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Excitatory cerebellar transcranial direct current stimulation boosts the leverage of prior knowledge for predicting actions

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Abstract

The cerebellum causally supports social processing by generating internal models of social events based on statistical learning of behavioral regularities. However, whether the cerebellum is only involved in forming or also in using internal models for the prediction of forthcoming actions is still unclear. We used cerebellar transcranial Direct Current Stimulation (ctDCS) to modulate the performance of healthy adults in using previously learned expectations in an action prediction task. In a first learning phase of this task, participants were exposed to different levels of associations between specific actions and contextual elements, to induce the formation of either strongly or moderately informative expectations. In a following testing phase, which assessed the use of these expectations for predicting ambiguous (i.e. temporally occluded) actions, we delivered ctDCS. Results showed that anodic, compared to sham, ctDCS boosted the prediction of actions embedded in moderately, but not strongly, informative contexts. Since ctDCS was delivered during the testing phase, that is after expectations were established, our findings suggest that the cerebellum is causally involved in using internal models (and not just in generating them). This encourages the exploration of the clinical effects of ctDCS to compensate poor use of predictive internal models for social perception.

Key words: cerebellum; tDCS; predictive coding; social cognition; action prediction

Introduction

The cerebellum is suggested to serve as a general-purpose controller implementing basic computational functions applicable in different domains and supporting not only motor but also high level cognitive and socio-affective functions (Bower, 1997; Timmann *et al.*, 2010; D'Angelo and Casali, 2012; Van Overwalle *et al.*, 2020). It aids in creating and retaining internal models of external world objects and events, supporting higher-level functions (Ito, 2008). This computational mode would mirror the one used to coordinate movements (Kitazawa *et al.*, 1998) and predict the sensory consequences of one's own movements (Blakemore *et al.*, 2001; Blakemore and Sirigu, 2003). In movement control, the cerebellum forms internal models mirroring body part dynamics, refining movement execution without continual reliance on body feedback (Marr, 1969; Bower, 2002). Extending from motor research, accumulating evidence has emphasized the cerebellar role in the prediction of future events, built upon the detection of

regularities in either the social or the physical world (Leggio *et al.*, 2008; Bellebaum *et al.*, 2012; Sokolov *et al.*, 2017).

Within the domain of social cognition (Van Overwalle *et al.*, 2020), numerous neuroimaging studies showed the cerebellum activating alongside the prefrontal and temporo-parietal cortices during socio-cognitive tasks (Hayter *et al.*, 2007; Stoodley, 2012; Habas, 2021). Clinical observations also linked cerebellar disorders to socio-cognitive deficits (Schmahmann and Sherman, 1998; Tavano *et al.*, 2007) and neuropsychiatric conditions with cerebellar structural and functional abnormalities (Schmahmann *et al.*, 2007; Phillips *et al.*, 2015).

For social processing, the cerebellum has been proposed to generate simulations of sensory events aiding in predicting forthcoming actions (Ito, 2008; Bellebaum *et al.*, 2012). Observing others during social interactions would trigger internal motor models, transforming observed body kinematics into anticipated intentions (Gazzola and Keysers, 2009). However, the understanding of

body kinematics alone is not sufficient to ensure successful social interactions. An important role is thought to be played by the acquisition and storing of internal models based on the detection of statistical regularities of the contextual elements (or priors) accompanying these interactions (Huang and Rao, 2011; Siman-Tov et al., 2019). Indeed, contextual priors significantly influence action recognition and motor activation during action observation, showcasing their impact on social interactions (Iacoboni et al., 2005; Amoruso et al., 2016, 2018, 2020; Amoruso and Finisguerra, 2019; Betti et al., 2022).

By integrating cerebellar functions in a predictive processing framework, in a previous study (Oldrati et al., 2021), we explored how cerebellar transcranial direct current stimulation (ctDCS) affects prediction abilities regarding actions and physical events based on prior experiences. In general, ctDCS consists in the application of constant weak current to the cerebellum via electrodes applied on the skin, in correspondence of specific cerebellar region. During tDCS, electric current passes between a positively charged anode and a negatively charged cathode and provokes a sub-threshold modulation of neuronal excitability without depolarizing action potentials. In principle, the modulation is polarity dependent and it consists in a change toward depolarization (i.e. excitation) after anodal stimulation or toward hyperpolarization (i.e. inhibition) after cathodal stimulation (Priori et al., 1998; Nitsche and Paulus, 2000). Using anodal (excitatory), cathodal (inhibitory) or sham ctDCS, in Oldrati et al. (2021), we conducted action and shape prediction tasks in two phases. First, in an implicit learning phase (i.e. familiarization phase), we manipulated the likelihood of action or shape occurrence with contextual elements, forming varying levels of predictive expectations. Participants then underwent a testing phase with reduced sensory evidence, assessing their ability to predict actions or events. Results indicated a polarity, expectancy-dependent effect of ctDCS, limited to the prediction of social actions but not of physical events: indeed, while cathodal stimulation was found to hamper the prediction of actions embedded in strongly informative contexts, anodic stimulation was able to boost the prediction of actions embedded in moderately informative contexts. No effects were instead observed on the prediction of physical events. These findings suggested the cerebellar role in forming and using learned contextual associations for action prediction. However, as ctDCS was administered throughout the task, including both the familiarization and testing phases, we could not dissociate the cerebellum's role in forming or retrieving action-cue associations.

Cerebellar activity has been detected in different phases of the learning process. As individuals become more proficient in executing movements, their neural representation becomes less reliant on the cerebellum (Doyon et al., 2002). Neuroimaging evidence also highlights increased cerebellar activation during learning new sequences compared to familiar sequences (Attout et al., 2014). This aligns with findings from transcranial magnetic stimulation (TMS) studies, indicating the cerebellum's lack of impact on recognizing familiar sequences (Ferrari et al., 2018). In social contexts, cerebellar patients struggled with ordering cartoons depicting false belief stories but performed normally on well-learned social scripts (Van Overwalle et al., 2019). Taken together, these findings emphasize the cerebellar role in forming internal models, particularly when minimal updates are needed.

To disentangle this point, here, we applied the same action prediction task used by Oldrati et al. (2021), but this time we delivered anodic ctDCS exclusively during the testing phase, thus

after expectations were learned in the familiarization phase without any stimulation. In keeping with a potential rehabilitative implication of the protocol, we applied only anodic stimulation, which, in our previous study (Oldrati et al., 2021), was linked to enhancing action prediction, but not cathodic stimulation, which was linked to opposite, negative effects. A significant effect of the stimulation would provide evidence of a causative role of the cerebellum (at least also) in utilizing the models necessary for optimal task execution under conditions of perceptual ambiguity. In addition, we expected the effect of the stimulation to be expectancy-dependent, as emerged in the preceding study, with anodic stimulation boosting the prediction of actions embedded in moderately, but not strongly, informative scenarios.

Participants

Twenty-four healthy University students took part in this study (10 meter/14 F; mean age = 22.6, SD = 2.6 years). The sample size of our repeated-measures analysis of variance (RM-ANOVA) design (numerator df = 1) was determined through the G*Power software (Faul et al., 2007). By using the SPSS option, we set the expected effect size f(U) = 0.7, based on the value of the interaction ($\eta_p^2 = 0.33$) within the action prediction task between the repeated-measure variables stimulation (anodic *vs* sham) and expectancy (high *vs* low) found by Oldrati et al. (2021); we set the alfa threshold of 0.05 and the desired power (1–β) at 0.85. All participants were right-handed and had a normal or corrected-to-normal vision. Prior to the experiment, all participants filled in a questionnaire to evaluate their suitability for tDCS. None of the volunteers reported a history of neurological disorders, brain trauma, a family history of epilepsy or any other contraindication to tDCS. The use of medications was screened to exclude the intake of any neuroleptic drug. Participants provided written informed consent according to a protocol approved by the local ethics committee (Comitato Etico I.R.C.C.S. 'E. Medea' Associazione La Nostra Famiglia, Italy, Prot. N.58/18) and compliant with the Code of Declaration of Helsinki.

Task and procedure

The study adopted a single-blind, within-subjects, sham-controlled design. Participants performed an action prediction task, consisting of familiarization and testing phases, and received real (anodic) or sham ctDCS during the testing phase only. Anodic or sham ctDCS were delivered in separate sessions, scheduled at least 24 h apart to ensure a wash-out period (mean = 4.6 days, SD = 2.3).

The action prediction task was adapted from previous studies (see Amoruso et al., 2019; Bianco et al., 2020 for a detailed description). It required participants to observe videos of a child performing two distinct actions upon two different objects, namely 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 at the opposite side of the table). Participants were then asked to predict action unfolding (i.e. individual or interpersonal outcome) in a two-alternative forced choice (2AFC) mode.

The task was divided into two consecutive phases: a familiarization phase and a testing phase. The aim of the familiarization phase was to establish an arbitrary association between a contextual cue (i.e. the color of a plate/tablecloth) and a given action (reaching to eat/drink or reaching to offer an apple or a glass).

To this aim, in this phase, the videos were presented for an unequal number of trials to manipulate different probabilities of co-occurrence between each action and the contextual cues. In a high-expectancy condition, a specific action toward an object (e.g. reaching to eat an apple) was presented in the 90% of trials together with a specific contextual cue (e.g. orange colored dish) and only in the 10% of trials with the contextual cue of a different color (e.g. violet). Conversely, in a low-expectancy condition, the action toward the other object (e.g. reaching the glass to drink) was presented in the 60% of trials with a specific contextual color (e.g. blue) and in the remaining 40% of trials with the other contextual color (e.g. white). Either in the high- or in the low-expectancy condition, for the opposite action (i.e. to offer action), the pattern of association with the contextual cue was reversed (i.e. the offering action of the apple was presented 90% of the time in association with the violet-colored plate, while the offering action of the glass was presented 60% of the time with the white-colored tablecloth). This manipulation conferred greater informativeness about the unfolding action to the contextual prior in the high-expectancy condition, whereas the contextual prior with low-expectancy value was characterized by lower informativeness. Furthermore, within the two levels of expectancy, each action could be 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. The color-action associations and object-expectancy manipulations were counterbalanced between-subjects; furthermore, to avoid carry over effects across sessions, they always varied between the two sessions for a single participant.

The arbitrary associations formed in the familiarization phase were expected to trigger contextual prior expectations on the unfolding action to be predicted in the testing phase. While in the familiarization phase, videos were interrupted after 833 ms of presentation (i.e. 25 frames), which corresponded to two frames before the actor made full contact with the target object, in the testing phase, videos were interrupted after 500 ms of presentation (i.e. 15 frames). Thus, by means of a temporal occlusion paradigm, most of the hand pre-shaping that could inform on how to differentiate between the two actions was occluded in the later testing phase. This way, we created a condition of perceptual uncertainty, in which we expected participants to leverage on previously formed contextual prior expectations to guide action discrimination. Figure 1A provides a schematic representation of the task structure. The stimulation (real or sham) was delivered exclusively during the testing phase in order to test the main hypothesis (see Figure 1B).

In both phases, a trial consisted of a 3000 ms fixation cross followed by video-clip presentation. After the video-clip, the labels (in Italian) of the two actions (i.e. 'to eat'/'to drink' and 'to give') were presented on the right/left bottom part of the screen, until a response was recorded. Participants could provide their response, without any time constraints, by pressing with the index finger the keys 'z' (for left choices) or 'm' (for right choices). They were, however, prompted to respond as quickly and accurately as possible. The location of the labels was counterbalanced between participants. An empty black screen was presented for 1000 ms between each consecutive trial. The familiarization phase consisted of 160 trials, while the testing phase consisted of 240 trials (60 trials per cell). The videos were displayed at a rate of 30 Hz (i.e. 33.33 ms per frame). They were presented on a black background on a 17″ monitor (refresh frequency, 60 Hz; resolution 1366 × 768) and subtended a 15.96° × 11.97° region viewed from a distance of 60 cm.

The task was built in E-Prime 3 software (Psychology Software Tools, Inc., Pittsburgh, PA, USA).

tDCS parameters and application

ctDCS was delivered by a battery-driven constant DC current stimulator (Brain-STIM, EMS s.r.l., Bologna) by means of two 5 × 5 electrodes (25 cm^2) inserted in a synthetic sponge covered with conductive gel (thickness: 3 mm). The current intensity was set at 1.5 mA (current density: 0.06 mA/cm^2). Each participant underwent a real (anodic) stimulation and a sham stimulation in two separate sessions. In both stimulation conditions, the active electrode was centered over the scalp position corresponding to 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. The choice of the target area is substantiated by a recent meta-analysis, which demonstrates that the application of anodal ctDCS to the medial cerebellum effectively modulates cognitive processes (Pezzetta *et al.*, 2024). Moreover, the midline portion of the cerebellum has been previously targeted in transcranial electrical stimulation studies, showcasing its effect on social cognition abilities, including emotion recognition (Ferrucci *et al.*, 2012; Malatesta *et al.*, 2023) and the attribution of mental states to others (Clausi *et al.*, 2022). Also, using the buccinator as the reference electrode position is in keeping with previous studies of cerebellar stimulation (Ferrucci *et al.*, 2015). A simulation model of the electric field distribution and magnitude generated by the applied montage was performed with SimNIBS (Thielscher *et al.*, 2015), using standard conductivity values (see Figure 2).

In the real stimulation condition, the current was ramped down after 20 min of tDCS, which corresponded approximately to the duration of the testing phase. In the sham condition, the stimulation was turned on only for 60 s at the beginning and at the end of the stimulation period (see Figure 1B).

The order of stimulation conditions (anodic *vs* sham) was counterbalanced between participants. Participants were divided such that half received anodic stimulation in the first session followed by sham stimulation in the second session, while the other half first received sham stimulation followed by anodic stimulation. The sequence of stimulation administration (anodic first or sham first) was linked to a set of consecutive participant numbers established prior to the experiment, associating odd numbers with the anodic-first order and even numbers with the sham-first order. Upon recruitment, participants were assigned the stimulation order according to their numerical position.

At the end of each session, participants were asked to fill in a modified version of the questionnaire proposed by Fertonani *et al.* (2015) to evaluate the level of perceptual sensations (burning, fatigue, headache, heat pain, itching, metal taste, neck pain, tingling sensations) they had experienced during the stimulation by a 5-point Likert scale (0 = 'none', 1 = 'mild', 2 = 'moderate', 3 = 'considerable', 4 = 'strong'). Moreover, they were also asked to answer the following three questions: Question 1: When they first perceived the listed sensations (0 = 'at the beginning'; 1 = 'about half way through'; 2 = 'around the end'); Question 2: How long the perceived sensations lasted (0 = 'immediately vanished'; 1 = 'vanished about half way through'; 2 = 'remained till the end'); Question 3: how much they thought the stimulation influenced their performance at the task (0 = 'not at all'; 1 = 'slightly'; 2 = 'considerably'; 3 = 'very much').
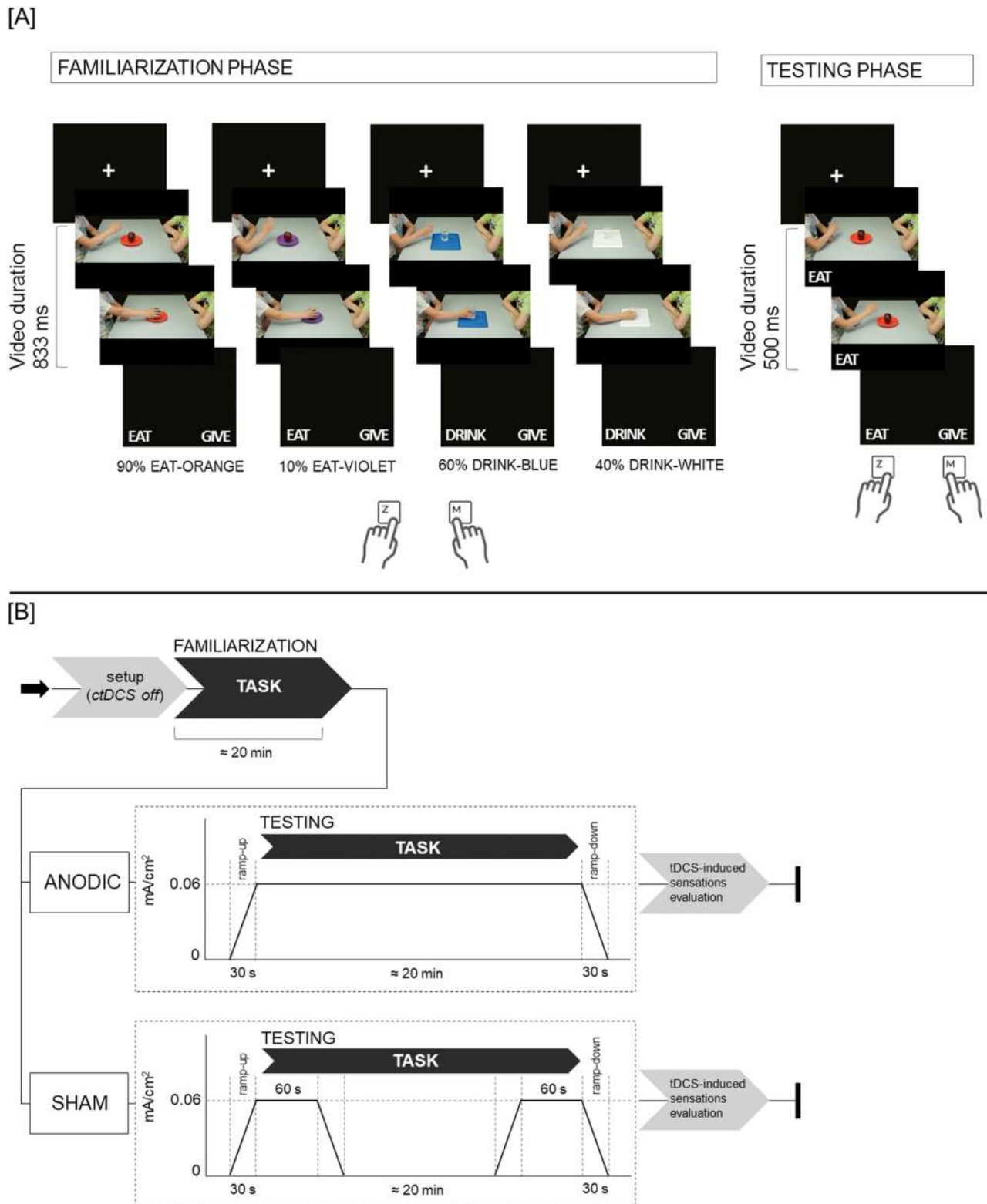
Fig. 1. (A) Depiction of the trial structure in the familiarization (on the left) and testing phase (on the right). (B) Schematic representation of the experimental procedure. According to the within-subjects design, all participants performed the task twice, each time receiving either real (anodic) or sham stimulation, and were administered with different versions of the task—displaying different combinations of cue-actions pairs—across sessions.

Data handling and statistical analysis

Preliminarily, we checked for the presence of any response bias by calculating criterion (C) according to signal detection theory (Stanislaw and Todorov, 1999). Criterion C was computed using the formula $C = -[z(H) + z(F)]/2$, with $z(H)$ and $z(F)$ denoting the z-scores for the hit and false alarm rates, respectively, obtained in each experimental condition. In the context of our study, a negative c-value suggests a tendency to favor an individual-action
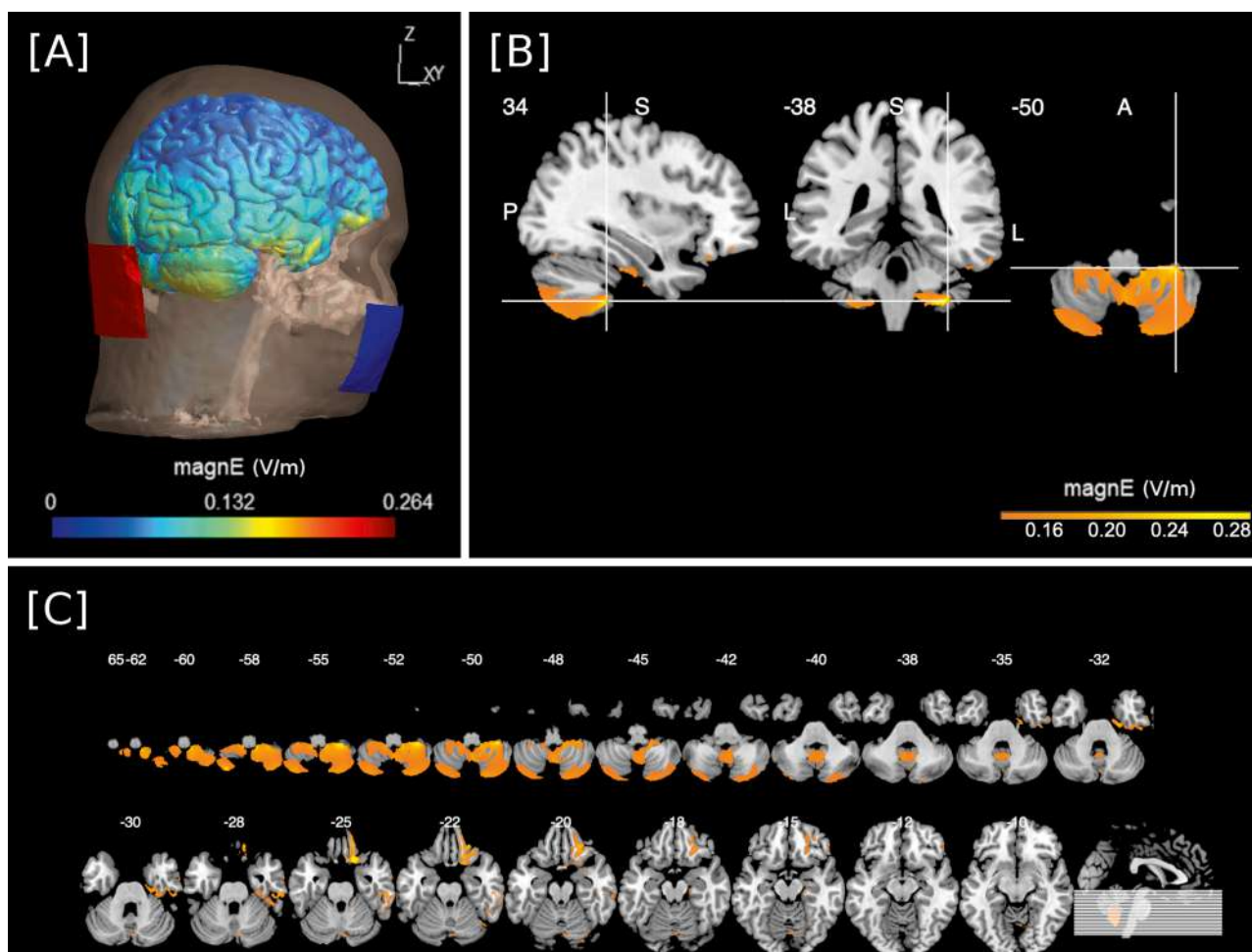
Fig. 2. (A) Illustration of the electric field magnitude (in V/m) for the midline-right buccinator montage using the original head model (Ernie); the red electrode refers to the anode (subject space: x = − 2.4, y = − 81.4, z = − 46.2), the blue one to the cathode (subject space: x = 64.5, y = 80.3, z = − 74.6). (B) Illustration of the point of maximum field magnitude located in the right cerebellar lobule VIII (MNI coordinates: x = 34, y = − 38, z = − 50; magnE (V/m) = 0.29) visualized in the sagittal, coronal and axial perspectives with MRIcron (v1.0.20190902, https://www.nitrc.org/projects/mricron). (C) Axial multi-slice view (selecting every fifth slice within the range from the 10th to the 120th slice; obtained with MRIcron) showing the distribution and magnitude of the electric field.

response, while positive values indicate a preference for the interpersonal-action response. A first 2×2 (PRE-STIMULATION SESSION * EXPECTANCY) RM-ANOVA on the c-values of the familiarization phase data did not yield any significant effect (all F < 0.1, all P > 0.4; intercept: F = 0.02, P = 0.9; overall mean = 0.001 ± 0.012; values varied between −0.01 ± 0.02 and 0.02 ± 0.02 across conditions). Also, the $2 \times 2 \times 2$ (STIMULATION * EXPECTANCY * PROBABILITY) RM-ANOVA on the c-values of the testing phase data did not yield any significant effect (all F < 3, all P > 0.1; intercept: F = 0.93, P = 0.4; overall mean = −0.05 ± 0.04; values varied between −0.25 ± 0.1 and 0.09 ± 0.12 across conditions). In light of these results, suggesting the absence of any systematic bias (Green and Swets, 1966; Stanislaw and Todorov, 1999), we considered the proportion of correct response (accuracy) as an appropriate measure of sensitivity (Stanislaw and Todorov, 1999).

Thus, accuracy and the reaction times (RTs) of correct responses were examined as the dependent variables, considering correctness based on the action kinematics, thus independently from the contextual cue expectations.

Data were filtered based on RTs applying a robust method for outliers filtering (Lachaud and Renaud, 2011). We calculated the median as robust estimates of center (rob-center) and the tau-estimate as robust estimates of scale (rob-scale) (Maronna and Zamar, 2002). Conversely to the use of the arithmetic mean as a center estimator of a distribution and standard deviation as a measure of variability, this method is not as influenced by the presence of outliers. In the familiarization phase, in trials with RTs exceeding ± 4 rob-scale, the rob-center value calculated within subject and expectancy were deleted. The procedure led to the removal of 179 trials (4.7%) in the high-expectancy condition and 169 trials (4.4%) in the low-expectancy condition, with no difference in the proportion of deleted trials between the two conditions ($X_1 = 0.39$, P = 0.53). In the testing phase, in trials with RTs exceeding ± 4 rob-scale, the rob-center value calculated within subject, stimulation type, expectancy and probability conditions were deleted. In total, 181 trials (3.1%) were deleted in the anodic condition and 200 (3.5%) in the sham condition. A chi-square test confirmed that the proportion of deleted trials was comparable among the experimental conditions ($X_3 = 3.44$, P = 0.33).

To begin with, separate 2×2 repeated-measures analyses of variance (RM-ANOVAs) were conducted on accuracy and mean RTs of correct responses extracted from the familiarization phase, with PRE-STIMULATION SESSION (pre-anodic *vs* pre-sham) and

EXPECTANCY (high 10 and 90% *vs* low 40 and 60%—predictability of the contextual cue) as within-subject variables. When analyzing data of the familiarization phase, the PROBABILITY condition was not considered because of the inherently different number of trials within each probability level. Next, two separate 2 × 2 × 2 RM-ANOVAs were conducted on mean accuracy and RTs of correct responses extracted from the testing phase, with STIMULATION (anodic *vs* sham), EXPECTANCY (high 10 and 90% *vs* low 40 and 60%) and PROBABILITY (high 60 and 90% *vs* low 10 and 40%) as within-subject variables.

Regarding the evaluation of the tDCS side-effects, a series of Fisher's exact tests were conducted to examine whether the proportion of rating values for each listed sensation and questions differed between stimulation conditions.

All statistical analyses were performed using STATISTICA 8.0 (StatSoftInc, Tulsa, Oklahoma). Tau-estimates were calculated with the 'robustbase' package of R (Maechler *et al.*, 2022) for the calculation of basic robust statistics. Data are reported as mean (M) ± SEM. The level of statistical significance was set to $P < 0.05$ and effect sizes were estimated using partial eta squared (η_p^2). Duncan post-hoc tests were performed to follow-up significant interactions.

Results

For the familiarization phase, neither the analysis on the mean percentage accuracy nor that on RTs showed any significant effect (all $F < 3.3$, all $P > 0.09$). Visual inspection of the data indicated that participants' ability to discriminate between the actions in this phase was close to 100% (Figure 3, top-left panel).

For the testing phase, the main analysis on accuracy showed a significant main effect of PROBABILITY ($F_{1,23} = 4.35$, $P < 0.05$, $\eta_p^2 = 0.16$), as participants were more accurate in high-probability (M = 89.9; SEM = 1.2) than in low-probability trials (M = 83.7; SEM = 2.9). The analysis also yielded a significant interaction effect of STIMULATION * EXPECTANCY ($F_{1,23} = 4.39$, $P < 0.05$, $\eta_p^2 = 0.16$). Indeed, participants were more accurate in discriminating between the two unfolding actions in low-expectancy trials during anodic (M = 88.5; SEM = 1.9) than sham stimulation (M = 84.2; SEM = 2.4; P = 0.04) (Figure 3, top-right panel). No other significant main effects or interactions were observed (all $F < 2.3$; $P > 0.14$).

The analysis on the RTs in the testing phase did not yield any significant effect (all $F < 3$; $P > 0.1$).

Regarding the analyses on the rating values of the tDCS-induced sensations, only the test conducted on the rating values

Fig. 3. Boxplots displaying data distribution of accuracy (top-panel) and RTs (bottom-panel) obtained in the familiarization- (left panels) and testing-phase (right panels) according to the type of stimulation (anodic *vs* sham) and as a function of the level of expectancy (high *vs* low). In the familiarization phase, data were collected before the delivery of the stimulation (pre-anodic *vs* pre-sham). Dots represent individual observations. * $P < 0.05$.

of metal taste approached statistical significance ($P = 0.05$), driven by the higher proportion of rating 'mild' (25%) and 'moderate' (21%) during anodic stimulation than during sham stimulation ('mild' 8%; 'moderate' 4%) (Figure 4) (all other $P > 0.1$). The rating value 4 ('strong') was never selected by any subject.

As for the questions evaluating the onset, duration and perceived impact of the stimulation, none of the tests reached statistical significance (all $P > 0.1$) (Figure 5).

Overall, these data suggest that the stimulation was well tolerated. Moreover, the similarity in sensations reported by participants after the real and after the sham stimulation suggested that they were actually blinded to the stimulation and that

also in the sham condition the stimulation could be perceived as reliable.

An explorative post-hoc analysis was carried out to verify that the significant interaction effect STIMULATION * EXPECTANCY was not influenced by the order in which participants underwent the two stimulation conditions. To this aim, we conducted a $2 \times 2 \times 2$ RM-ANOVA on accuracy with the within-subject variables STIMULATION and EXPECTANCY and the between-subject factor ORDER (anodic-first *vs* sham-first) to test for their 3-way interaction. The analysis yielded a non-significant effect of the interaction ($F_{1,22} = 0.003$, $P = 0.96$, $\eta_p^2 = 0.0002$). The findings indicate that the expectancy-dependent impact of the stimulation
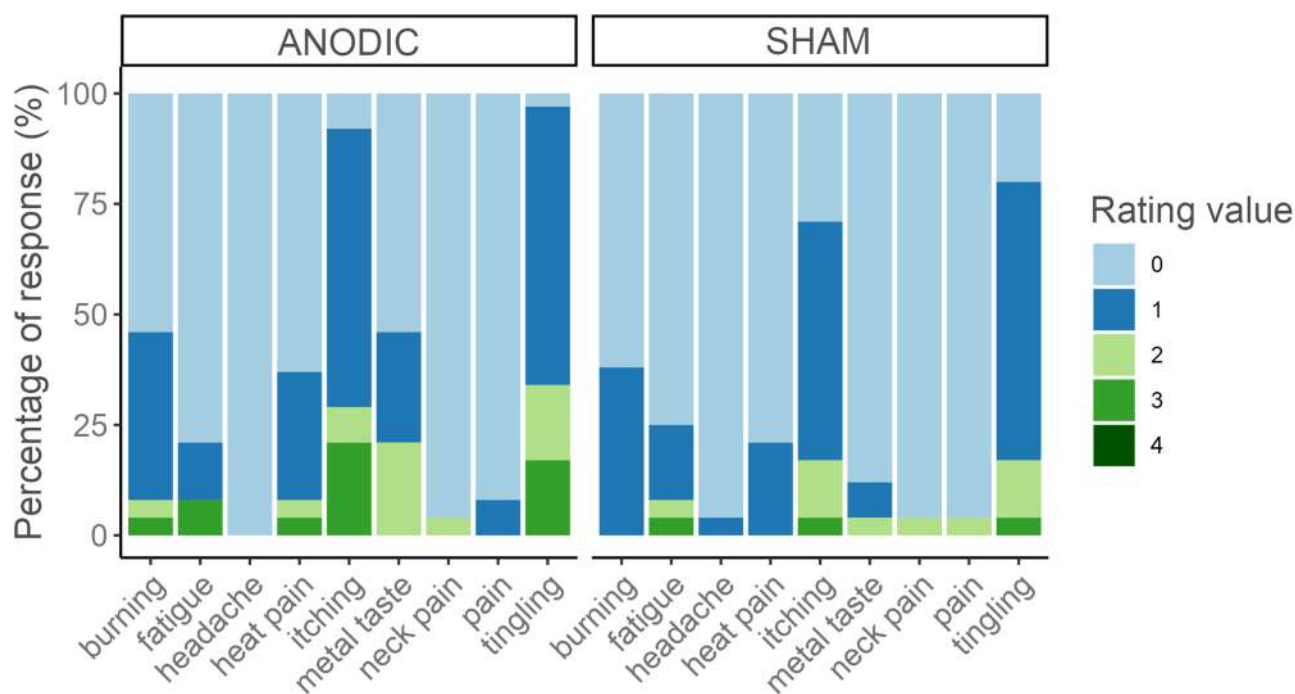
Fig. 4. Bar-plot displaying the percentage of rating value (y-axis) obtained for each perceptual sensation (x-axis) during anodic stimulation (left panel) and sham stimulation (right panel).
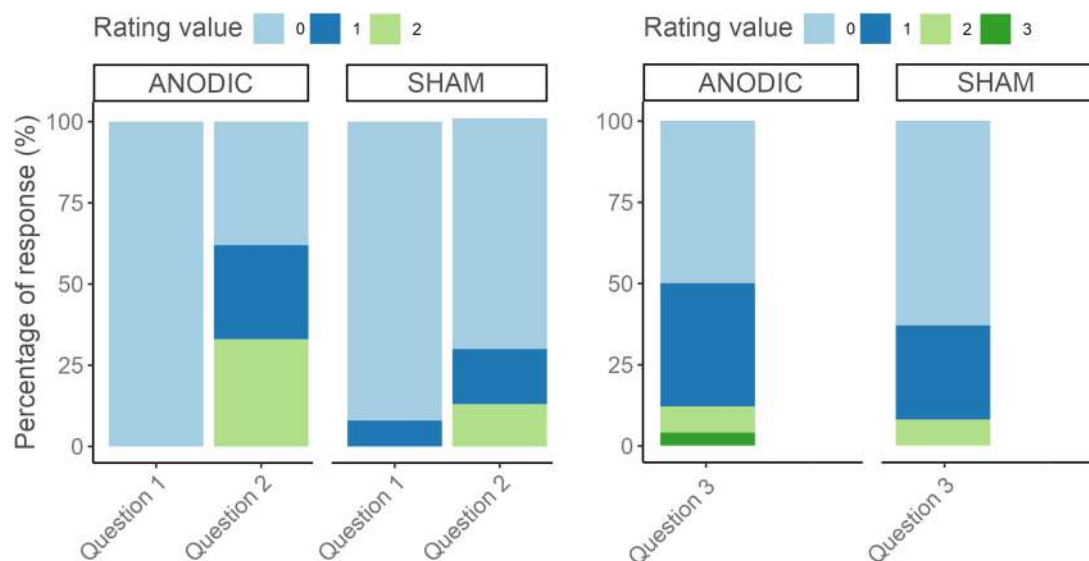
Fig. 5. Bar-plot displaying the percentage of rating value (y-axis) obtained at each question (x-axis) during anodic and sham stimulation.

remained unaffected by the order in which the stimulation was delivered.

Discussion

The study aimed to explore how anodic ctDCS affected action prediction based on prior contextual expectations. The present work was a follow-up to a previous experiment where anodal, cathodal or sham ctDCS was administered during the same action prediction task (Oldrati *et al.*, 2021). In this previous study, we found that, while cathodic ctDCS impaired participants' performance in predicting actions embedded in a highly informative context, we observed that anodic ctDCS improved the ability to predict actions when embedded in a moderately, but not highly, informative context (Oldrati *et al.*, 2021). However, in this experiment, stimulation was only delivered during the testing phase to disentangle the cerebellar role in forming associations between actions and cues, occurring during familiarization, *vs* their retrieval, required to optimally execute the task in face of reduced sensory evidence. With respect to the polarity of the stimulation, the choice of delivering only anodic stimulation was motivated by the possible rehabilitative implications of the study.

To begin with, the analysis showed that anodic ctDCS improved participants' ability to predict the unfolding action when embedded in a moderately, but not highly, informative context, replicating the effect emerged by Oldrati *et al.* (2021). The context-expectancy-dependent effect of the stimulation is consistent with the evidence, indicating that cerebellar activity during the processing of perceptual events is modulated by their level of predictability (Lam *et al.*, 2013). Indeed, using a task that required participants to learn the probabilistic association between combinations of four playing cards and two outcomes, an fMRI study detected stronger activation of the cerebellum during learning of combinations with high predictive value, linking this result with the formation of internal models (Lam *et al.*, 2013). Similarly, studies on the neural basis of probabilistic reasoning under conditions of uncertainty showed strong activation of the cerebellum and linked it to the construction of internal working models of uncertain events (Blackwood *et al.*, 2004; Kobza and Bellebaum, 2015). Our finding is also in line with the results of an fMRI-ctDCS combined experiment that showed not only greater cerebellar activation but also greater susceptibility to the stimulation during the processing of sentences that provided strong *vs* weak cues to the missing word (D'Mello *et al.*, 2017). We speculated that, by increasing cerebellar cortical excitability, anodic ctDCS enhanced the retrieval of moderately informative models of action-contextual cues associations, which were likely associated with lower cerebellar activation (D'Mello *et al.*, 2017). Following this assumption, the lack of ctDCS effects on highly informative models might be due to the already elevated cerebellar activation, making further enhancement via ctDCS challenging.

An alternative explanation for this outcome might involve the varying difficulty levels between the high and low predictability conditions. Pope and Miall (2012) discovered that cathodal ctDCS impacted working memory and attention differently based on task difficulty, while anodal stimulation did not. However, in contrast to the commonly held belief about polarity-based tDCS effects, a meta-analysis found that neither anodal nor cathodal cerebellar stimulation consistently resulted in overall improvement or impairment in behavior (Oldrati and Schutter, 2018). Moreover, despite stronger perceptual evidence in high-expectancy trials, no significant difference emerged between the two expectancy conditions during sham stimulation. This finding rules out the possibility that difficulty level influenced the observed effect. Rather, we noted performance modulation based on association probabilities within each expectation condition. Performance was better with high-probability (90% or 60%) action-cue associations compared to low-probability (10% or 40%) ones. Interestingly, this effect was not linked to a differential modulation exerted by ctDCS.

Reproducing ctDCS effects when delivered solely during testing suggests stimulation influenced model retrieval rather than formation, aligning with a study that found no stimulation impact on associative probabilistic learning (Seyed Majidi *et al.*, 2017). With a sham controlled design, this study delivered anodic tDCS over the right cerebellar hemisphere during the execution of the same task administered by Lam *et al.* (2013) (see also Gluck *et al.*, 2002). Although participants performed better over time, neither the main effect of the stimulation nor the interaction between stimulation condition and blocks resulted to be significant. In our opinion, the lack of stimulation effect might not likely depend (exclusively) on the stimulation settings but also on the nature of the task. Indeed, the task regarded prediction of non-social events (i.e. the outcome of four playing cards), while the cerebellum has been hypothesized to play a preferential role for the processing of actions and social scripts (see Introduction). As a matter of fact, in our prior investigation (Oldrati *et al.*, 2021), participants performed both the action prediction task and a control task involving context-based prediction of geometrical shapes. Interestingly, even though the tasks shared identical structures, our findings revealed that ctDCS had a selective impact on the action-prediction task while leaving the shape prediction task unaffected. While there is growing evidence supporting the role of the cerebellum in the working memory circuit (King *et al.*, 2019), this specific outcome suggests that non-specific effect of cerebellar stimulation on broader memory circuits could be ruled out. We propose that the observed sensitivity of the cerebellum to action-related processing may indicate an interdependence between various cognitive processing aspects (such as action semantics) and the motor functions of the cerebellum (García and Ibáñez, 2018).

In line with this view, the impaired recognition of actions and social sequences in cerebellar patients contrasts with their preserved ability to process non-social mechanical sequences (Cattaneo *et al.*, 2012; Van Overwalle *et al.*, 2019; Butti *et al.*, 2020a). However, using the exact same experimental paradigm of action and physical event prediction, a comparable deficit of contextual modulation was found in either task in a sample of patients with congenital cerebellar malformations (Urgesi *et al.*, 2021). In a similar vein, neuro-stimulation studies revealed non-specific effects of cerebellar stimulation across various social and non-social sequence tasks (Heleven *et al.*, 2021; Ma *et al.*, 2023), potentially influenced by task design variations impacting implicit *vs* explicit learning mechanisms (Bianco *et al.*, 2022) and the level of automatic *vs* inferential processing (Ferrari *et al.*, 2023).

The positive impact of ctDCS on retrieving weak contextual expectations for action discrimination suggests its potential as a tool for treating social perception deficits in cerebellar disorders (Ciricugno *et al.*, 2024), as well as in neurodevelopmental and psychiatric conditions featured by cerebellar alterations (Schmahmann *et al.*, 2007; Tavano *et al.*, 2007; Phillips *et al.*, 2015). This emphasizes the need for further exploration of non-invasive cerebellar stimulation, potentially in combination with existing

training programs Butti *et al.*, 2020b; Urgesi *et al.*, 2021), for rehabilitating socio-cognitive deficits in cerebellar disorders (Manto *et al.*, 2021; Cattaneo *et al.*, 2022).

Nevertheless, limitations must be considered. While our stimulation model indicated that the cerebellum was the region where the electric current was most prominently conducted, we cannot rule out the possibility that the observed effects could be partly attributed to the current spreading to other brain areas, in keeping with the low spatial acuity of the tDCS. This concern has been previously noted in a computational electric field modeling study investigating the conventionally used cerebellum-buccinator montage (Klaus and Schutter, 2021). Then, the study task structure prevented a control experiment to isolate the cerebellar-specific role in internal model formation using the same paradigm. On the one hand, delivering ctDCS only during familiarization would lead to carry-over effects (Takano *et al.*, 2022), challenging the differentiation between online and offline effects. On the other hand, extending the time between phases could impact memory maintenance of action-cue associations. Thus, while this study confirmed that ctDCS influence cerebellar retrieval and use of internal models, it could not rule out modulation in their formation. Task repetition across sessions might have weakened implicit learning, but counterbalancing stimulation conditions prevented repetition effects. Additionally, while the study highlighted the cerebellar involvement in using contextual expectations, it could not assess ctDCS effects on other connected brain structures, necessitating future studies combining stimulation with neuroimaging and electrophysiological methods for a more comprehensive understanding. While the limited spatial precision of tDCS hinders precise anatomical inferences, it remains plausible that targeting other cerebellar macro-areas might yield distinct outcomes. Indeed, recent neurostimulation evidence proposes a medial-to-lateral gradient in the functional organization of the posterior cerebellum for social cognition (Ferrari *et al.*, 2023). Moreover, although the simulation showed an effect spreading from the vermis toward both hemispheres, it is important to note that the point of maximum field magnitude was situated within the right cerebellum. Consequently, future studies are warranted to pinpoint the optimal electrode position to modulate specific social functions.

Despite these limitations, the present result confirmed the expectancy specificity of ctDCS effects, pointing to a role of the cerebellum in using previously learned contextual associations to predict actions. Adding to previous findings, the occurrence of the effect when delivering the stimulation during testing phase only suggests that the cerebellum is involved in the retrieval of internal models for action prediction.

Data Availability

The datasets generated and analyzed during the current study are available in the OSF repository, https://osf.io/3a62c/?view_only=cef342e82108451fbd8614205bdca1d8.

Author contribution

V.O. data curation, formal analysis, investigation, methodology, writing original draft; N.B. investigation, writing - review and editing; E.F. investigation, writing - review and editing; Z.C. methodology, writing - review and editing; C.U. conceptualization, methodology, supervision, funding acquisition, writing - review and editing; A.F. conceptualization, methodology, supervision, funding acquisition, writing - review and editing.

Conflict of interest

The authors declared that they had no conflict of interest with respect to their authorship or the publication of this article.

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