance. This might reflect that, while the motor coding of contextual action priors might be altered in individuals with high autistic traits, their action prediction performance is not necessarily affected, likely being compensated through context processing in different networks. In fact, the behavioral deficits of children with autism, as compared to children with typical development, in using contextual priors to predict action unfolding was not accounted by their levels of autistic traits, but by their behavioral problems (Amoruso et al. 2019). This may hint at the notion that, while autistic traits are associated to an altered sensitivity of motor resonance to action contexts, the prediction deficits of persons with ASD might stem from concurrent failure in other mechanisms (e.g., inferential processing). However, these results, either the significant correlation of AQ with the CSE contextual modulation or the non-significant correlation with behavioral performance, should be interpreted with caution given that our relatively small sample of individuals may not be representative of the AQ score distribution in the general population, thus limiting the range of AQ variation and the power of the correlation.

5. Conclusions

This study showed that our perceptions and motor responses are shaped by the implicitly learnt statistical regularities of the environment (i.e., the probability manipulation of the contextual cues), hence supporting the interpretation of incoming sensory evidence. Low-level information provided by stimuli features and high-level information acquired through probabilistic contextual learning then critically interact to support predictive processing, in consistency with the Bayesian framework of predictive coding (e.g., Kilner et al., 2007). Contextual priors affected prediction of both social and non-social stimuli as emerged from the behavioral responses; however, in motor terms, context-based predictions only modulated motor responses for action stimuli. Specifically, when initial kinematic information was provided to the observer for intention prediction, motor responses reflected the representation of the more probable action in a given context. Contextual priors then appeared to be more influential than kinematic information in shaping the motor output at the initial stages of action processing, highlighting the role played by top-down contextual expectations in driving our processing of others’ actions in social situations.

Data availability statement

The datasets generated and analyzed during the current study (Experiment 1 and Experiment 2) are available from the Open Science Framework, at this link: https://osf.io/w8nmq/?view_only=354fef1786a946c3ad28f41d3e205c42

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