



How social is the cerebellum? Exploring the effects of cerebellar transcranial direct current stimulation on the prediction of social and physical events

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Abstract

Congenital or acquired cerebellum alterations are associated with a complex pattern of motor, cognitive and social disorders. These disturbances may reflect the involvement of the cerebellum in generating and updating the internal models that subserve the prediction of sensory events. Here, we tested whether the cerebellar involvement in using contextual expectations to interpret ambiguous sensory sceneries is specific for social actions or also extends to physical events. We applied anodic, cathodic and sham cerebellar transcranial Direct Current Stimulation (ctDCS) to modulate the performance of an adult sample in two tasks requiring the prediction of social actions or moving shapes. For both tasks, in an earlier implicit-learning phase (familiarization), we manipulated the probability of co-occurrence between a particular action/shape and contextual elements, which could provide either strongly or moderately informative expectations. The use of these expectations was then tested when participants had to predict the unfolding of temporally occluded videos, in situations of perceptual uncertainty (testing). Results showed that in the testing, but not in the familiarization phase, cathodic as compared to anodic and sham ctDCS hindered participants' sensitivity in predicting actions embedded in strongly, but not moderately, informative contexts. Conversely, anodic as compared to sham ctDCS boosted the prediction of actions embedded in moderately, but not strongly, informative contexts. We observed no ctDCS effects for the shape prediction task, thus pointing to a specific involvement of the cerebellum in forming expectations related to social events. Our results encourage the exploration of rehabilitative effects of ctDCS in patients with social perception deficits.

Keywords Cerebellum · tDCS · Predictive coding · Social cognition · Action prediction · Priors

Introduction

The contribution of the cerebellum to sensorimotor (Wolpert et al. 1998; Blakemore and Sirigu 2003) and cognitive (Strick et al. 2009) functions has been recognized to extend to socio-emotional processing (Schutter and van Honk 2005; Adamaszek et al. 2017). Indeed, going beyond the traditional consideration of the cerebellum as a purely motor control structure (Flourens 1824; Luciani 1891; Holmes 1907), it is now acknowledged that this brain region is involved in many different abilities, including those required for regulating social behaviour and action perception (Fuentes and Bastian 2007; Van Overwalle et al. 2020). Neuropsychological evidence falls in line with this view. In particular, a cerebellar cognitive-affective syndrome (CCAS) has been described in patients with cerebellar damage (Schmahmann and Sherman 1998). Alongside general intellectual deficits

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(Ahmadian et al. 2019), the CCAS includes socio-emotional symptoms, such as emotional blunting, behavioral disinhibition and compromised reasoning about social situations (Hoche et al. 2016).

A possible explanation accounting for these symptoms in the CCAS calls into play the so-called primitive functions of the cerebellum in the sensorimotor domain, namely acquisition, storage and update of forward internal models. In this view, a forward model generates a prediction about the sensory consequences of a to-be-implemented motor command. In case a mismatch between the prediction and sensory evidence is detected, a signal error is produced, which is later used to update the model and further guide the implementation of the movement (Miall and Wolpert 1996). These primitive functions have been proposed to extend also to other domains by handling multi-modal representations (Ito 2008; Popa and Ebner 2019). In particular, according to the Universal Cerebellar Transform (UCT) hypothesis (Koziol et al. 2014), the computational mode of the cerebellum would provide an integration of internally stored representations with external stimuli in order to optimize the performance according to the contextual demands. This cerebellar role would be independent from the nature of the processed information, thus underlying a broad range of functional domains. In other words, the cerebellum would contribute, possibly thereby a unique computational predictive mechanism, to produce harmonious motor, cognitive as well as emotive and social responses.

Given the role of the cerebellum in the sequencing of motor commands during action execution (Ivry 1997), a previous study compared the effects of cerebellar damage on the sequencing of drawings that reproduced behavioural sequences and of drawings depicting abstract figures (Leggio et al. 2008). In line with the idea of the cerebellum as a sequencer of elements not necessarily requiring motor representations, cerebellar patients failed in both tasks. A partially different pattern of results was obtained in a following study (Cattaneo et al. 2012) that compared the effects of cerebellar damage on the perception of the timing of action sequences and of the timing of complex physical events. In particular, patients with cerebellar damage and healthy controls were presented with a series of pictures depicting different phases of human actions (e.g., opening a bottle) or of events occurring in inanimate objects (e.g., the falling of a broom). They were required to detect which pictures were not part of the sequence for being inappropriate to the context or for containing altered dynamics. Results showed that patients with cerebellar damage performed worse than healthy controls in both tasks, but their performance was particularly poor in sequencing biological actions compared to physical events. While the impairments of cerebellar patients in both biological and non-biological tasks (Cattaneo et al. 2012) were in keeping with the UCT, the dissociation between the

biological and non-biological sequencing tasks was held as evidence that cerebellar damage may affect more the processing of scripts of biological actions as compared to scripts of physical events devoid of any social relevance. This suggests that sequences of motor acts may be represented differently from other sequences in the cerebellum. Accordingly, a recent study showed cerebellar patients to fail in generating the correct chronological order of social actions depicting complex situations, whereas their performance was close to normal for non-social mechanical stories and overlearned social scripts (Van Overwalle et al. 2019).

In the view of a more specific role of the cerebellum for social processing (Van Overwalle et al. 2020), the observation of others' actions would be processed by the cerebellum as a forward model in which the perceptual inputs of the observed movement are transformed into a simulated motor pattern that allows predicting the forthcoming actions (Umiltà et al. 2001; Wolpert et al. 2003; Gazzola and Keysers 2009). Such a process has been thought to be crucial for efficient everyday social interactions, which often require to anticipate and to understand the intention underlying others' behaviour by observing their movements. Accordingly, neuroimaging evidence has shown that the cerebellum is consistently activated during action observation (Molenberghs et al. 2012), together with the fronto-parietal areas that have been described to become active during both observation and execution of similar actions (Rizzolatti and Craighero 2004). Importantly, in keeping with the pattern of activation of fronto-parietal areas, the cerebellar activation during action observation is modulated by motor expertise, thus pointing to its involvement into a simulation mechanism that matches observed movements onto an observer's motor representations (Calvo-Merino et al. 2006).

Crucially, however, the understanding of others' actions does not merely rely on the reading of movement kinematics, but it also takes into account the contextual objects in which an action is embedded. Indeed, contextual information may provide an early prediction of the outcome of an observed action (Kilner and Frith 2009; Kilner 2011) through acquisition and storing of internal models based on the detection of statistical regularities of what has previously occurred in specific contexts (Siman-Tov et al. 2019). These internal models, thus, include information on either the social or the physical world. Several studies have shown that the embedding context facilitates action recognition and modulates motor activation during action observation (Iacoboni et al. 2005; Amoruso et al. 2016, 2018, 2019, 2020; see Amoruso and Finisguerra 2019 for a review). Furthermore, a recent study has shown that paediatric patients with a brain tumour affecting the cerebellum, as compared to those with a supratentorial tumour, were impaired in using contextual information to predict actions (Butti et al. 2020b). While providing evidence for

the involvement of the cerebellum in context-based predictions, this study has left open the question of whether the cerebellum plays a specific or more relevant role for the prediction of social actions or it is generally involved in the context-based predictions of both social and non-social physical events.

To clarify this issue, we used cerebellar transcranial Direct Current Stimulation (ctDCS) on healthy individuals. This brain stimulation technique has been increasingly applied as a mean to modulate and investigate functions of the cerebellar cortex in the healthy and pathological brain (Grimaldi et al. 2014; Ferrucci et al. 2015; van Dun et al. 2016). It allows, indeed, testing the causal involvement of the cerebellum in the target functions by inducing prolonged functional changes in the cerebellum, either as increased (after anodic ctDCS) or decreased (after cathodic ctDCS) excitability of the stimulated area. To disentangle the involvement of the cerebellum in processing social and non-social events, we delivered anodic, cathodic or sham ctDCS over the cerebellum during the execution of two tasks requiring participants to implicitly extract and learn probabilistic regularities in incoming sensory information. In particular, participants were familiarized with specific associations between a contextual cue and a social or non-social sensorial event, and to use this association to predict the upcoming outcome in situations of perceptual uncertainty. For the social domain, we used a task requiring participants to predict action unfolding, namely to discriminate between individual or interpersonal intentions underlying observed movements (Amoruso et al. 2019). For the non-social domain, we used a task requiring participants to predict the identity of moving shapes. These stimuli have been previously used as a control condition for assessing the action-specific or the domain-general involvement of brain areas in predictive mechanisms (Schubotz and von Cramon 2004; Paracampo et al. 2018; Bianco et al. 2020). In particular, using these tasks, it has been shown that manipulating the probability of co-occurrence of the target event and contextual cues biases the ability to predict social or non-social events in conditions of perceptual ambiguity (Bianco et al. 2020).

In light of previous evidence showing cerebellar patients' general impairments in the processing of both social and non-social events (Leggio et al. 2008) or domain-specific deficits in the processing of action patterns (Cattaneo et al. 2012; Van Overwalle et al. 2019), two hypotheses were tested: (H1) ctDCS influences both the social and the non-social prediction tasks, confirming the idea of the cerebellum as a “general purpose” controller operating across domains, and (H2) ctDCS influences only (or to a greater extent) the execution of the social task, endorsing the idea of a “social” cerebellum constituting a critical node for socio-emotional processing.

Methods

Participants

A total of 24 healthy University students were enrolled in this study (6 Male, mean age = 22.5, SD = 1.9 years). The sample size for our repeated-measure ANOVA design (numerator $df = 2$) was determined a-priori considering a medium–low effect size of $f = 0.32$ —as reported in a meta-analytic investigation of ctDCS effects on non-motor functions (Oldrati and Schutter 2017)—and applying an alpha level of 0.05 to achieve a power of 0.90. All participants were right-handed as measured by the Edinburgh inventory of handedness (Oldfield 1971) and had normal or correct-to-normal vision. Once recruited, all participants filled out a questionnaire to evaluate their suitability for tDCS. None of the volunteers had a history of neurological disorders or brain trauma, or a family history of epilepsy. Prior to the beginning of the experiment, written informed consent was obtained from all participants, who remained naïve to the experimental hypotheses until the end of the experiment, when they were debriefed about the study. The experimental procedure was approved by the local ethical committee and conducted in accordance with the Declaration of Helsinki.

Procedure and tasks

The study adopted a single-blind, within-subjects design. Participants performed a social and a non-social prediction task, lasting about 15 min each, while receiving anodic, cathodic or sham stimulation. The three stimulation types were applied in three separate daily sessions, at least 4 days apart (average 10 days). In each session, a 30 min break separated the administration of the two tasks, each one coupled with online stimulation delivery. At the end of each stimulation session, participants were asked to rate the level of discomfort (e.g., tingling, pain, itching, and burning sensations in the vicinity of the electrodes) they experienced during the stimulation by means of a 10-cm Visual Analogue Scale (VAS), with the descriptor extremes “no discomfort at all” (score 0) and “elevated discomfort” (score 10) (Fig. 1). A one-way ANOVA on the VAS scores with stimulation type as a within-subject variable yielded a non-significant result [$F(2,46) = 1.52$, $p = 0.23$, $\eta_p^2 = 0.06$], suggesting that participants were blinded successfully. Moreover, the mean of perceived discomfort in all three conditions was below 2, confirming that ctDCS was well tolerated.

The prediction tasks were adapted from previous studies (see Amoruso et al. 2019 and Bianco et al. 2020 for

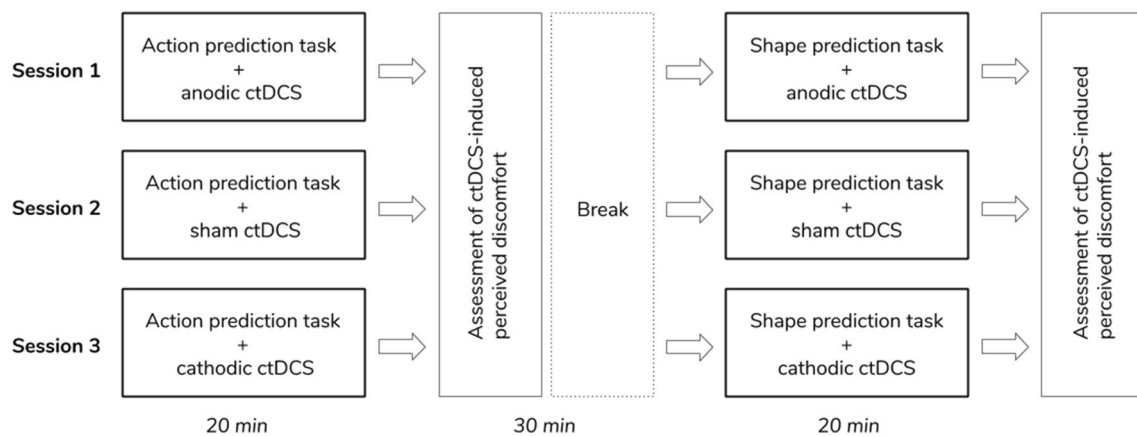


Fig. 1 Schematic depiction of the experimental procedure of a participant. The order of presentation of the tasks was kept fixed across sessions for each participant. The order of presentation of tasks and of ctDCS types were counterbalanced between participants

detailed description). The task tapping on the social component, i.e., the action-prediction task, required participants to observe videos showing a child (male 10 years old) acting in different ways upon two different objects, i.e., grasping an apple from a plate or a glass from a tablecloth to perform either individual (i.e., eating/drinking) or interpersonal actions (i.e., giving the object to a peer sitting in front of the child). Participants were asked to predict action unfolding (i.e., individual or interpersonal) in a two-alternative forced choice (2AFC) mode. For the task tapping on the non-social component, a shape-prediction task was used. Moving shapes (instead of objects) were used to avoid the effects of any pre-existent semantic association that could affect the probabilistic manipulation. This task required participants to observe videos depicting one of four coloured geometric shapes, which could be either right-angle polygons (i.e., a square or a rectangle) or acute-angle polygons (i.e., a parallelogram or a trapezoid). In each pair, one shape was equal length sided (i.e., with even horizontal and vertical segments: square and parallelogram), while the other was unequal length sided (i.e., with longer horizontal than vertical segments, rectangle and trapezoid). The target shape appeared from the left side of the screen and moved towards the right, where a complementary receptor figure, which was static and had the same colour of the moving shape, was presented. This receptor figure contained in its lower and upper parts two concavities that were, respectively, complementary (i.e., in which the target shape could fit) to either the two right-angle polygons (i.e., one to the rectangle and the other to the square) or to the two acute-angle polygons (i.e., one to the parallelogram and the other to the trapezoid). Thus, the right- or acute-angle nature of the moving shape was visible since the very beginning of the video. However, whether the right-angle polygon was a square or a

rectangle or whether the acute-angle polygon was a parallelogram or a trapezoid could not be distinguished when only the rightmost part was visible at the beginning of the video. The differences between the two shapes in each pair became evident only with the increasing visibility of their leftmost part during video unfolding. At the end of each video, participants were asked to discriminate whether the moving shape was equal or unequal length sided by indicating, in a 2AFC mode, which concavity (lower vs. upper) of the receptor figure was complementary to the moving shape.

For both tasks, videos were displayed at a rate of 30 Hz (i.e., 33.33 ms per frame). They were presented on a neutral black background on a 17" monitor (refresh frequency, 60 Hz; resolution 1366 × 768) and subtended a $15.96^\circ \times 11.97^\circ$ region viewed from a distance of 60 cm. Videos were presented using the E-Prime 2 software (Psychology Software Tools, Inc., Pittsburgh, PA, USA).

Both tasks were administered in a familiarization phase and a following testing phase using a temporal occlusion paradigm in which the videos were stopped before the completion of the action/shape motion. In the familiarization phase, videos were interrupted after 833 ms of presentation (i.e., 25 frames). For the action prediction task, this corresponded to two frames before the model made full contact with the object, thus occluding the grasping movement itself. Despite this, the amount of visual information about the hand pre-shaping was sufficient to correctly discriminate the action as either individual or interpersonal (see also Amoruso et al. 2019). For the shape-prediction task, the interruption in the familiarization phase corresponded to a midway position of the shape motion to the central figure, showing the whole shape on the screen. Thus, analogously to the action-prediction task, participants did not observe the fitting of the shape into the

receptor, but had enough sensory information to discriminate the moving shape.

Notably, each action took place in the presence of a specific contextual cue, provided by the colour of the plate (orange or violet) or by the colour of the tablecloth (white or blue). Analogously, the polygons could be of four different colours (orange or violet for the right-angle polygons and white or blue for the acute-angle polygons). Thus, a total of 8 different videos were created for each task. Crucially, during the familiarization phase, we aimed to establish an arbitrary association between a contextual cue and a given action or shape, thus triggering the formation of contextual prior expectations regarding the unfolding action or the moving shape. To this aim, the eight videos were presented for an unequal number of trials in the familiarization phase to manipulate different probabilities of co-occurrence between each action or shape and a contextual cue. In particular, for the action prediction task, in a high expectancy condition, each action (e.g., grasping the apple to eat) or shape (e.g., square) in a pair was presented in the 90% of trials with a specific contextual colour (e.g., orange) and only in the 10% of trials with the other contextual colour (e.g., violet). Conversely, in a low expectancy condition, which was applied to the other pair of actions or polygons, each action (e.g., grasping the glass to drink) or shape (e.g., trapezoid) was presented in the 60% of trials with a specific contextual colour (e.g., blue) and in the 40% of trials with the other contextual colour (e.g., white). Thus, at the two levels of expectancy, each target stimulus was associated with high probability (i.e., 90 or 60%) to a contextual cue and with low probability (i.e., 10 or 40%) to the other. Examples of this probabilistic manipulation are illustrated in Fig. 2. The association between each action or shape and each contextual cue was counterbalanced across participants.

In the testing phase, videos were interrupted after 500 ms of presentation (i.e., 15 frames). For the action prediction task, this occluded most of the hand pre-shaping that could differentiate between the two types of action outcomes. Similarly, for the shape-prediction task, this occluded most of the left half of the moving shape, hindering the detection of the major/minor side ratio and thus the ease of discriminating between the two alternative moving shapes of each pair. This manipulation was aimed at leading participants to rely on the contextual prior expectations acquired during the familiarization to compensate for perceptual uncertainty in face of reduced sensory evidence. Using comparable manipulations for the two tasks allowed us to test the role of the cerebellum in forming and using contextual priors for predicting the unfolding of social vs. physical events. In this phase, each action or shape was presented embedded in each context for the same number of trials. Both tasks included two blocks. In each block,

80 familiarization trials were immediately followed by 40 testing trials, for a total of 160 familiarization and 80 testing trials per task (20 trials per cell).

In both familiarization and testing phases (Fig. 2), trials started with a fixation cross, which lasted 3000 ms and was followed by video-clip presentation. After the video-clip, the verbal descriptors (in Italian) of the two possible response alternatives (i.e., ‘to eat’/‘drink’ and ‘to give’ for the action prediction task; ‘down’ and ‘up’ for the shape prediction task) were presented on the right/left bottom part of the screen, until a response was recorded. Participants were requested to respond by pressing with the index finger the computer keys ‘z’ (for left choices) or ‘m’ (for right choices). The location of the two descriptors was counterbalanced between participants. The fact that participants could respond only at the presentation of the prompt frame after video offset ensured that participants could observe the whole video in all conditions. An empty black screen was presented for 1000 ms between each consecutive trial.

ctDCS administration

Transcranial direct current stimulation (tDCS) was delivered by a battery-driven constant DC current stimulator (BrainSTIM, EMS s.r.l., Bologna), using two 5×5 electrodes (25 cm^2)—current density: 0.06 mA/cm^2 —in saline-soaked synthetic sponge at a low continuous current intensity of 1.5 mA. In the anodic stimulation condition, the active electrode was centred over the medial cerebellum—2 cm below the inion with electrode’s lateral borders 2 cm medially to the mastoid apophysis—whereas the reference electrode was placed over the right buccinator muscle (BC). A tDCS modelling study found an inion-based right BC montage to produce relatively high field strengths in its target area (Rampersad et al. 2014). Furthermore, the montage applied in the present study was found effective in modulating visuomotor sequence learning in a sample of healthy adults (Shimizu et al. 2016). In the cathodic condition, the polarity of the electrodes was reversed. Both real and sham ctDCS involved a ramp up period of 15 s in which intensity was gradually increased to the established maximum. In the real conditions, the stimulation was ramped down (15 s) after 20 min of 1.5 mA ctDCS. In the sham condition, the ramp up period was followed by 30 s of real stimulation after which the intensity was ramped down to 0 mA. This way, participants felt the characteristic tingling sensations in the vicinity of the electrodes for a brief period of time, thus enhancing the plausibility of the control condition. Half of participants underwent sham stimulation with the anodic electrode over the cerebellum, the other half with the anodic electrode over

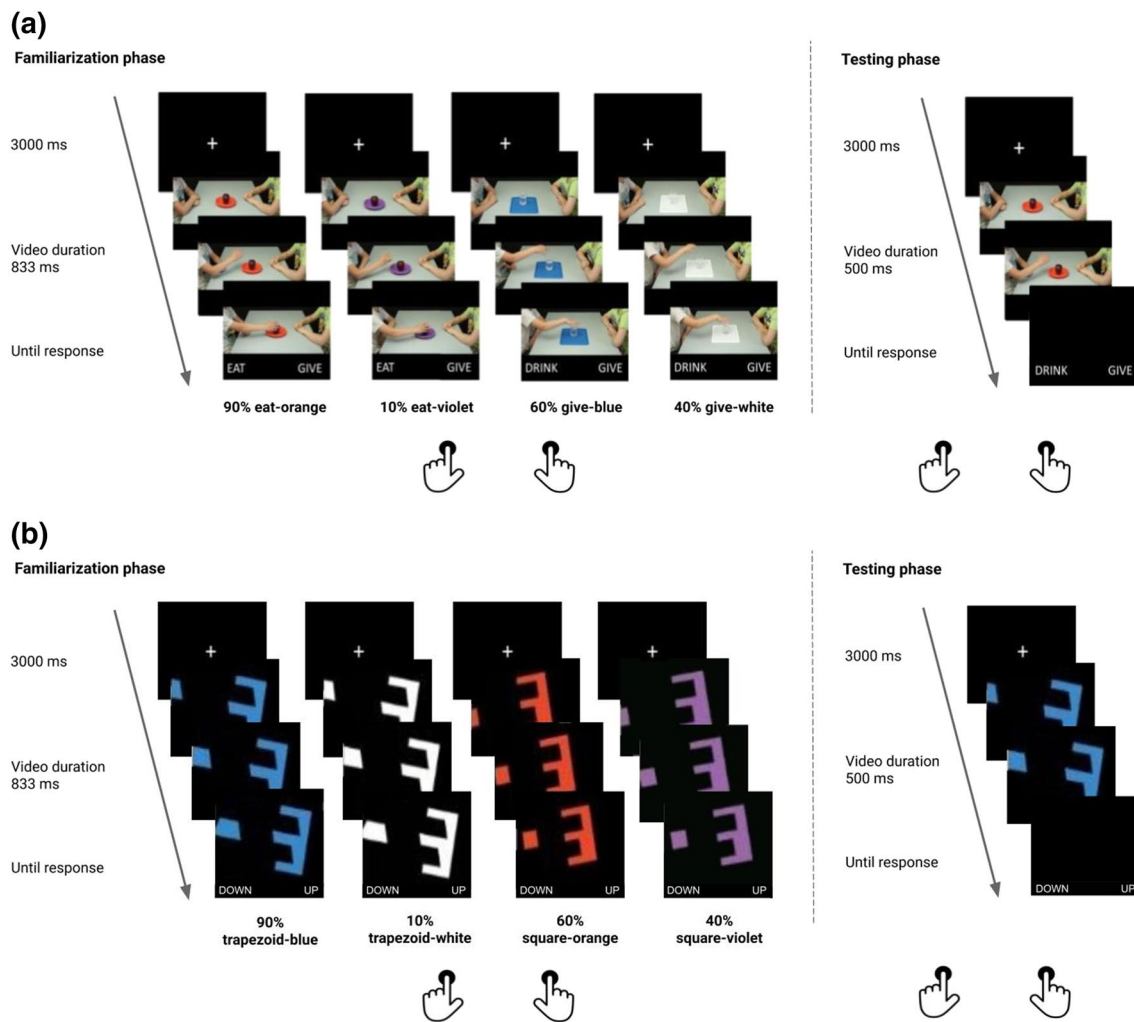


Fig. 2 Examples of trials in the familiarization phase and trial structure for the familiarization and testing phases of the action **(a)** and shape **(b)** prediction tasks. **a** In the example of the familiarization phase for the action prediction task, the high expectancy condition was assigned to the pair of actions directed to the apple, while the low expectancy condition was assigned to the pair of actions directed to the glass. In particular, the 90% of apple-action trials displayed a grasping-to-eat action from an orange plate or a grasping-to-offer action from a violet plate (high expectancy–high probability). The opposite action-cue associations were presented in the remaining 10% of apple-action trials (high expectancy–low probability). This way, an orange coloured plate strongly biased to grasping-to-eat and a violet one to grasping-to-offer. For what concerns the actions directed to the glass, 60% of trials displayed a grasping-to-offer action from a blue coloured tablecloth or a grasping-to-drink action from a white coloured tablecloth (low expectancy–high probability). The opposite intention-cue associations were presented in the remaining 40%

of trials (low expectancy–low probability). This way, a blue coloured tablecloth moderately biased to grasping-to-offer and a white one to grasping-to-drink. **b** In the example of the familiarization phase for the shape prediction task, the high expectancy condition was assigned to the acute-angle polygons, while the low expectancy one was assigned to the right-angle polygons. In particular, 90% of acute-angle polygon trials showed a blue coloured trapezoid or a white coloured parallelogram (high expectancy–high probability). The remaining 10% of trials showed a white coloured trapezoid or a blue coloured parallelogram (high expectancy–low probability). This way, the blue colour strongly biased to the trapezoid and the white colour to the parallelogram. For the right-angle polygons, 60% of trials displayed an orange coloured square or a violet coloured rectangle (low expectancy–high probability). The remaining 40% of trials showed a violet coloured square or an orange coloured rectangle (low expectancy–low probability). This way, the orange colour moderately biased to the square and the violet colour to the rectangle

the buccinator muscle. The schematic illustration of the setup is shown in Fig. 3.

Data handling

Proportions of correct responses for each experimental condition were extracted and analysed. For both tasks, a correct response was considered on the basis of the action kinematics or moving shape, thus independently from the

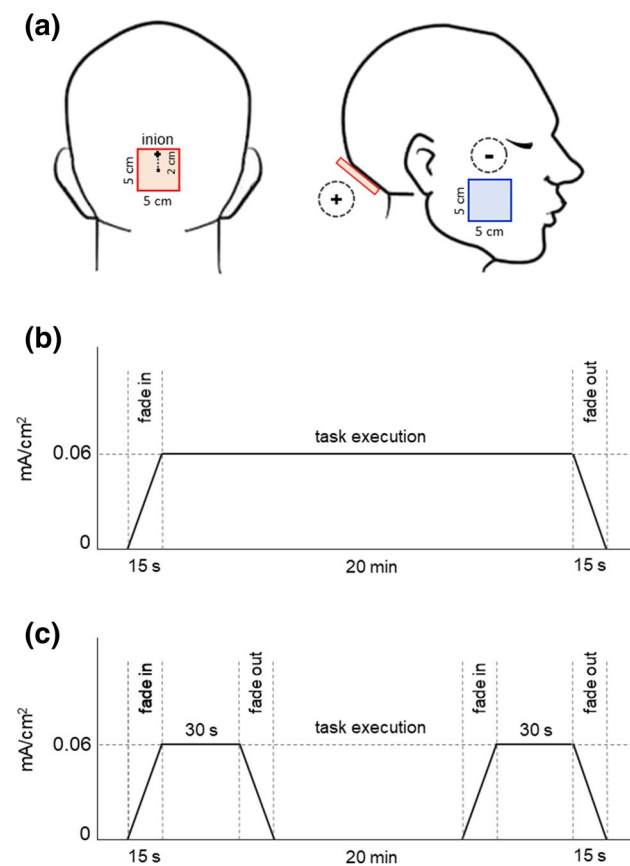


Fig. 3 Schematic depiction of **a** placement of electrodes for anodic ctDCS with the anode (red) over the medial cerebellum and the cathode (blue) over the right BC muscle; **b** time course of real ctDCS conditions and **c** time course of sham ctDCS condition

contextual prior. Latencies of responses were not entered into the analyses, since participants were not left free to respond at the onset of the video. Still, they were inspected

to identify anticipated or delayed responses. Thus, trials with latencies falling below 150 ms and above 3000 ms from the onset of the prompt frame were removed. After filtering, 0.5% of trials were removed from the familiarization phase of the action prediction task and 0.6% from the shape prediction tasks. For the testing phases, 1.3% and 0.9% of trials were removed in the action and shape prediction task, respectively.

A signal detection theory approach was used (Tanner and Swets 1954; Green and Swets 1966). D-prime values (d') were calculated from data collected in the familiarization and testing phases. This index is a bias-corrected measure of sensitivity reflecting the ability to discriminate between two categories of stimuli. In keeping with previous studies (Amoruso et al. 2019; Bianco et al. 2020), for the action prediction task individual actions identified as individual were considered 'hits', while interpersonal actions identified as individual were considered 'false alarms'. For the shape prediction task, equal-length-sided shapes (i.e., square and parallelogram) identified correctly were considered 'hits', while unequal length-sided shapes identified incorrectly were considered 'false alarms'. We also calculated a measure of response criterion (c), which reflects the existence of a bias in providing a specific response, with negative values pointing to a tendency toward reporting the signal and positive values a tendency toward reporting the absence of the signal; values close to 0 suggest no bias. In our case, negative c values point to a tendency to report individual or equal-length-sided shapes, while positive values a tendency to report interpersonal or unequal-length-sided segment shapes. The values of d' and c for all experimental conditions are reported in Table 1.

First, $2 \times 3 \times 2$ repeated-measures analyses of variance (RM-ANOVAs) were conducted on d' and c values extracted from the familiarization phases, with TASK (action vs. shape

Table 1 Mean and standard error of the mean (SEM) of sensitivity d' and criterion c as a function of task (action vs. shape prediction), ctDCS stimulation (anodic/cathodic and sham) level of expectancy (low vs. high) and level of probability (low vs. high) in the testing phase

	Expectancy	Action prediction				Shape prediction			
		Low	High	Low	High	Low	High	Low	High
Anodic	Probability	Low	High	Low	High	Low	High	Low	High
	Sensitivity d'	2.60 (0.14)	2.71 (0.11)	2.19 (0.26)	2.69 (0.12)	2.61 (0.19)	2.61 (0.16)	2.64 (0.16)	2.62 (0.15)
	Cathodic	2.27 (0.21)	2.63 (0.13)	1.83 (0.31)	2.38 (0.15)	2.31 (0.28)	2.52 (0.20)	2.22 (0.30)	2.71 (0.13)
Sham		2.41 (0.16)	2.29 (0.25)	2.53 (0.17)	2.62 (0.16)	2.68 (0.14)	2.57 (0.17)	2.61 (0.20)	2.63 (0.18)
Anodic	criterion c	Low	High	Low	High	Low	High	Low	High
		0.12 (0.07)	0.06 (0.06)	0.25 (0.09)	0.02 (0.07)	0.06 (0.10)	0.07 (0.09)	-0.02 (0.08)	-0.08 (0.07)
		Cathodic	0.16 (0.10)	-0.01 (0.08)	0.13 (0.11)	0.12 (0.10)	0.07 (0.08)	0.12 (0.09)	-0.06 (0.05)
Sham		0.13 (0.08)	-0.07 (0.08)	0.19 (0.06)	0.06 (0.06)	-0.01 (0.09)	-0.04 (0.10)	0.09 (0.10)	0.11 (0.11)

prediction), STIMULATION TYPE (anodic vs. cathodic vs. sham) and EXPECTANCY (low 40 and 60% vs. high 10 and 90%—predictability of the contextual cue) as within-subject factors. In the context of this experiment, the level of expectancy is thought to underlie the presence of a highly informative contextual prior of the upcoming target event, as compared to a moderately informative prior. The specific probability condition (i.e., 10 vs. 90% or 40 vs. 60%) was not considered in the familiarization phase because of an inherently different number of trials.

Then, separate $2 \times 3 \times 2 \times 2$ RM-ANOVAs were conducted on d' and c values extracted from the testing phases, with TASK (action vs. shape prediction), STIMULATION TYPE (anodic vs. cathodic vs. sham), EXPECTANCY (low vs. high) and PROBABILITY (low 10% and 40% vs. high 60 and 90%—probability of co-occurrence between target and contextual cue) as within-subject factors.

All statistical analyses were performed using STATISTICA 8.0 (StatSoftInc, Tulsa, Oklahoma). All data are reported as mean (M) \pm standard error of the mean (SEM). A significance threshold of $p < 0.05$ was set for all effects and effect sizes were estimated using the partial eta squared measure (η_p^2). Duncan post hoc tests were performed to follow-up significant interactions.

Results

The analysis of the familiarization-phase d' data (Fig. 4a) yielded a significant main effect of TASK [$F(1,23) = 8.49$, $p = 0.008$; $\eta_p^2 = 0.27$] indicating that participants performed better in the action (3.25 ± 0.01) compared to the shape prediction task (3.20 ± 0.02). No other significant result emerged (all $F < 3$, $p > 0.07$).

The analysis on the c values of the familiarization-phase (Fig. 4b) showed a significant interaction effect of TASK*EXPECTANCY [$F(1,23) = 8.64$, $p = 0.007$; $\eta_p^2 = 0.27$]. Post hoc analysis revealed that, in the shape prediction task, the response bias was lower in the high-expectancy (-0.02 ± 0.01) compared to the low-expectancy trials (0.02 ± 0.01 ; $p = 0.01$). No difference emerged for the action prediction task ($p = 0.3$). This suggests that, albeit the c values were close to zero in all conditions, ruling out an important response bias in either task, participants were slightly more prone to report an equal-length-sided shape when contextual priors were more informative and an unequal-length-sided shape when contextual priors were less informative. No other significant main effects or interactions were observed (all $F < 1.96$; $p > 0.15$).

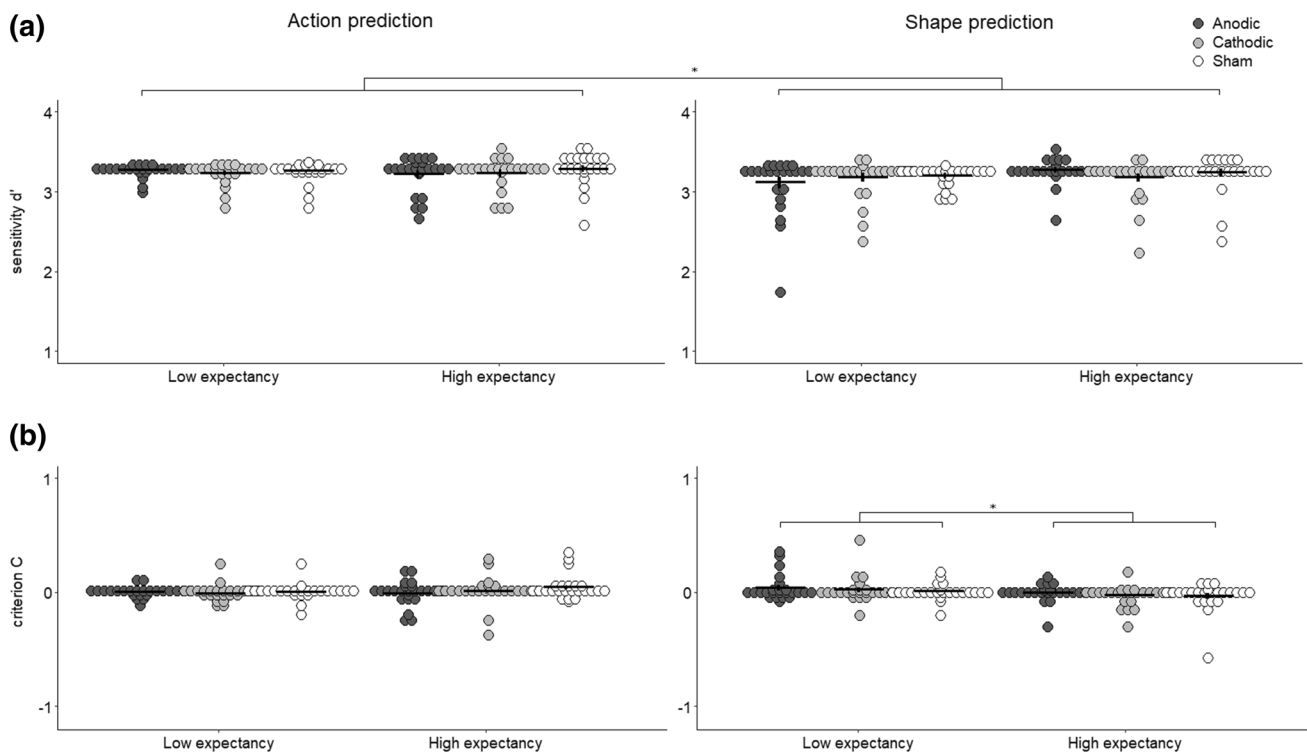


Fig. 4 Dot plot displaying data distribution of d' sensitivity (a) and criterion c (b) values obtained in the familiarization-phase in the action prediction task (left panel) and in the shape prediction task (right panel) during anodic (dark grey), cathodic (light grey) and

sham (white) ctDCS as a function of the level of expectancy (low vs. high). The horizontal lines represent mean scores. Error bars represent \pm standard error of the mean. Asterisks indicate significant comparisons

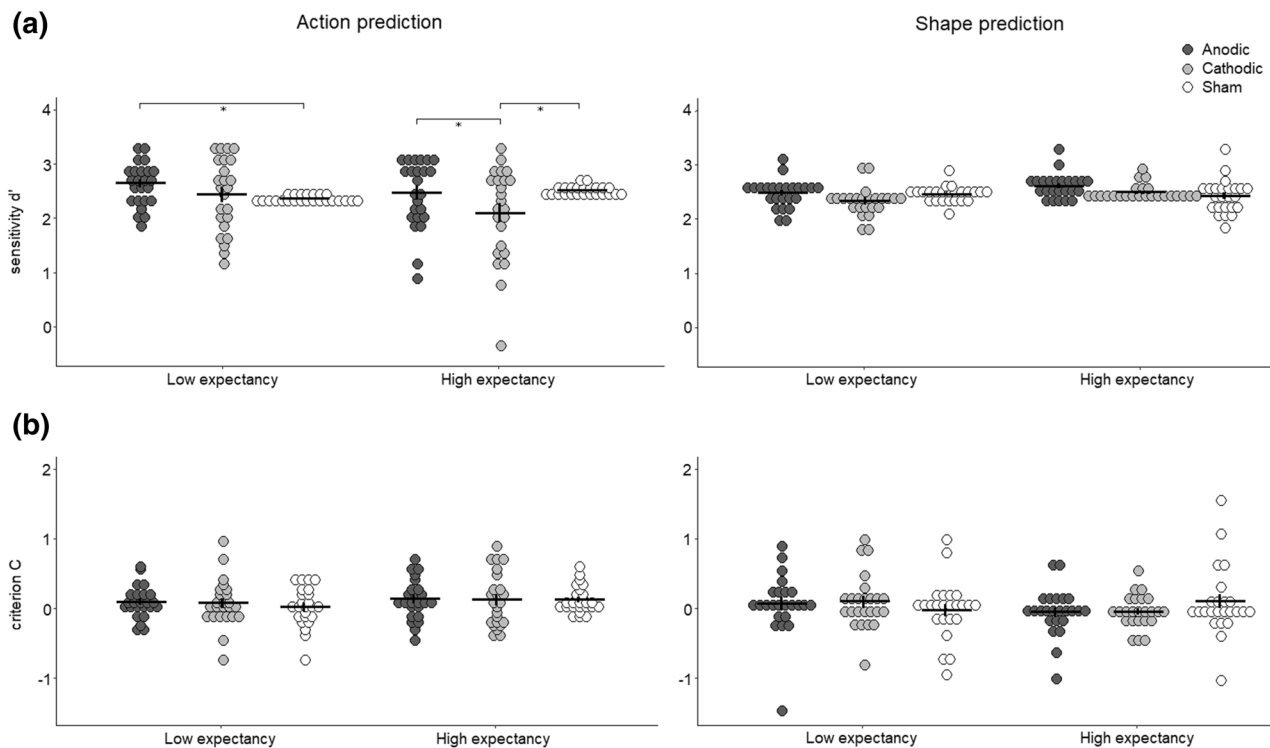


Fig. 5 Dot plot displaying data distribution of d' sensitivity (**a**) and criterion c (**b**) values obtained in the testing-phase in the action prediction task (left panel) and in the shape prediction task (right panel) during anodic (dark grey), cathodic (light grey) and sham (white)

The analysis of the testing-phase d' data (Fig. 5a) showed a near-to-significance main effect of PROBABILITY [$F(1,23)=4.18, p=0.05, \eta_p^2=0.15$], indicating higher sensitivity in trials with high (2.58 ± 0.33) compared to low (2.41 ± 0.41) level of probability of co-occurrence between target and contextual cues. This confirmed the successful probabilistic manipulation of the context-target associations. Importantly, a significant interaction effect of TASK* STIMULATION TYPE* EXPECTANCY [$F(2,46)=4.03, p=0.03, \eta_p^2=0.15$] emerged. Post hoc comparisons of this interaction highlighted specific effects of stimulation on the action prediction task according to the level of expectancy. Specifically, when considering the low expectancy trials, a higher sensitivity was found during anodic stimulation (2.65 ± 0.11) compared to sham stimulation (2.35 ± 0.20 ; $p=0.03$), whereas no significant difference emerged between anodic and cathodic (2.45 ± 0.19 ; $p=0.13$) or between cathodic and sham stimulations ($p=0.44$). Conversely, for the high-expectancy trials, results showed lower sensitivity during cathodic stimulation (2.10 ± 0.25) compared to both anodic (2.44 ± 0.19 ; $p=0.008$) and sham stimulations (2.57 ± 0.17 ; $p<0.001$), whereas no difference emerged between anodic and sham stimulations ($p=0.29$). No significant difference between stimulation types emerged within

ctDCS as a function of the level of expectancy (low vs. high). The horizontal lines represent mean scores. Error bars represent \pm standard error of the mean. Asterisks indicate significant comparisons

the shape prediction task (all $p>0.11$). No other significant main effects or interactions were found (all $F<2.46$; all $p>0.10$).

The analysis of the testing-phase c data (Fig. 5b) yielded a significant main effect of PROBABILITY [$F(1,23)=5.47, p=0.03$; $\eta_p^2=0.19$], which was further qualified by a significant interaction effect TASK* PROBABILITY [$F(1,23)=5.91, p=0.02$; $\eta_p^2=0.20$]. Post hoc test revealed that participants were more prone to report an interpersonal than an individual action in the low-probability trials (0.16 ± 0.02) than in the high-probability ones (0.03 ± 0.02 ; $p=0.003$) of the action prediction task. No such difference emerged in the shape prediction task ($p=0.98$). Importantly, no other main effects or interactions were significant (all $F<3.18$; all $p>0.09$), ruling out that the expectancy-modulated effects of ctDCS on the sensitivity in the action prediction task were affected by a change in response bias.

Discussion

In this study, we attempted to disentangle the general or domain-specific involvement of the cerebellum in learning and using probabilistic regularities to make predictions

about social or physical events. To this aim, we modulated the excitability of the cerebellar cortex by means of facilitatory (anodic) and inhibitory (cathodic) ctDCS during the execution of an action and a shape prediction task. Importantly, thanks to their inner structure, these tasks allowed us to assess the use of strong or moderate context-target associations, acquired during a first learning phase, to predict the future of social and non-social (physical) events in situation of perceptual uncertainty. Indeed, the associations between actions/shapes and contextual elements were manipulated in terms of their probability of co-occurrence, so to test participants' behavior in predicting upcoming events on the base of past experiences. Based on the conception of the cerebellum as a “general purpose” controller operating across domains (Kozioł et al. 2014), both the action and the shape prediction tasks should have been influenced by ctDCS (H1). Differently, according to the idea of a “social” cerebellum constituting a critical node for socio-emotional processing (Van Overwalle et al. 2020), we expected to find a specific effect of ctDCS in the execution of the action, but not of the shape, prediction task (H2). Overall, in line with H2, we found that ctDCS affected participants' ability in using prior knowledge to make predictions of social, but not of physical events. Importantly, in keeping with a role of the cerebellum in anticipating incoming information in condition of perceptual uncertainty, we found ctDCS to affect participants' performance only in the testing, but not in the familiarization phase of the action prediction task.

The differential effect of ctDCS on the two tasks is unlikely due to different levels of task difficulty. Indeed, in the testing phase, where sparse perceptual information was provided for both tasks, no differences between the two tasks emerged in terms of sensitivity to target discrimination. Nevertheless, a different sensitivity for the two tasks emerged in the familiarization phase, with the action prediction task being easier than the shape prediction task, independently from the stimulation condition. This is possibly due to a greater familiarity and relevance in everyday life for using sensorial evidence to discriminate human actions than to discriminate abstract figures. Accordingly, participants' response bias was modulated by the context-target associations in the familiarization phase of the shape prediction task, with a different tendency to report a shape with equal- vs unequal-length sides depending on the probability of context-target associations. This finding reassured that participants relied on the context-target associations to solve the shape prediction task, ruling out that the absence of ctDCS effects in this task was due to an oversight of contextual information. Interestingly, with the reduced perceptual information provided in the testing phase, even the action prediction task revealed a modulation of the response bias according to the probability of context-target associations, with a greater tendency to report an interpersonal rather

than an individual action outcome in the low- than high-probability trials. Thus, in conditions of poor sensorial and contextual information, participants changed their criterion of response toward an interpersonal action, probably due to the presence of another individual in the scene for all action videos. Notably, response bias was never modulated by ctDCS, ruling out that the ctDCS effects on sensitivity were mediated by changes in response bias.

That ctDCS modulated participants' performance only in the action, but not in the shape prediction task, supports a prominent role of the cerebellum in the processing of action sequences. This is in accordance with previous evidence of impaired recognition of action (Cattaneo et al. 2012; Butti et al. 2020b) and social sequences (Van Overwalle et al. 2019) in cerebellar patients in spite of preserved—or less damaged—ability to recognize “non-social” mechanical sequences. In contrast, differently from previous studies in cerebellar patients that have found at least partial deficits in the sequencing of both social and non-social events (Leggio et al. 2008; Cattaneo et al. 2012), no effects at all were found in the non-social task. The prominent involvement of the cerebellum in social predictions fits with the broad framework of the Embodied Cognition theory, which endorses the notion that action-related processing is grounded in the sensorimotor system (see Gentsch et al. 2016 for a review). Given its critical role in sensory-motor control, the “social-specific” role of the cerebellum might reflect its susceptibility to the prediction of unfolding actions. On this matter, it has been proposed that different aspects of cognitive processing (e.g., action semantics) are interdependent with the motor functions of the cerebellum (García and Ibáñez 2018). In a convergent manner, cerebellar patients have been demonstrated to exhibit a selective impairment in processing action semantics, as compared to object semantics (Cervetto et al. 2018), as well as in processing action verbs as compared to other classes of words (García et al. 2017) possibly due to an alteration of predictable motor-semantic integration patterns.

Nevertheless, the task-dependent effect may also depend to some extent on the site of stimulation. In the present study, ctDCS was targeted over the medial (vermal) portion of the cerebellum. A recent study has shown that cerebellar malformations in specific portion of the vermis were associated to impairments in social cognition (Clausi et al. 2019). Despite the low spatial acuity of tDCS prevents any specific anatomical inferences, it cannot be excluded that targeting other cerebellar macro-areas could have led to a domain-general modulation of predictive abilities based on prior experiences. That being said, evidence gathered on the functional topography of the cerebellum is still far from providing a clear picture of the functional specificity of its regions, although some steps in the characterization of cerebellum topography have been made (Stoodley and

Schmahmann 2018; Diedrichsen et al. 2019), also using magnetic stimulation techniques (Cattaneo et al. 2014; Ferrari et al. 2018, 2019a, b). Thus, future studies using more focal brain stimulation techniques may provide further evidence on the contributions of different cerebellar regions to the prediction of social and non-social events.

Importantly, beside a task-specific effect of ctDCS, a polarity-dependent effect was also found, with increased performance after anodic ctDCS and reduced performance after cathodic ctDCS. Even though neither anodic nor cathodic ctDCS has been proven to reliably predict the respective enhancement or impairment in performance (Oldrati and Schutter 2017), the present finding is in accordance with the conventional anodic-excitation and cathodic-inhibition dichotomy (Galea et al. 2009). Interestingly, these facilitatory or inhibitory modulations of anodic or cathodic ctDCS were state-dependent according to the informativeness of the context. Specifically, we found that enhancing the activation of the cerebellum via anodic ctDCS strengthened the use of moderately informative priors in making predictions pertaining the social domain with respect to a sham (control) condition. Conversely, reducing the activation of the same area via cathodic ctDCS decreased the use of highly informative priors compared to both anodic and sham stimulations in the same (social) task. It can be hypothesized that these modulatory effects reflect the different levels of activation of cerebellar networks during the prediction of actions embedded in moderately or highly informative contexts, which might lead to lower or higher cerebellar activation, respectively. Indeed, it has been shown, within the linguistic domain, that the cerebellum is more active and is differently susceptible to ctDCS during completion of sentences that provide strong vs. weak cues to the missing word (D’Mello et al. 2017). Accordingly, in our study, anodic stimulation, by increasing cerebellar cortical excitability, boosted the retrieval of moderately informative models of target-context associations, resulting in improved performance for low expectancy trials, which were likely associated with lower activation of cerebellar circuits. The same excitatory stimulation did not affect high expectancy trials, which were associated with high cerebellar activation, such that no further boosting of activity could be achieved via ctDCS. On the opposite, cathodic stimulation, by reducing cerebellar cortical excitability, particularly disturbed highly informative models, leading to a performance decrease for high expectancy trials, which were likely associated with higher activation of cerebellar circuits. The same inhibitory stimulation did not affect low expectancy trials, which were associated with lower cerebellar activity, such that no further decrease could be achieved via ctDCS. Thus, the effect of ctDCS was state dependent with respect to the informativeness of the context regardless of the clarity of kinematic information. Indeed, participants’ ability in discriminating

between competing actions, independently from contextual information, was still high and well above the chance level for both low and high expectancy trials. This suggests that ctDCS did not affect the perception of action kinematic per se, which was comparably available in low and high expectancy trials, but it rather affected the reliance on contextual priors to make predictions. Despite caution is urged about such a mechanistic explanation of tDCS effects, our findings highlighted the role of the cerebellum in making context-dependent predictions in the social domain.

Alterations in predicting unfolding actions may explain the social perception deficits reported in neurodevelopmental disorders. In particular, a recent view has linked difficulties in action comprehension in individuals with autism to atypical predictive processing (Pellicano and Burr 2012; Sinha et al. 2014). The core idea would be that individuals with autism are less influenced by prior knowledge (e.g., contextual elements) and, on the contrary, rely to a greater extent on bottom-up sensory signals. In keeping with this view and using the same action prediction task of the present study, Amoroso et al. (2019) demonstrated that children with typical development, but not children diagnosed with autism, were able to use previously learned contextual priors to predict upcoming actions. Our findings qualify this view by providing evidence of a role of cerebellar functioning in context-based predictions of actions. Interestingly, atypical cerebro-cerebellar connectivity has been described in autistic individuals (Khan et al. 2015; Olivito et al. 2017). Although distinct pathophysiological mechanisms have been proposed to drive neurocognitive deficits in autism and in cerebellar disorders causing CCAS (Casartelli et al. 2018), it can be conjectured that their action comprehension difficulties may have roots in a misuse of contextual priors of social scripts to predict forthcoming behaviours.

In this regard, our study supports the feasibility of ctDCS to investigate action prediction abilities in healthy individuals and the definition of ctDCS protocols for the rehabilitation of social skill abilities in patients with cerebellar abnormalities. In fact, evidence of ctDCS efficacy in supporting the recovery from not only motor, but also cognitive and social impairments following cerebellar damage (Wessel and Hummel 2018), endorses the further examination of the effects of cerebellar stimulation protocols alone or in combination with other intervention programs. In particular, our findings point to the possible efficacy of ctDCS to boost the efficacy of intervention programs aiming at enhancing predictive internal models of other’s behaviours in order to boost social competences (Butti et al. 2020a).

The conclusions that can be drawn from this study must be considered in light of two main limitations. First, even if we powered our study to detect ctDCS effects based on previous meta-analytic investigation of ctDCS effects on non-motor functions (Oldrati and Schutter 2017), no

information for estimating the effect size of ctDCS on the implicit-learning tasks used here was available. Moreover, despite the intrinsic power of a within-subject design and despite the use of different versions of the same tasks within each participant, the repetition of the implicit-learning tasks across three sessions might have blurred the probabilistic implicit-learning manipulation. Second, differences between the two tasks must be acknowledged. Despite the probabilistic manipulation and the structure of the two tasks was kept identical, the shape prediction task suffered from low ecological validity. In fact, participants were likely less familiar with either the task requirements or the stimuli of the shape as compared to the action prediction task. Despite these limitations, the task-, polarity- and expectancy specificity of the ctDCS effects provided causative evidence for a role of the cerebellum in using previously learned contextual associations to predict social events.

Author contributions AF and CU contributed to the study conception and design. Data collection was performed by VO, EF and NB. Data analysis were carried out by VO, EF, NB and AF. The first draft of the manuscript was written by VO and AF. CU, ZC and RB contributed to writing and editing. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials The datasets generated during and analysed during the current study are available in the OSF repository, https://osf.io/vg2nt/?view_only=0e3a4b975f5847288e33d68162720a54.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval The experimental protocol respected the Helsinki Declaration and its later amendments.

Informed consent All subjects provided their written informed consent before participating in the study.

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