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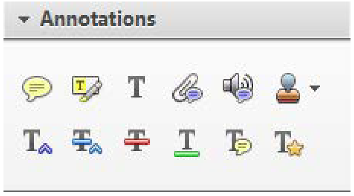

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Behavioral/Cognitive

Functional Segregation of the Human Cerebellum in Social Cognitive Tasks Revealed by TMS

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AQ:B AQ:C **The role of the posterior cerebellum in social cognition is well established; however, it is still unclear whether different cerebellar subregions contribute to different social cognitive processes by exerting specific functions. Here, we employed transcranial magnetic stimulation (TMS) in male and female healthy humans to test the hypothesis of the existence of a medial-to-lateral gradient in the functional organization of the posterior cerebellum, according to which the phylogenetically newer cerebellar AQ:D hemispheres are involved in tasks requiring higher-level social inferences whereas vermal/medial sectors are involved in basic perceptual emotional mechanisms. We found that interfering via TMS with activity of the medial cerebellum significantly impaired basic emotional recognition/discrimination. In turn, only TMS over the lateral cerebellum affected a task requiring recognizing an emotion considering the social context in which it was experienced. Overall, our data support the existence of a medial-to-lateral gradient in the posterior cerebellum, with medial sectors supporting basic emotion recognition and lateral sectors being recruited when the task taps on higher inferential processing/mentalizing. Interestingly, the contribution of the cerebellum in these different processes seems to be restricted to negative emotional stimuli.**

Key words: cerebellum; emotion; social cognition; TMS

Significance Statement

The cerebellum has been recently recognized as a critical component of the social brain, however, the functional topography of this structure in relation to social and emotional processes is still debated. By adopting a causative approach through the use of transcranial magnetic stimulation (TMS), the present study critically insights into the functional organization of the posterior cerebellum by testing the hypothesis of a medial-to-lateral gradient that reflects increasing complexity of social cognitive processes. Our findings demonstrate that lateral and medial cerebellar regions exert partially distinguishable functions in the social cognitive domain, with the medial cerebellum that mainly mediates basic perceptual emotional mechanisms while the lateral cerebellum, although supporting more basic functions, further subserves higher-level social operations.

Introduction

A growing body of evidence suggests that the cerebellum is a key region mediating both social thinking and basic sensory-affective processes involved in others' mind comprehension (Adamaszek et al., 2017; Van Overwalle et al., 2020). Indeed, the posterior cerebellum systematically activates during theory of mind (Van Overwalle et al., 2014) and emotion perception tasks, including the recognition of emotional faces (Fusar-Poli et al., 2009). Accordingly, cerebellar patients are impaired in perceiving other individuals' feelings based on their facial appearance or tone of voice (Adamaszek et al., 2014; Hoche et al., 2016; Clausi et al., 2021a). Moreover, neurostimulation studies repeatedly showed that interfering with posterior cerebellar activity affects healthy individuals' ability to discriminate others' emotions from facial and body expressions (Ferrucci et al., 2012; Ferrari et al., 2018a, 2022a). Finally, cerebellar anomalies have been reported in schizophrenia and autism, characterized by difficulties perceiving what people think and feel (S.S. Wang et al., 2014; Clausi et al., 2021b).

Although, on the one hand, the role of the cerebellum in social cognition is well established, on the other, whether its contribution may be ascribed to a single functional mechanism or a set of multiple functions (possibly mediated by different cerebellar subregions) remains a matter of debate (Diedrichsen et al., 2019). Classical views of cerebellar functioning have suggested that this structure predominantly operates by generating internal models of motor, sensory, and cognitive operations that allow predictions about potential outcomes based on the individual's

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prior experience and knowledge (Ito, 2008). In this perspective, the role of the cerebellum in social cognition may be that of anticipating others' behaviors during social interactions by forming predictions about their possible consequences (outcomes; Van Overwalle et al., 2020), a hypothesis supported by recent studies on prediction of (social) actions (Oldrati et al., 2021; Haihambo et al., 2022).

As stated above, predictions are possible whenever a (sufficiently informative) context (a specific place or situation) is available. Nonetheless, there is also consistent evidence suggesting that the cerebellum is involved in basic social cognitive mechanisms, such as facial emotion discrimination, in the absence of any additional contextual cues beyond the face stimulus itself (Fusar-Poli et al., 2009; Ferrari et al., 2018a; Pierce et al., 2022). Although also basic perceptual mechanisms are inherently predictive (Friston, 2012), expecting a specific behavior based on a provided context requires an inferential process that is not implied in a simple discrimination task. Hence, a critical question is whether the whole posterior cerebellum supports social inferential processing regardless of the type/level of prediction required (perceptual/low-level vs mentalizing/high-level) or whether the posterior cerebellar functional organization may be related to the type/level of the inferential process at play. In support of the latter hypothesis, recent evidence suggests a sort of medial-to-lateral gradient reflecting increasing complexity of the socio-emotional process. For instance, low-level social cognitive operations, like the processing of emotional faces, recruit slightly more medial regions than complex social processes like perceiving geometrical shapes that socially interact (Metoki et al., 2022). In line with this, Kruithof et al. (2022) have proposed the existence of a dissociation between the lateral and medial cerebellum in mediating different motivational and emotional processes.

In light of the above, here we systematically assessed for the first time using transcranial magnetic stimulation (TMS) the existence of a medial-to-lateral gradient in the functional organization of the posterior cerebellum, according to which the phylogenetically newer cerebellar hemispheres are involved in higher-level social inferences and vermal (more medial) sectors of the cerebellum in basic perceptual emotional mechanisms. Specifically, we expected that interfering with medial and lateral regions of the posterior cerebellum should overall affect emotional processing, but this interference should be stronger for basic emotional processing when TMS is delivered over medial regions and stronger for higher-order processing (high-level social prediction) when posterolateral cerebellar sectors are targeted.

Materials and Methods

Experiment 1

In the first experiment, we employed a same-different facial emotional discrimination task, in which participants had to categorize faces as expressing the same or a different emotion (happiness or anger) while receiving online TMS over the lateral cerebellum, the paravermal cerebellum, and the vertex (control condition). We have already demonstrated (Ferrari et al., 2018a) that the paravermal cerebellum is causally involved in the discrimination of angry and happy facial expressions, a finding that we expected to replicate here. In turn, we expected the stimulation of the lateral cerebellum to interfere less than the stimulation of the medial cerebellum with basic emotion discrimination, considering that the former region has been associated with higher-level social tasks, such as social thinking, mentalizing, and social sequencing (Van Overwalle et al., 2014; Heleven et al., 2019).

Participants

Twenty-four right-handed white volunteers with normal or corrected-to-normal vision, took part in the study (four males, mean age = 22.8 years, SD = 3.2). Before the experiment, each participant filled in a questionnaire to evaluate compatibility with TMS (translated from Rossi et al., 2011). The protocol was approved by the local ethics committee and participants were treated in accordance with the Declaration of Helsinki. An a priori power analysis conducted using G-Power 3.1 software indicated that for our experimental design, a sample size of 22 individuals is required to obtain 90% of power at a significance threshold α of 0.05, with an expected large effect size of f(U) = 0.57 ($\eta_p^2 = 0.25$) based on data of a prior TMS study in which participants discriminated emotional body stimuli with a level of accuracy similar to that expected here (i.e., ∼70%; Ferrari et al., 2022a).

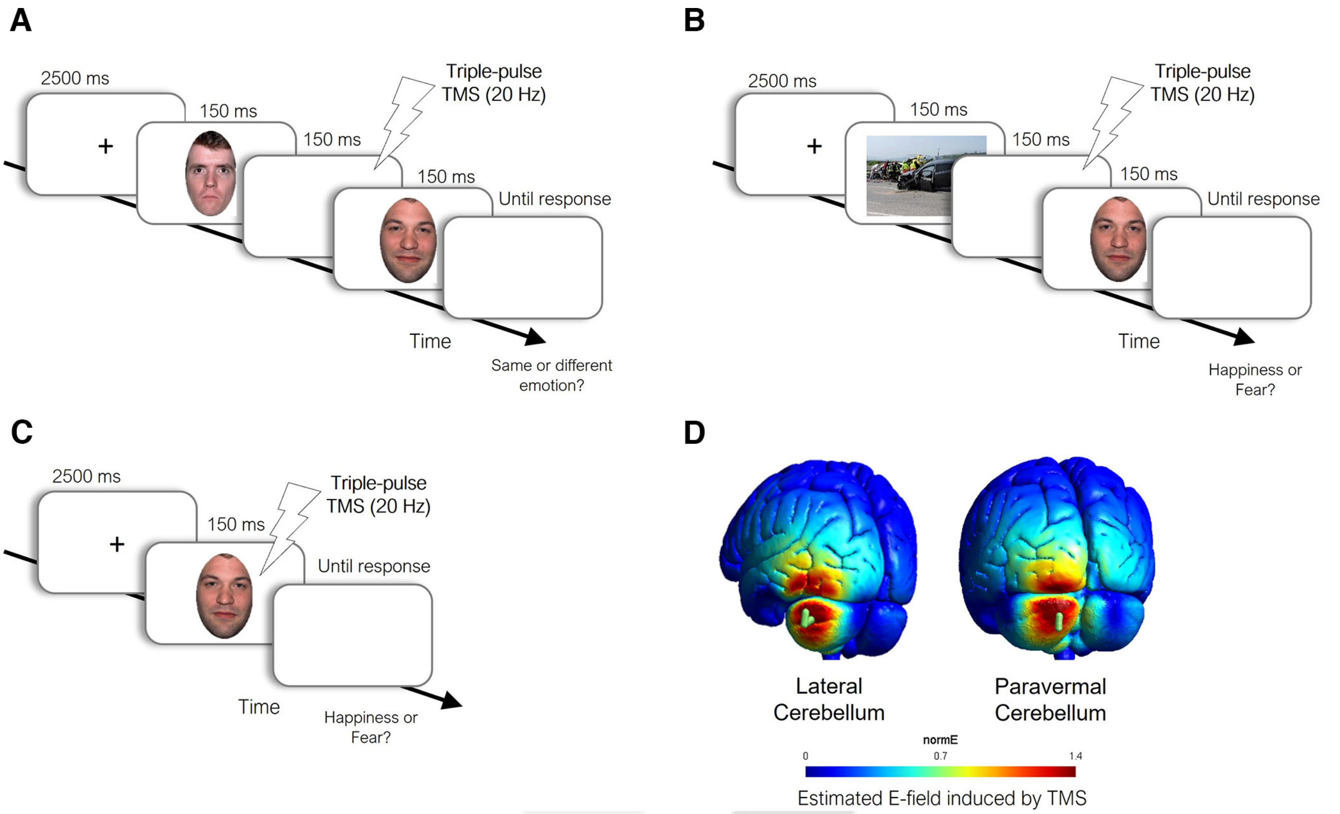
Stimuli

Stimuli consisted of 28 morphed facial expressions of anger (14) and happiness (14). FantaMorph software 5.0 was used to create morphed faces from seven male and seven female white individuals expressing happiness, anger, and no emotional facial expression (neutral) taken from the NimStim dataset (Tottenham et al., 2009). For each identity, images from the dataset were used as endpoints to generate two different morph continua: from angry to neutral, and from happy to neutral. For each identity, nine intermediate pictures were produced with each image representing a 10% step within the morphing continuum (e.g., 90% angry–10% neutral, 80% angry–20% neutral, 70% angry–30% neutral, 60% angry–40% neutral, 50% angry–50% neutral, 40% angry–60% neutral, 30% angry–70% neutral, 20% angry–80% neutral, and 10% angry–90% neutral). These steps provided a subtle gradation of emotional intensity for each emotion and allowed us to create different levels of emotional ambiguity in the faces. Faces were then cropped so that hair was not visible. Faces corresponding to the 40% morph level were employed in the task. This morph level was selected because participants discriminated between 40% morph level angry and happy faces with an accuracy rate of around 70% which is optimal for being modulated by TMS (see Robertson et al., 2003). This allowed us to avoid ceiling effects on participants' performance often reported when participants discriminate between stereotypical faces (Ferrari et al., 2018a). To establish the optimal morph level, we run a pilot (behavioral) experiment in which a different group of participants (*N* = 15, three males, mean age = 24.5 years, SD = 3.7) performed nine blocks of emotion discrimination task, one for each morphing level. The task procedure was identical to the one used in the TMS experiment (see below) with the only exception that trials were repeated only once. The pilot experiment was implemented using an online research platform (https://pavlovia.org/; Peirce et al., 2019). Analysis of participants' accuracy rates revealed that participants performed the anger-happiness discrimination task with the optimal accuracy rate of 70% in the block corresponding to the 40% face morphing level (M = 71%, SD = 10.5).

Procedure

Participants were seated in front of a 19-inch screen at an approximate distance of 57 cm and were instructed to perform an emotion discrimination task in which they saw pairs of emotional faces (sequentially presented) that they had to evaluate as expressing the same or a different emotion. Figure 1*A* shows an example of an experimental trial. Each trial started with a black fixation cross appearing in the middle of the screen (2500 ms), followed by the first face (visible for 150 ms), a blank screen (150 ms), and the second face (150 ms). Participants responded as quickly as possible by using their right hand to press the left or right arrow key. Response key assignment was counterbalanced across participants. The emotion discrimination task consisted of 56 trials (randomly presented) repeated twice, for a total of 112 trials. The faces expressed either anger or happiness and were paired to convey the same emotion (i.e., happy–happy or angry–angry) in half of the trials and a different emotion (i.e., happy–angry or angry–happy) in the other half. Within each trial, images always depicted individuals of the same gender (but of different identities). After a brief practice task consisting of sixteen trials, participants performed three blocks of the emotion discrimination task, one for each TMS site (see "TMS" below). The order of TMS conditions was counterbalanced across participants. The software E-prime 2.0 (Psychology Software Tools) was used for stimulus presentation, data collection, and TMS triggering.

F1



AQ:M **Figure 1.** Timeline of an experimental trial of: (***A***) the same-different emotion discrimination task used in Experiments 1 (happy/angry faces) and 2 (happy/fearful faces); (***B***) the task used in Experiment 3, requiring participants to consider the information conveyed by the context in deciding about the emotion expressed by the face; (***C***) the basic emotion recognition task used in Experiment 4, in which participants had to indicate whether a series of faces and scenes (the contexts used in Experiment 3), individually presented, conveyed a positive or negative emotion; (***D***) estimated electric field induced by the Magstim Rapid^2 stimulator 70-mm figure-of-eight coil obtained using SimNIBS (Thielscher et al., 2015; Weise et al., 2020).

TMS

Online neuronavigated TMS was applied by means of a Magstim Rapid^2 stimulator (Magstim Co, Ltd) connected to a 70-mm butterfly coil. Before the experiment, single-pulse TMS was applied over the left M1 at increasing intensities to determine each participant's resting motor threshold (rMT). rMT was defined as the minimal intensity of the stimulator output that produced motor evoked potentials (the motor response measured through electrodes applied to the hand muscles) with an amplitude of at least 50 mV in the first dorsal interosseous with 50% probability (Rossini et al., 1994; see also Hanajima et al., 2007 for methodological details on this standard procedure). Participants were stimulated at 100% of their rMT, which is consistent with prior TMS studies targeting the cerebellum (Demirtas-Tatlidede et al., 2011; Ferrari et al., 2018a, b). The intensity of stimulation was 49.52% of the maximum stimulator output (SD = 1.47) and it was kept constant for the stimulation of all the target sites. TMS was delivered over the left lateral cerebellum, the paravermal cerebellum, and the vertex (control site). We stimulated the left lateral cerebellum (rather than the right) because previous neuroimaging studies reported more consistent activations in the left cerebellar posterior hemisphere during the processing of emotional faces (Schraa-Tam et al., 2012). Accordingly, a recent large-scale neuroimaging study reported laterality differences in the posterior cerebellum during emotional and social tasks, with the left cerebellum displaying more and stronger effective connections to the right cerebral mentalizing areas, compared with the right cerebellum (Metoki et al., 2022). Triple-pulse 20-Hz TMS was delivered in each experimental trial 150 ms before the presentation of the second image, in line with previous studies (Ferrari et al., 2018a, 2022a; see Fig. 1A). The cerebellar target regions were localized by means of stereotaxic navigation on individual estimated magnetic resonance images (MRIs) obtained through a 3D warping procedure fitting a high-resolution MRI template with the participant's scalp model and craniometric points (Softaxic 3.0, EMS, obtained using individual MRI scans, see Carducci and Brusco, 2012). The same localization procedure has been successfully used in many prior TMS studies (Balconi and Ferrari, 2012; Ferrari et al., 2016, 2017, 2018c). Anatomical Talairach coordinates (Talairach and Tournoux, 1988) of the left lateral cerebellum were $x = -31$, $y = -64$, $z = -27$ (corresponding to lateral lobule VI/VII) and were taken from a prior meta-analysis of neuroimaging studies reporting activations in this cerebellar sector during emotional processing (Keren-Happuch et al., 2014). The coordinates of the left paravermal cerebellum were $x = -15$, $y = -82$, $z = -32$, and correspond to the left medial sector of lobule VI/VII. These coordinates were obtained from a previous neuroimaging study on facial emotional processing (Schraa-Tam et al., 2012) and were used in previous TMS studies of our group (Ferrari et al., 2018a, 2021). Although the two cerebellar target sites are located quite close on the scalp surface (within 3–4 cm when marked on the heads of all participants), previous studies demonstrated that lateral and medial cerebellar sectors could be selectively stimulated using TMS (Esterman et al., 2017; Ciricugno et al., 2020; Ferrari et al., 2022b). AQ:E

The vertex was localized as the point falling half the distance between the nasion and the inion on the same midline. For the vertex stimulation, the coil was placed tangentially to the scalp and held parallel to the midsagittal line with the handle pointing backward. For cerebellar stimulation, the coil was placed tangentially to the scalp and held parallel to the midsagittal line with the handle pointing superiorly, consistently with evidence suggesting that this is an effective coil orientation to modulate activity in cerebellar structures (Bijsterbosch et al., 2012; van Dun et al., 2017). The experiment took on average 1 h and 30 min (including instructions, fill-in of TMS questionnaire and informed consent, neuronavigation, and debriefing). No participant reported discomfort or adverse effects during TMS.

Experiment 2

In Experiment 2, participants were presented with the same paradigm and stimulation parameters as Experiment 1, but they had to discriminate between fearful and happy faces. Experiment 2 thus aimed to replicate the findings of Experiment 1 meanwhile testing for the cerebellar contribution to the discrimination of different emotions (fear rather than anger).

Participants

Twenty-two right-handed white volunteers with normal or corrected-to-normal vision, took part in the study (five males, mean age = 22.7 years, SD = 2.19). None of them participated in Experiment 1. The exclusion criteria were the same as in the previous experiment. The protocol was approved by the local ethics committee and participants were treated in accordance with the Declaration of Helsinki. The sample size was estimated as in Experiment 1.

Stimuli, procedure, and TMS

Participants performed a facial emotion discrimination task identical to that of Experiment 1 with the exception that angry faces were replaced with fearful faces. Participants discriminated between 40% morphed fearful and happy faces that were created with the same morphing procedure of Experiment 1. The morph level of the faces was established based on a pilot experiment on a separate sample of participants ($N = 15$, three males, mean age = 28.0 years, SD = 10.8). In the pilot experiment, participants reached the desired accuracy of ~70% (M = 69%, SD = 7.0) when presented with 40% morph-level faces in a same-different emotion discrimination task as the one employed in the main TMS experiment. The experimental procedure and TMS parameters were identical to those of Experiment 1. The intensity of TMS was 49.41% of the maximum stimulator output (SD = 1.74), corresponding to 100% of the participants' rMT (obtained as described in Experiment 1).

Experiment 3

Experiment 3 aimed to assess the contribution of the medial and lateral posterior cerebellum in a task requiring a higher-level social inference compared with that required by Experiments 1 and 2. Participants were presented with a situational context (e.g., a party, a car accident, etc.) and then with a face; their task was to indicate whether the face expressed a positive or a negative emotion considering that the latter was experienced in the provided context. Hence, participants could predict the facial emotion when viewing the context; the prediction could then be confirmed (congruent trials) or disconfirmed (incongruent trials). If a medial-to-lateral gradient exists in the posterior cerebellar organization reflecting increasing complexity of the socio-emotional process (Kruithof et al., 2022), TMS over the lateral cerebellum should affect the contextual inference more than TMS delivered over the medial cerebellum.

Participants

Twenty-eight right-handed volunteers participated in the experiment (five males, mean age = 22.5 years, SD = 3.2); none of them had taken part in the previous two experiments. Before the experiment, participants were screened to evaluate compatibility with TMS (translated from Rossi et al., 2011). The protocol was approved by the local ethics committee and participants were treated in accordance with the Declaration of Helsinki. The sample size was similar as in the prior experiments although the task was slightly different.

Stimuli

Stimuli consisted of images of emotional faces (happy and fearful, as in Experiment 2) and emotional scenarios. The morph level of the emotional faces was 20%, based on the results of a pilot experiment ($N = 15$, 2 males, mean age = 26.1 years, SD = 6.3), in which participants had to decide whether a single face presented expressed fear or happiness (two-alternative force-choice task). For the scenarios, we used 28 pictures selected on the basis of a pilot rating experiment in which participants had to rate a larger set of emotional and neutral images taken either from the International Affective Picture System (Lang et al., 1997) or from the Web. The pilot rating experiment was administered through the online Qualtrics platform (https://www.qualtrics.com/) and involved 20 participants (seven males, mean age = 23.5 years, SD = 3.2) not taking part in the TMS experiment. Participants had to evaluate the images on a 1–9 Likert scale for valence (i.e., 1 = very negative; 9 = very positive) and arousal (i.e., 1 = not aroused; 9 = extremely aroused) and to indicate the emotion conveyed. For the TMS experiment, we selected 14 happy scenarios and 14 fearful scenarios. The mean valence rating for happy scenarios was 7.48 (SD = 0.43) and it was significantly higher than that of the fearful scenarios (mean = 2.19, SD = 0.88), $t_{(13)} = 21.3$, $p < 0.001$, $d = 5.7$. Fearful scenarios were rated as more arousing (mean = 7.11, SD = 0.68) than happy ones (mean = 5.29, SD = 1.14), $t_{(13)} = 4.69$, $p < 0.001$, $d = 1.25$.

Procedure

Participants were seated in front of a 19-inch screen at an approximate distance of 57 cm. The task consisted of the presentation of context-face pairs in which the context could be predictive of the emotion expressed by the face (i.e., a party/a happy face; a car accident/a fearful face) or not predictive (i.e., a happy context was followed by a fearful face or vice versa). Each trial started with a fixation cross (displayed for 2500 ms), followed by an emotional scenario (presented for 150 ms), a blank screen (150 ms), and the emotional face (150 ms; see Fig. 1*B*). Participants were instructed to recognize the emotion expressed by the face by choosing between two alternatives (happiness or fear) and were told that each emotional face would be preceded by an image representing the context in which that emotion was experienced. Thus, participants were explicitly instructed to use the information conveyed by the context to make inferences about the emotion expressed by the face. Participants responded as quickly as possible by using their right hand to press the left or right arrow key, with response keys counterbalanced across participants. The task was first piloted in a group of 20 participants (five males, mean age = 24.9 years, SD = 2.9) without TMS to ensure that the provided context indeed facilitated the recognition of a congruent facial emotion. The pilot task consisted of only one block of 112 trials (half congruent and half incongruent). Results of the pilot experiment are reported in Results of Experiment 3. The TMS experiment consisted of three blocks (each composed of 112 trials, half congruent and half incongruent), one for each stimulation site (see below), preceded by a short practice block (16 trials). Moreover, at the end of the experimental session, emotional recognition of faces (in isolation) was tested (without TMS). Specifically, participants were presented with all emotional faces employed in the TMS experiment (stimuli were presented as in the TMS experiment for 150 ms) and participants had to indicate whether they conveyed fear or happiness using the same response keys of the TMS experiment.

TMS

Participants performed the task while receiving TMS over the paravermal cerebellum, the lateral cerebellum, and the vertex, localized with the same procedure as in the previous experiments. TMS parameters were identical to those employed in Experiments 1 and 2. The intensity of stimulation was 49.7% of the maximum stimulator output (SD = 1.65), corresponding to 100% of the participants' rMT (obtained as described in Experiment 1).

Experiment 4

We conducted Experiment 4 to rule out the possibility that TMS over distinct cerebellar sectors may differently affect the processing of emotional faces and scenarios (regardless of the low-level vs high-level social inference required by the task). Indeed, although prior neuroimaging evidence reported a cerebellar involvement in the emotional processing of different stimuli (Fusar-Poli et al., 2009; Baumann et al., 2012; Metoki et al., 2022; for review, see Adamaszek et al., 2017), lateral and medial sectors may contribute differently depending on stimulus type. Participants were presented with a two-alternative force-choice task, in which they had to classify a series of faces and scenarios as conveying a positive or negative emotion. Since the task is very basic and does not require any mentalizing/high-level inferential process, we expect to find a major role for the medial compared with the lateral cerebellum (as for Experiments 1 and 2). If the specific type of emotional stimulus employed is not critical in determining the extent to which medial

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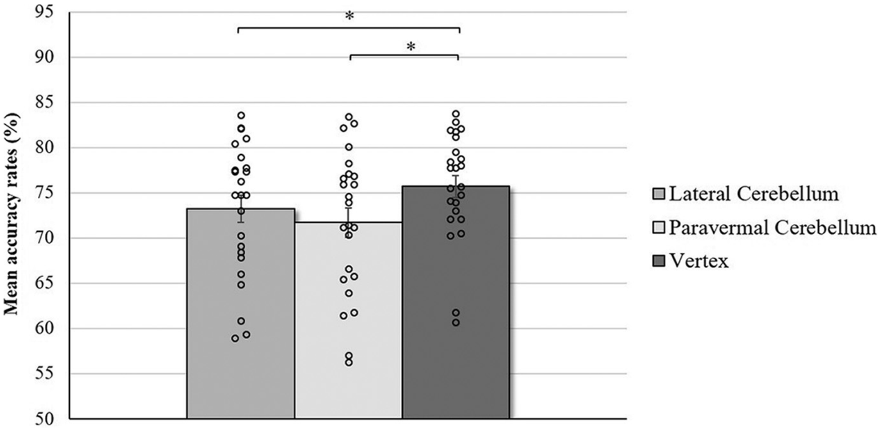

Figure 2. Mean accuracy rates (%) as a function of TMS site (lateral cerebellum, paravermal cerebellum, and vertex) in the discrimination of angry and happy faces (Experiment 1). Asterisks indicate significant differences ($p < 0.05$, Bonferroni–Holm corrected) across TMS conditions.

and lateral cerebellar sectors are involved (see Fusar-Poli et al., 2009; Baumann et al., 2012; Metoki et al., 2022; for review, see Adamaszek et al., 2017), this should be the case for both emotional scenarios/contexts and faces.

Participants
Twenty-two right-handed volunteers participated in the experiment (three males, mean age = 21.9 years, SD = 1.7). Before the experiment, participants were screened to evaluate compatibility with TMS (translated from Rossi et al., 2011). None of them participated in the previous experiments. The protocol was approved by the local ethics committee and participants were treated in accordance with the Declaration of Helsinki. The sample size was similar to the first two experiments, although the task was slightly different.

Stimuli, procedure, and TMS
Participants were seated in front of a 19-inch screen at an approximate distance of 57 cm. The task was a two-alternative forced-choice task requiring participants to indicate by left/right key pressing with their right hand whether a stimulus individually presented at the center of the screen conveyed a positive or negative emotion (response keys were counterbalanced across participants). Stimuli consisted of the emotional faces and emotional scenarios used in Experiment 3. In each block, each image was individually presented for 150 ms on a gray background. Response was followed by a fixation cross (2500 ms); hence, the next stimulus was presented (see Fig. 1*C*). Triple-pulse 20-Hz TMS was delivered over the same sites of the previous Experiments at the onset of the image (since no second stimulus was expected and participants could respond immediately after onset). Faces and scenarios were presented in different blocks. There were six experimental blocks, one for each combination between stimulus type (face vs scenario) and TMS site (medial cerebellum, lateral cerebellum, vertex). Each block consisted of 28 trials, half depicting images conveying fear and half happiness. A short practice block (12 trials) preceded the TMS experiment. The order of the presentation of the experimental blocks was counterbalanced across participants, and targeted sites were localized as in the previous experiments. The intensity of stimulation was 50.1% of the maximum stimulator output (SD = 2.01), corresponding to 100% of the participants' rMT (obtained as described in Experiment 1).

Results

Deidentified data for all experiments are available at https://zenodo.org/. Mean accuracy rates and mean correct reaction times (RTs, recorded from the offset of the image preceding the response) were computed for each participant in each experimental condition. For all experiments, RTs that were ±3 SD compared with each participant's block mean were excluded from the analyses (following this criterion, 1.1% of total trials were excluded for Experiment 1, 1.0% for Experiment 2, 1.1% for Experiment 3, and 1.0% for Experiment 4).

Experiment 1

A repeated-measures ANOVA with TMS site (lateral cerebellum, paravermal cerebellum, and vertex) as within-subjects variable on the mean accuracy scores revealed a significant main effect of TMS, $F_{(2,46)} = 6.79$, $p = 0.003$, $\eta_p^2 = 0.23$. *Post hoc* comparisons (Bonferroni–Holm correction applied) indicated that compared with TMS over the vertex both TMS over the paravermal cerebellum, $t_{(23)} = 3.07$, $p = 0.015$, $d = 0.63$, and the lateral cerebellum, $t_{(23)} = 2.54$, $p = 0.036$, $d = 0.52$, lowered participants' ability to discriminate between angry and happy faces. No difference was observed between TMS over the paravermal cerebellum and over the lateral cerebellum, $t_{(23)} = 1.57$, $p = 0.13$ (see Fig. 2). F2

A similar ANOVA performed on mean correct RTs (vertex = 710 ms, SD = 225; lateral cerebellum = 712 ms, SD = 215; paravermal cerebellum = 715 ms, SD = 221) revealed no significant effect of TMS, $F_{(2,46)} < 1$, $p = 0.99$.

Experiment 2

A repeated-measures ANOVAs with TMS site (lateral cerebellum, paravermal cerebellum, and vertex) as within-subjects variable on the mean accuracy scores revealed a significant main effect of TMS, $F_{(2,42)} = 5.62$, $p = 0.007$, $\eta_p^2 = 0.21$. *Post hoc* comparisons (Bonferroni–Holm corrected) indicated that compared with TMS over the vertex both TMS over the paravermal cerebellum, $t_{(21)} = 3.41$, $p = 0.009$, $d = 0.73$, and the lateral cerebellum, $t_{(21)} = 2.43$, $p = 0.048$, $d = 0.52$, lowered participants' ability to discriminate between emotional faces. No difference was observed between TMS over the paravermal and lateral cerebellum, $t_{(21)} < 1$, $p = 0.41$, $d = 0.29$ (see Fig. 3). F3

Correct RTs for stimulation of the vertex were 643 ms (SD = 214), for the stimulation of the lateral cerebellum were 655 ms (SD = 211), and for the paravermal stimulation were 652 ms (SD = 219). The ANOVA on mean correct RTs revealed no significant effect of TMS, $F_{(2,42)} < 1$, $p = 0.91$.

Experiment 3

Pilot experiment
A repeated-measures ANOVA on participants' mean accuracy rates with Face emotion (fear vs happiness) and Context (congruent vs incongruent) as within-subjects factors revealed a significant main effect of Face emotion, $F_{(1,19)} = 4.62$, $p = 0.045$, $\eta_p^2 = 0.19$, with participants performing better with fearful faces (mean = 72%, SD = 16.4) than happy faces (mean = 60%, SD = 14.7), and a significant main effect of Context, $F_{(1,19)} = 10.14$, $p = 0.005$, $\eta_p^2 = 0.35$, with accuracy being higher when the context was congruent with the emotion of the face (mean = 73%, SD = 9.1) rather than incongruent (mean = 59%, SD = 16.5). The same ANOVA on participants' correct RTs revealed a significant main effect of Context, $F_{(1,19)} = 4.54$, $p = 0.046$, $\eta_p^2 = 0.19$, with participants responding faster when the context was congruent with the emotion of the face (mean = 713 ms,

SD = 210) compared with when it was incongruent (mean = 794 ms, SD = 282). Neither the main effect of Face emotion, $F_{(1,19)} < 1$, $p = 0.42$, nor the interaction Face emotion × Context, $F_{(1,19)} < 1$, $p = 0.92$, reached significance. Overall, the results of the pilot experiment confirm that face emotion recognition is sensitive to the influence of the provided context.

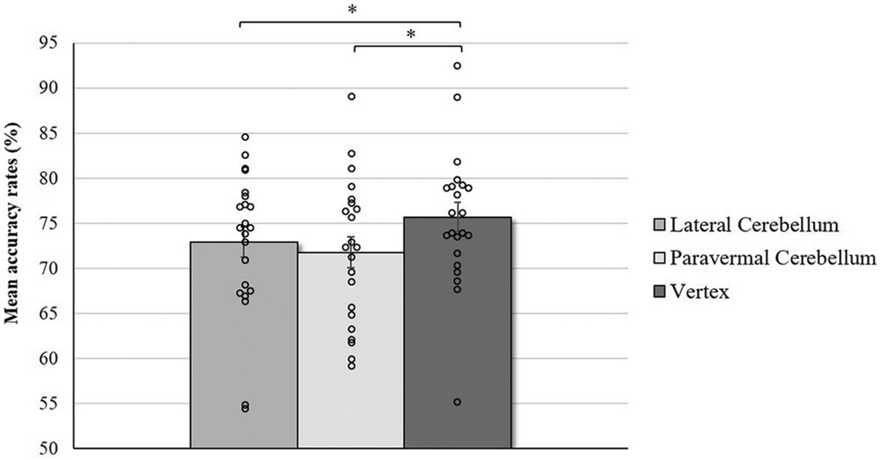

Figure 3. Mean accuracy rates (%) as a function of TMS site (lateral cerebellum, paravermal cerebellum, and vertex) in the discrimination of fearful and happy faces (Experiment 2). Asterisks indicate significant differences ($p < 0.05$, Bonferroni–Holm corrected) across TMS conditions.

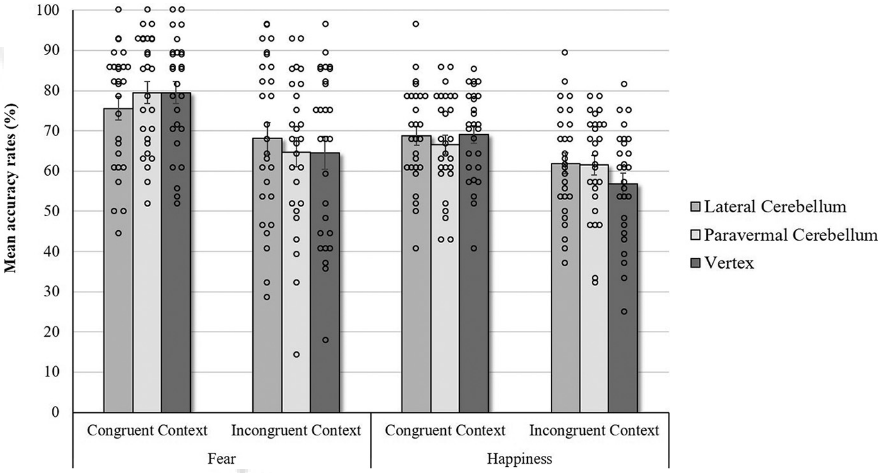

Figure 4. Mean accuracy rates (%) as a function of Context (congruent, incongruent), Face emotion (fear, happiness), and TMS site (lateral cerebellum, paravermal cerebellum, and vertex) in Experiment 3.

TMS experiment

Data of one participant were excluded because of extremely long response latencies, exceeding the group mean of >2 SD. Analysis of participants' performance in recognizing the emotions expressed by the faces alone (performed without TMS at the end of the experimental session) confirmed that participants could correctly recognize fearful (mean accuracy = 78%, SD = 1.5) and happy faces (mean accuracy rates of 64%, SD = 1.1). Fearful faces were overall recognized better than happy faces, $t_{(25)} = 3.40$, $p = 0.002$, probably as a result of the morphing procedure making these faces more recognizable.

Accuracy rates for the TMS experiment are shown in Figure 4. A re- F4
peated-measures ANOVA with Context (congruent vs incongruent), Face emotion (fear vs happiness), and TMS site as within subjects-factors on accuracy scores revealed a significant main effect of Context, $F_{(1,26)} = 17.89$, $p < 0.001$, $\eta_p^2 = 0.41$, indicating that faces paired with congruent contexts (mean = 73%, SD = 7.2) were recognized better than those paired with incongruent contexts (mean = 63%, SD = 10.6; in line with results of the pilot study). The main effect of Face emotion also reached significance, $F_{(1,26)} = 4.76$, $p = 0.038$, $\eta_p^2 = 0.16$, indicating that fearful faces (mean = 72%, SD = 1.4) were recognized better than happy faces (mean = 64%, SD = 8.6; as in the pilot task, see above). These main effects were qualified by the significant interaction Context by Face emotion by TMS, $F_{(2,52)} = 3.46$, $p = 0.039$, $\eta_p^2 = 0.12$. No other main effect or interaction reached significance: TMS, $F_{(2,52)} < 1$, $p = 0.58$; Face Emotion by TMS, $F_{(2,52)} < 1$, $p = 0.74$; TMS by Context, $F_{(2,52)} = 2.77$, $p = 0.07$.

To clarify the three-way significant interaction, we conducted a repeated-measures ANOVA with Context and TMS as within-subjects factors separately for fearful and happy faces. When participants were presented with happy faces, the analysis revealed a significant main effect of Context, $F_{(1,26)} = 13.68$, $p = 0.001$, $\eta_p^2 = 0.35$, confirming that participants recognized happy faces better in congruent than incongruent trials. Neither the main effect of TMS, $F_{(2,52)} < 1$, $p = 0.44$, nor the interaction Context by TMS, $F_{(2,52)} = 2.34$, $p = 0.11$, reached significance. For fearful faces, the analysis revealed a significant main effect of Context, $F_{(1,26)} = 16.46$, $p < 0.001$, $\eta_p^2 = 0.39$, indicating that participants were better at recognizing fearful faces paired with congruent compared with incongruent scenarios. Critically, however, this effect was modulated by TMS, as demonstrated by the significant Context by TMS interaction, $F_{(2,52)} = 3.71$, $p = 0.031$, $\eta_p^2 = 0.13$. The main effect of TMS was not significant, $F_{(2,52)} < 1$, $p = 0.99$. *Post hoc* comparisons (Bonferroni–Holm correction applied) showed that the main effect of Context was significant in all the TMS conditions, however, it was weaker (as shown by the magnitude of the effect size) during TMS over the lateral cerebellum, $t_{(26)} = 2.09$, $p = 0.046$, $d = 0.40$, compared with TMS over the vertex $t_{(26)} = 4.05$, $p < 0.001$, $d = 0.78$, and the medial cerebellum $t_{(26)} = 4.29$, $p < 0.001$, $d = 0.83$. To further clarify this effect, we computed (for responses to fearful faces) a differential score (Δ) that represents the magnitude of the facilitation induced by congruent contexts subtracting for each participant accuracy rates in incongruent trials (i.e., happy context/fearful face) from those in congruent trials (i.e., fearful context/fearful face; see Fig. 5). Hence, F5 F6
we assessed whether this differential score varied as a function of the TMS site. Pairwise comparisons showed that the magnitude of the facilitatory contextual effect was smaller during the stimulation of the lateral cerebellum compared with both the stimulation of the vertex, $t_{(26)} = 2.38$, $p = 0.050$, $d = 0.46$, and the paravermal cerebellum, $t_{(25)} = 2.54$, $p = 0.051$, $d = 0.49$. No difference in the magnitude of the contextual effect was observed between the stimulation of vertex and the paravermal cerebellum, $t_{(26)} < 1$, $p = 0.95$.

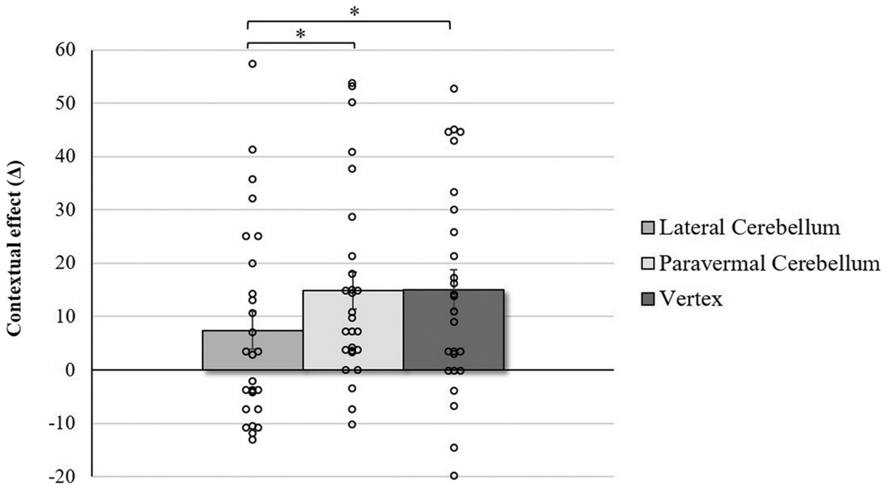

Figure 5. The facilitatory effect (Δ) of a congruent context on correct recognition of fearful faces, calculated by subtracting each participant's accuracy rates in incongruent trials from those in congruent trials, as a function of TMS site (lateral cerebellum, paravermal cerebellum, and vertex) in Experiment 3. Asterisks indicate significant differences ($p < 0.05$, Bonferroni–Holm corrected) across conditions.

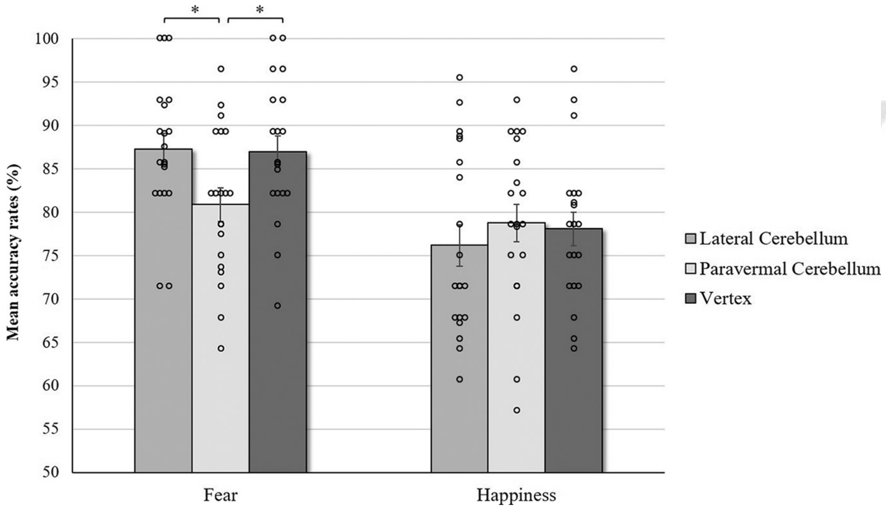

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Figure 6. Mean accuracy rates (%) collapsed for Stimulus type (faces and scenarios) as a function of Emotion (fear, happiness), and TMS site (lateral cerebellum, paravermal cerebellum, and vertex) in Experiment 4.

The ANOVA on mean correct RTs revealed a significant main effect of Context, $F_{(1,26)} = 11.09$, $p = 0.003$, $\eta_p^2 = 0.30$, with participants responding faster in congruent (mean = 594, SD = 178) than incongruent trials (mean = 617, SD = 180). No other main effects or interactions reached significance: Face emotion, $F_{(1,26)} < 1$, $p = 0.47$; TMS, $F_{(2,52)} < 1$, $p = 0.88$; Face Emotion by TMS, $F_{(2,52)} < 1$, $p = 0.77$; Face Emotion by Context, $F_{(1,26)} < 1$, $p = 0.62$; TMS by Context, $F_{(2,52)} < 1$, $p = 0.66$; Face Emotion by Context by TMS, $F_{(2,52)} < 1$, $p = 0.76$.

Experiment 4

Data of two participants were excluded because of extremely long response latencies, exceeding the group mean of >2 SD. A repeated-measures ANOVA with Emotion (fear vs happiness), Stimulus type (face vs scenario), and TMS site (lateral cerebellum vs paravermal cerebellum vs vertex) as within-subjects variables conducted on mean accuracy rates revealed a significant main effect of Stimulus type, $F_{(1,19)} = 413.16$, $p < 0.001$, $\eta_p^2 = 0.95$, and a significant effect of Emotion, $F_{(1,19)} = 8.13$, $p = 0.010$, $\eta_p^2 = 0.30$, whereas the main effect of TMS was not significant, $F_{(2,38)} = 2.02$, $p = 0.15$. The main effect of Stimulus type was because of accuracy being overall higher for scenarios (mean = 95%, SD = 2.7) than faces (mean = 68%, SD = 6.0), this likely depending on the morphing procedure applied to emotional faces that made their recognition more demanding. The main effect of Emotion was qualified by the significant interaction Emotion by Stimulus type, $F_{(1,19)} = 9.24$, $p = 0.007$, $\eta_p^2 = 0.33$. This interaction depended on participants being overall better at recognizing fearful (mean = 76%, SD = 1.3) compared with happy faces (mean = 60%, SD = 1.4), $t_{(19)} = 3.00$, $p = 0.007$, $d = 0.67$, whereas no difference was observed between fearful (mean = 94%, SD = 0.39) and happy scenarios (mean = 95%, SD = 0.33), $t_{(19)} = 1.28$, $p = 0.22$. The interaction Emotion by TMS site also reached significance, $F_{(2,38)} = 3.44$, $p = 0.042$, $\eta_p^2 = 0.15$. An analysis of the simple main effect of TMS within each emotion revealed that that TMS selectively interfered with recognition of fearful stimuli, $F_{(2,38)} = 5.44$, $p = 0.008$, $\eta_p^2 = 0.22$, and not with recognition of happy stimuli, $F_{(2,38)} < 1$, $p = 0.54$. *Post hoc* comparisons (Bonferroni–Holm correction applied) showed that accuracy was lower when TMS was applied over the medial cerebellum compared with vertex, $t_{(19)} = 2.78$, $p = 0.036$, $d = 0.62$, and to lateral cerebellum, $t_{(19)} = 2.77$, $p = 0.024$, $d = 0.62$. Accuracy for TMS over the lateral cerebellum and the vertex did not differ, $t_{(19)} < 1$, $p = 0.87$. The interactions Stimulus type by TMS site, $F_{(2,38)} < 1$, $p = 0.64$, and Emotion by Stimulus type by TMS site, $F_{(2,38)} = 1.04$, $p = 0.36$, were not significant.

A similar ANOVA on mean correct RTs revealed a main effect of Stimulus Type, $F_{(1,19)} = 36.42$, $p < 0.001$, $\eta_p^2 = 0.66$, indicating that participants recognized scenes (mean = 313 ms, SD = 101) faster than faces (mean = 416, SD = 156), paralleling the results on accuracy. None of the other main effects or interactions reached significance (all Fs < 2.4, ps > 0.13).

Discussion

The involvement of the posterior cerebellum in social cognition is nowadays well established (Adamaszek et al., 2017; Van Overwalle et al., 2020), but whether different sectors of the posterior cerebellum are differently involved in social cognitive processes depending on the type/level of the required social inference is not clear. In a series of experiments, we showed that interfering via TMS with the activity of the medial posterior cerebellum affected basic emotion recognition in a two-alternative force-choice task, although this effect was restricted to negative stimuli (i.e., classification of fearful faces and scenarios). In turn, TMS over both the medial and lateral posterior cerebellum affected performance in a same-different discrimination task, requiring to indicate whether two faces expressed the same or a different (ambiguous) emotion (anger/happiness or fear/happiness). Finally, only TMS over the lateral posterior cerebellum affected performance in a task requiring a higher-level social inference and in which participants had to recognize an (ambiguous) facial emotion as expressing happiness or fear considering the context in which it was experienced, with this effect being again only evident for fearful faces.

Our findings provide critical evidence in support of the causal role of the paravermal/medial cerebellum in the discrimination of emotional faces (Experiments 1 and 2) and scenes (Experiment 4). Our data are in line with the results of prior TMS studies (Ferrari et al., 2018a, 2021, 2022a) and neuroimaging and neuropsychological evidence showing that the vermis and medial cerebellum are fundamental components of the brain network that mediates the processing of different emotional expressions and more, in general, a variety of emotional stimuli (Fusar-Poli et al., 2009; Baumann et al., 2012; Metoki et al., 2022; for review, see Adamaszek et al., 2017). Here, we add to this evidence by showing that basic emotion discrimination (i.e., classification of a face or a scene as expressing fear or happiness) selectively recruits the medial cerebellum. In turn, when emotional processing becomes more demanding (even if the degree of mentalizing is quite limited), as in deciding about the emotion of two consecutively presented faces in the absence of any other contextual information, both the medial and the lateral cerebellum play a role. Accordingly, available neuroimaging evidence suggests that the cerebellar regions that respond to emotional faces extend from the midline into paravermal and lateral (left) lobule VI/VII (Fusar-Poli et al., 2009; Schraa-Tam et al., 2012). The posterior cerebellum participates in basic emotional processing possibly via interactions with the salience network (Habas et al., 2009). This network (that encompasses dorsal anterior cingulate and frontoinsular cortices and is linked to subcortical limbic structures) is dedicated to the detection and integration of relevant interoceptive, autonomic, and emotional information (Seeley et al., 2007; Habas et al., 2009) that supports rapid decisions about which stimuli are important to attend (for review, see Barrett and Satpute, 2013). The paravermal and lateral sectors of lobules VI and VII might therefore participate in the salience network by facilitating the detection and attentional orientation toward emotional/salient stimuli and by mediating the selection of the more appropriate emotional response based on the individual's current state.

In Experiment 3, participants had to recognize (ambiguous) facial emotional expressions by considering the contextual information provided before the face, with TMS being delivered after the presentation of the contextual scenario. The emotion expressed by the face could be congruent with what participants may have expected on the basis of the provided scenario (e.g., a happy face following the image of a party) or incongruent (e.g., a happy face following the image of a car accident). The task employed in Experiment 3 thus required some degree of mentalizing and represents a more abstract and complex form of socio-emotional process compared with the basic discrimination of isolated facial expressions (Schurz et al., 2021). AQ:G Critically, we found that this higher-level inference selectively recruited the lateral posterior cerebellum, at least when the emotion to be recognized was negative (i.e., fear). This finding suggests that whereas the whole posterior cerebellum may overall play a role in emotion discrimination (at least when the task is sufficiently demanding), higher-level social inferential processes may selectively tap on phylogenetically newer lateral cerebellar sectors. Hence, our data support the existence of a medial-to-lateral gradient in the functional organization of the posterior cerebellum depending on the type/level of required social inference (Kruithof et al., 2022) and show that the lateral cerebellar sector, although maintaining more basic functions (i.e., simple emotion discrimination) may have further evolved to subserve higher-level social mechanisms.

Critically, data from Experiments 3 and 4 consistently suggest that interfering with either the medial or the lateral cerebellum only modulated processing of fearful stimuli (note that this information is not available for Experiments 1 and 2, since the same-different specific paradigm used in those experiments did not allow to analyze performance separately for each emotion). The finding of a selective or more prominent role of the cerebellum in the processing of negative emotions is not new, since prior studies (also from our group) reported similar results (Beauregard et al., 1998; Ferrucci et al., 2012; Schraa-Tam et al., 2012; Adamaszek et al., 2017; Ferrari et al., 2022a; but see Fusar-Poli et al., 2009; Baumann and Mattingley, 2012). The current study adds to this previous evidence and corroborates the hypothesis that the cerebellum is more involved in responding to those stimuli that trigger motor "fight or flight" responses (Schraa-Tam et al., 2012). In this view, the cerebellum might contribute to the emotional domain by implementing prediction mechanisms important for the preparation and planning of fast responses to potential threats, such as anger or fear-related stimuli. In line with this, the effects we reported may have also depended on the stimulation of a larger subcortical network comprising both the cerebellum and the amygdala and involved in different aspects of emotional processing, from fear conditioning (Timmann et al., 2010) to emotional enhancement of episodic memory (Fastenrath et al., 2022), a possibility that deserves though further investigation.

In the experiments reported here, we selectively stimulated left lateral cerebellar sectors. This choice depended on consistent literature suggesting that emotional and social tasks may drive more consistent activations in the left than in the right cerebellum, with connectivity between the left cerebellum and the right cortex being also more evident than that between the right cerebellum and the left cortex (Schraa-Tam et al., 2012; Metoki et al., 2022). These results are in line with the right hemisphere bias of the mentalizing network in the cerebrum (Y. Wang et al., 2021) and more in general, with evidence showing that cognitive networks (such as the language network) that are strongly lateralized in the cerebrum may also be lateralized within the cerebellum (Wang et al., 2012). AQ:H Whether the right cerebellar hemisphere is also involved in different social inferential predictive processes has never been tested via TMS. Future investigations should shed light on possible patterns of task-related lateralization in the posterior cerebellum in the social and affective domains.

Finally, in interpreting the cerebellar TMS effects we reported, one may wonder whether these depended, at least in part, on indirect stimulation of the visual cortex. Indeed, estimation of the E-field generated by cerebellar TMS (see Fig. 1*D*) shows that the visual cortex was also partially affected by stimulation. However, we believe this possibility is unlikely. Indeed, in the first three experiments, TMS was delivered during the blank between the two stimuli: this timing of stimulation is unlikely to have affected early visual processing of either stimulus (Amassian et al., 1989; de Graaf et al., 2014), as we have also directly demonstrated in a prior study (Ferrari et al., 2018a). Furthermore, even when cerebellar TMS was delivered at the onset of the stimulus to be categorized (Experiment 4), the effects were specific for emotion (see also Experiment 3), discouraging an interpretation of the data as driven by interference with early visual processing. In light of the above, although our stimulation possibly reached the early visual cortex, it was too indirect to effectively modulate performance. Cerebellar TMS (especially when repetitive) given at higher intensities (above phosphene threshold) may be riskier in this respect (see Renzi et al., 2014); accordingly, cerebellar TMS parameters (i.e., intensity, frequency, timing) should be carefully evaluated in each paradigm to rule out confounding effects depending on indirect stimulation of the visual cortex.

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In sum, our findings demonstrate for the first time that processing others' emotions draws on the involvement of segregated cerebellar regions (depending on the level of social inference/mentalizing required) that exert partially distinguishable functions, providing a more detailed functional mapping of the cerebellar causal contribution to emotional processing. These findings are also informative for the understanding of specific psychiatric conditions associated with cerebellar damage such as schizophrenia whose symptoms have been recently hypothesized to reflect dysfunctional predictive mechanisms (Moberget and Ivry, 2019).

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