A chronometric study of the posterior cerebellum's function in emotional processing

Andrea Ciricugno[1,2§], Chiara Ferrari[1,3§], Lorella Battelli[4,5] & Zaira Cattaneo[6*]

1- IRCCS C. Mondino Foundation, Via Mondino, Pavia, 27100, Italy
2- Department of Brain and Behavioral Sciences, University of Pavia, Via Bassi 21, Pavia, 27100, Italy
3- Department of Humanities, University of Pavia, Piazza Botta 6, Pavia, 27100, Italy
4- Department of Neurology, Berenson-Allen Center for Noninvasive Brain Stimulation, Beth Israel Deaconess Medical Center and Harvard Medical School, 330 Brookline Ave Kirstein Building KS 158, Boston, MA, 02215, United States
5- Center for Neuroscience and Cognitive Systems@UniTn, Istituto Italiano di Tecnologia, Corso Bettini 31, Rovereto, 38068, Italy
6- Department of Human and Social Sciences, University of Bergamo, Piazzale S. Agostino 2, Bergamo, 24129, Italy

§ These two authors contributed equally to this work and shared first co-authorship

* Lead Contact: zaira.cattaneo@unibg.it

Summary

The posterior cerebellum is a recently discovered hub of the affective and social brain, with different subsectors contributing to different social functions. However, very little is known about *when* the posterior cerebellum plays a critical role in social processing. Due to its location and anatomy, it has been difficult to use traditional approaches to directly study the chronometry of the cerebellum. To address this gap in cerebellar knowledge, here we investigated for the first time the *causal* contribution of the posterior cerebellum to social processing using a chronometric transcranial magnetic stimulation (TMS) approach. We show that the posterior cerebellum is recruited at an early stage of emotional processing (starting from 100 ms after stimulus onset), simultaneously with the posterior superior temporal sulcus (pSTS), a key node of the social brain. Moreover, using a condition-and-perturb TMS approach, we found that the recruitment of the pSTS in emotional processing is dependent on cerebellar activation. Our results are the first to shed light on chronometric aspects of cerebellar function and its causal functional connectivity with other nodes of the social brain.

Introduction

The contribution of the posterior cerebellum to social cognition is well established. We can now count on solid evidence from different approaches demonstrating the role of the posterior (vs. anterior) cerebellum in a variety of social tasks, including facial and bodily emotion recognition and discrimination[1-4], mentalizing[4,5-6], perception of biological motion[7-9], action understanding and prediction[10-11], and social categorization[12] (for recent reviews and meta-analyses, see[13-15]). Moreover, neuroimaging studies suggest that the posterior cerebellum exhibits a fine-grained functional topography[16-17] even within the domain of social cognition. In line with this, we have recently provided causal evidence for a medial-to-lateral gradient in the posterior cerebellum, with medial cerebellar sectors supporting basic social cognitive functions (emotion recognition and processing) and more lateral/hemispheric sectors playing a role in higher-level social inferential processing and mentalizing[18].

Despite the extensive progress in our understanding of cerebellar topography in humans, very little is known about the *time course* of mental operations in the cerebellum. Chronometric approaches play a unique role in clarifying the cognitive operations that each cortical node within a network performs and how they are organized in real-time. However, in the case of the cerebellum, these approaches can be challenging to implement, mainly because the anatomy of the cerebellum makes it difficult to use traditional electrophysiological methods (i.e., electroencephalogram, EEG, and magnetoencephalography, MEG)[19]. Nevertheless, knowing *when* the posterior cerebellum is involved in social processing would be crucial for a better understanding of how cerebellar output affects social circuits in the neocortex. Indeed, a largely accepted view is that the cerebellum may contribute to cognition by signaling temporally-specific predictions about behavioral outcomes related to the function of different cortical areas[20-23].

To fill this gap in current knowledge of cerebellar functioning, here we systematically investigated the time course of the *causal* involvement of the posterior cerebellum in an emotion discrimination task using a chronometric TMS approach. Indeed, thanks to its excellent temporal resolution (in the order of a few milliseconds), TMS can be used to study the chronometry of mental processes in the brain[24-25]. Furthermore, we compared the timing of cerebellar activation with the timing of activation of a key node of the social brain, the posterior superior temporal sulcus (pSTS), and we assessed for the first time whether activation of the pSTS during performance of a social task is *causally* dependent on cerebellar activation. Indeed, although many studies have shown that the posterior cerebellum is anatomically and functionally connected to cortical hubs of the social brain,

such as the pSTS and the dorsomedial prefrontal cortex (dmPFC)[4,8-9,26], this evidence is mostly based on fMRI studies, which cannot assess *causal* functional connectivity.

In the first two experiments, we used TMS to investigate the chronometry of cerebellar recruitment in facial emotion discrimination (see Figure 1A; using different time-windows), a task in which we have consistently demonstrated a role for the posterior left paravermal cerebellum[1-2,18]. Across the two experiments, we consistently found that TMS over the posterior (left paravermal) cerebellum significantly impaired facial emotion discrimination when delivered as early as 100 ms from face onset, up to around 200 ms. Experiment 2 also showed that TMS over the pSTS impairs performance in a similar time-window, suggesting that the pSTS and the posterior cerebellum work in tandem to support facial emotion processing. Finally, in a third experiment, we used a condition-and-perturb TMS approach (see Figure 1B) (a methodology based on TMS state dependence[27]) to directly assess causal functional connectivity between the posterior cerebellum and the pSTS. We found that inhibitory TMS over the cerebellum modulated the effects of TMS delivered over the pSTS during the task, suggesting that these two regions are *causally* functional connected.

< Figure 1>

Results

A total of 87 participants took part in three experiments designed to investigate the timing of cerebellar recruitment in emotional facial processing (Experiments 1 and 2) and explore cerebellar *causal* functional connectivity with a critical node of the social brain, the pSTS (Experiment 3).

rTMS over the posterior left paravermal cerebellum disrupts discrimination of facial emotions when delivered at 120 ms from probe face onset

In Experiment 1, 25 participants (7 males, mean age = 23.9 years, SD = 2.9) performed a facial emotion discrimination task, in which they had to indicate whether two consecutive emotional faces expressed the same or a different emotion (see STAR Methods for details). During the task, they received triple-pulse TMS (20 Hz) starting at four different time points from the probe face onset (20ms, 120ms, 220ms, 320ms) over the posterior left paravermal cerebellum, and over two control sites (V1/V2, and the vertex). V1/V2 was also targeted to rule out the possibility that cerebellar TMS effects may depend on spread of activation to nearby early visual cortex[30].

A repeated measures ANOVA, with TMS site (vertex, V1/V2, left paravermal cerebellum) and TMS timing (first pulse delivered at 20, 120, 220, 320 ms from probe face onset) as within-subjects variables on mean accuracy rates revealed no significant main effect of either TMS site, $F(2,48)<1$, $p=.44$, or TMS timing, $F(3,72)<1$, $p=.53$. The interaction TMS site x TMS timing, $F(6,144)=2.99$, $p=.009$, $\eta_p^2=.11$, reached significance and was further examined by looking at the simple main effect of TMS site at each time onset. The analysis revealed a significant main effect of TMS site for TMS delivered at 20 ms (20-120ms time window), $F(2,48)=3.56$, $p=.036$, $\eta_p^2=.13$, and at 120 ms from probe face onset (120-220 ms time window), $F(2,48)=4.55$, $p=.016$, $\eta_p^2=.16$. In turn, TMS site was not significant for TMS delivered at 220 ms, $F(2,48)=1.13$, $p=.33$, or 320 ms, $F(2,48)<1$, $p=.40$, from probe face onset. Post-hoc *t*-tests showed that when the first pulse was delivered at 20 ms from the probe face onset, TMS over V1/V2 impaired performance relative to the vertex, $t(24)=2.51$, $p=.019$ ($p=.057$ Bonferroni-Holm corrected), and relative to the left paravermal cerebellum (although in this case the difference only approached significance), $t(24)=2.01$, $p=.056$ ($p=.11$ Bonferroni-Holm corrected). TMS over the left paravermal cerebellum did not affect accuracy compared to the control vertex condition, $t(24)<1$, $p=.93$. For the 120 ms TMS onset, accuracy rates were lower when TMS was applied over the left paravermal cerebellum compared to the vertex, $t(24)=3.11$, $p=.005$ ($p=.014$ Bonferroni-Holm corrected) and V1/V2, $t(24)=2.51$, $p=.019$ ($p=.038$ Bonferroni-Holm corrected) (Figure 2). No difference was observed between TMS over the vertex and V1/V2, $t(24)<1$, $p=.76$.

< Figure 2>

The same analysis performed on correct RTs revealed no significant main effects or interactions: TMS site, $F(2,48)=1.27$, $p=.29$; TMS timing, $F(3,72)<1$, $p=.63$; TMS site by TMS timing, $F(6,144)<1$, $p=.55$. Mean correct RTs were 1121 ms (SD=249) for vertex TMS, 1135 ms (SD=344) for cerebellar TMS, and 1048 ms (SD=270) for V1/V2.

Double-pulse TMS over the posterior left paravermal cerebellum and over the right pSTS disrupts discrimination of facial emotions at a similar timing

In Experiment 2, we performed a finer temporal analysis of the cerebellar contribution to facial emotion processing, focusing on the 120-220 ms time window identified in Experiment 1. To this aim, 24 participants (9 males, mean age = 22.30 years, SD = 2.35) performed the same facial emotion discrimination task used in Experiment 1, while receiving double-pulse TMS (40 ms between the two pulses, resulting into a 25 Hz frequency, see Pitcher[31]) at 100ms, 130ms, and 170ms from the probe

face onset. Critically, here we also targeted the pSTS, a core region of the social brain implied in facial emotion processing.

A repeated measures ANOVA with TMS site (vertex, left paravermal cerebellum, pSTS) and TMS timing (first pulse at 100ms, 130ms, 170ms from probe face onset) as within-subject variables on mean accuracy rates revealed a significant main effect of TMS site, $F(2,46)=4.93$, $p=.012$, $\eta_p^2 =.18$, indicating that TMS over both the pSTS, $t(23)=3.13$, $p=.005$ ($p=.014$ Bonferroni-Holm corrected), and the left paravermal cerebellum, $t(23)=2.20$, $p=.038$ ($p=.077$ Bonferroni-Holm corrected) impaired performance compared to TMS over the control site (vertex). TMS over the pSTS and the left paravermal cerebellum similarly impaired performance, $t(23)=1.03$, $p=.32$ (Figure 3). The main effect of TMS timing, $F(2,46)<1$, $p=.92$, and the interaction of TMS site by TMS timing, $F(4,92)<1$, $p=.82$, were not significant.

< Figure 3>

Correct RTs were 1074 ms (SD=200) for vertex TMS, 1084 ms (SD=256) for left paravermal cerebellar TMS, and 1076 ms (SD=280) for pSTS TMS. The repeated measure ANOVA on RTs revealed no significant main effects or interactions: TMS site, $F(2,46)<1$, $p=.98$; TMS timing, $F(2,46)<1$, $p=.53$; TMS site by TMS timing, $F(4,92)=1.46$, $p=.22$.

Inhibition of the posterior left paravermal cerebellum modulates the effects of perturbing TMS over the right pSTS during facial emotion discrimination

Experiment 3 was designed to assess possible causal functional connectivity between the posterior left paravermal cerebellum and the pSTS. To this aim, we used a dual-site condition-and-perturb TMS approach (see STAR Method for details), in which 38 participants (10 males, mean age = 23.19 years, SD = 3.08) received conditioning (inhibitory) 1Hz TMS over the left paravermal cerebellum followed by five-pulses (10 Hz) perturbing TMS over the right pSTS during the same facial emotion discrimination task performed in the previous experiments.

Data from two participants were excluded due to technical problems. A repeated measure ANOVA with conditioning TMS (left paravermal cerebellum and vertex) and perturbing TMS (right pSTS and vertex) as within-subject variables on mean accuracy rates revealed no significant main effect for conditioning TMS, $F(1,35)<1$, $p=.65$. The main effect of perturbing TMS was significant,

$F(1,35)= 9.89$, $p=.003$, $\eta_p^2=.22$, as was the interaction of perturbing TMS by conditioning TMS, $F(1,35)=13.22$, $p<.001$, $\eta_p^2=.27$ (Figure 4).

Post-hoc comparisons showed that when online TMS was applied over the vertex, performance after 1 Hz conditioning of the cerebellum tended to be lower compared to conditioning of the vertex, $t(35)=1.88$, $p=.068$ ($p=.14$ Bonferroni-Holm corrected). Furthermore, following 1 Hz vertex conditioning, participants' accuracy was lower when we delivered online TMS over the right pSTS compared to the vertex, $t(35)=4.07$, $p<.001$, $d=.68$ ($p=.002$ Bonferroni-Holm corrected), indicating the effective contribution of pSTS in the emotion discrimination task. Critically, this pattern disappeared following 1 Hz conditioning of the posterior left paravermal cerebellum: in this condition perturbing pSTS activity with online TMS did not affect performance compared to online TMS of the vertex, $t(35)<1$, $p=.82$. Accordingly, performance was higher when pSTS was stimulated online following cerebellar conditioning compared to vertex conditioning, $t(35)=2.58$, $p=.014$ ($p=.042$ Bonferroni-Holm corrected).

< Figure 4>

The same analysis carried out on correct RTs revealed no significant main effects or interactions: perturbing TMS, $F(1,35)<1$, $p=.64$; conditioning TMS, $F(1,35)<1$, $p=.50$; conditioning TMS by perturbing TMS, $F(1,35)<1$, $p=.45$. Mean correct RTs after vertex conditioning TMS were=996 ms (SD=326) for perturbing vertex TMS and 976 ms (SD=332) for perturbing pSTS TMS. Mean correct RTs after cerebellar inhibitory conditioning TMS were 959 ms (SD=210) for perturbing vertex TMS and 960 ms (SD=218) for perturbing pSTS TMS.

Discussion

In this study, we conducted the first chronometric investigation of the *causal* recruitment of the posterior cerebellum in social processing. Moreover, to further characterize the role of the posterior cerebellum within the social brain, we assessed for the first time the *causal* functional connectivity between this region and the pSTS by using a condition-and-perturb TMS approach.

In a first experiment, we applied triple-pulse TMS over the posterior left paravermal cerebellum (and over V1/V2 and vertex as control sites) during a facial emotion discrimination task in four different 100ms-long time windows (starting at 20, 120, 220, and 320 ms from probe face

onset). We found that cerebellar TMS significantly impaired emotion discrimination when administered between 120 and 220 ms from probe face onset, but not at earlier or later time-windows. This result provides the first *causal* evidence of the time course of the posterior cerebellum's involvement in a social task and, more broadly, in a cognitive process. Importantly, although the electric field induced by TMS over our targeted paravermal site may have spread to nearby visual regions (see Figure 1D, see also Renzi et al[30]; for a recent discussion on TMS focality see Numssen et al[32]), the effects we reported are unlikely to depend on indirect stimulation of V1/V2. Indeed, direct stimulation of V1/V2 only affected performance in the earliest time window (20-120 ms, as expected, see de Graaf et al[33]). Moreover, in prior studies we were able to clearly dissociate the effects of cerebellar and V1/V2 TMS on visual tasks' performance[1-2], demonstrating that these two regions can be selectively targeted.

We then conducted (Experiment 2) a more detailed temporal analysis of the role of the cerebellum in facial emotion processing within the critical time-window identified in Experiment 1, using double-pulse TMS and focusing on shorter (40 ms-long) time intervals (similarly to Pitcher[31]). Here, we also compared the time-course of cerebellar involvement in facial emotion processing with that of the right pSTS, a key node of the social brain. Results of Experiment 2 supported what found in the first experiment: TMS over the posterior left paravermal cerebellum affected facial emotion discrimination between 100 and 210 ms, and so did TMS over the right pSTS. The observed TMS effects over the pSTS are mostly in line with prior literature: indeed, if Pitcher[31] found a significant contribution of the pSTS to facial emotion discrimination up to 140 ms after face onset, other MEG studies reported a strong pSTS response up to 250 ms after face onset in similar tasks[34-35]. While stimulation effects for the pSTS are therefore consistent with previous evidence, the critical finding here is that the posterior cerebellum causally contributes to emotion discrimination within the same time window as the pSTS.

We suggest that the simultaneous causal recruitment of the posterior left paravermal cerebellum and the right pSTS reflects an effective functional interaction between these two regions (as suggested by prior neuroimaging studies[36]), as part of the same network, rather than the simultaneous activation of two distinct networks. Indeed, in a third experiment, we showed that the recruitment of the right pSTS in face emotion discrimination depends on posterior cerebellar activation. Specifically, we observed that interfering with the right pSTS activity with online (i.e., during the task) perturbing TMS impaired participants' performance in discriminating emotional face expressions, in line with previous studies[31,37]. Crucially, however, when we inhibited the posterior left paravermal cerebellum activity with offline 1 Hz TMS before the task, online perturbation of

right pSTS activity no longer impaired performance. This result points to the existence of *causal* functional connections between the posterior left paravermal cerebellum and right pSTS during social processing, in line with prior neuroimaging evidence suggesting functional connections between these two regions[36].

Data from Experiment 3 are likely indicative of state-dependent effects of TMS[38-39]. State dependence in TMS studies refers to the consistent observation that when the activity of a brain region is primed by inhibitory offline 1Hz rTMS, subsequent online TMS applied over the same region either has no effect or can even paradoxically cause a behavioral facilitation, as opposed to the disruptive effect typically observed when online TMS alone is administered. In other words, online TMS applied to a region causally involved in a task may counteract or even reverse the interference effect normally induced by the stimulation, if this region has previously been inhibited by offline 1 Hz TMS[40]. In this context, the effects observed in our study suggest that, under normal conditions, the posterior cerebellum may send excitatory signals to the pSTS during emotion discrimination, possibly fine-tuning its activity. Consequently, when cerebellar activity is suppressed by offline 1 Hz TMS, the pSTS is indirectly inhibited. Thus, the subsequent online TMS applied over the pSTS results in a facilitatory effect due to this prior cerebellar inhibition.

Prior studies have proposed that during social tasks, such as emotion face and body processing, the visual input travels from extrastriate visual regions to the pSTS[41-42] (see also Pitcher and Ungerleider[43]). The pSTS is thought to subserve the rapid integration of information derived from changeable aspects of the stimuli (e.g., facial expressions, body movements) to attribute social and emotional meaning to faces and bodies and thereby understand the intentions of others[44-45]). These operations represent an intermediate step between basic perceptual mechanisms and higher-level social processes (e.g., perspective taking, theory of mind), occurring in other nodes of the social brain, such as the temporoparietal junction (TPJ) and the dmPFC[45-47]. Here we propose that, within this circuit, the role of the posterior left paravermal cerebellum may be to fine-tune via bidirectional connections the contribution of the pSTS to mental state inference by constructing situational internal models. Indeed, a consistent body of evidence suggests that the posterior cerebellum anticipates the behavior of others by generating internal models of social interactions that predict potential outcomes based on individuals' prior experience and knowledge[15, 20-22, 48]. Our findings suggest that, if this is indeed the case, the posterior paravermal cerebellum generates these internal models for emotion discrimination around 100 ms from face onset, concurrently with the operations performed by the pSTS. Furthermore, although in our study we focused on functional connectivity between the posterior left paravermal cerebellum and the pSTS, there is evidence that the posterior cerebellum is

also functionally connected to both the TPJ and the dmPFC49 (see also Metoki et al[4] and Van Overwalle et al[50] for meta-analyses). Accordingly, the posterior cerebellum may modulate processing of social information at different stages within the social brain, with cerebro-cerebellar connections playing an important role in determining whole-brain dynamics[51].

It is worth noting that cerebellar inhibition, which in our study tended to reduce performance when followed by vertex/control online stimulation, has been associated with reduced resting-state functional connectivity between the cerebellum and core regions of the Default Mode Network (DMN), which largely overlaps with the mentalizing network[52]. Thus, our findings may contribute to the ongoing debate about the modulatory tone exerted by the posterior cerebellum on the cerebrum. In fact, while it is widely accepted that the cerebellum exerts an inhibitory tone on the primary motor cortex (M1), a phenomenon known as cerebellar brain inhibition (CBI)[53], the potential excitatory/inhibitory nature of the posterior cerebellar connectivity with non-motor cerebral regions is more controversial. In a previous study, we showed that inhibition of the posterior left paravermal cerebellum via TMS reduced motor-evoked potentials during fearful face viewing[54]. Thus, the direction or tone of the cerebellar modulatory effect (whether inhibitory or excitatory) over the cerebrum may depend on the specific network involved. This perspective is consistent with a previous PET study showing that cerebellar inhibition via 1Hz TMS resulted in both decreased activity in cerebral regions associated with voluntary movements and emotion-related regions, and increased activity in regions associated with cognition and language in the cerebrum[55]. Overall, the nature of the modulation exerted by the posterior cerebellum on various cortical and subcortical networks warrants further investigation, possibly using double-coils/paired-pulse/cortico-cortical paired associative stimulation methods[56].

In prior work we have suggested that there may be a gradient in posterior cerebellar organization whereby sectors of the vermal/paravermal cerebellum play a role in emotion recognition, whereas lateral sectors are mostly engaged when higher-level inferential processing and mentalizing tasks are tested[18]. This suggests a potentially different time course for the involvement of distinct posterior cerebellar sectors depending on the specific demands of the task. In our study, TMS affected left paravermal regions, possibly spreading to the (left) lateral hemisphere, as suggested by modeling of the TMS induced electric field (see Figure 1D). We predict that more lateral cerebellar regions (e.g., lying in lobule VI/VII, see Ferrari et al[18]) may be recruited at different stages of processing, when tasks involve higher-level inferential processes such as mentalizing. This is a hypothesis that should be investigated in future studies and may also shed light on lateralization patterns in the cerebellum. Indeed, previous neuroimaging studies found that socio-affective tasks drive more

consistent activations in the left rather than the right cerebellum, with the left cerebellum also displaying more and stronger effective connections to the right cerebral mentalizing areas, compared to the right cerebellum[4,57]. However, whereas findings from several studies converge in suggesting that language functions are likely to be mediated more by the right than the left cerebellar hemisphere[58-59] (but see Bongaerts et al[60]), available evidence on lateralization of emotional and social processes in the posterior cerebellum is more controversial, with recent meta-analyses of neuroimaging studies mostly suggesting bilateral activations[61-62]. Lateralization of cerebellar functions, as well as cerebellar inter-hemispheric dynamics, deserve further investigation.

In conclusion, our data are the first to provide insights into the chronometry of social processes occurring in the posterior paravermal cerebellum and to show that perturbing cerebellar activity directly affects responses in other nodes of the social brain, such as the pSTS. These findings are critical for a comprehensive understanding of the mechanisms that govern the mentalizing network in the human brain. They also highlight the central role of the posterior cerebellum in social cognition, with important implications for clinical and therapeutic settings.

Acknowledgments

This research was funded by the Italian Ministry of University and Research (PRIN 20203LT7H3 to Z.C.) and by Italian Ministry of University and Research and the European Union-Next Generation EU (PRIN PNRR – Socio-emotional functions of the cerebellum: Pathophysiological mechanisms and practical therapeutic implications in Spinocerebellar Ataxia - P2022TWSWS to C.F.).

Author contribution

Conceptualization, A.C., C.F. and Z.C.; methodology, A.C., C.F., L.B. and Z.C.; formal analysis, A.C. and C.F.; investigation, A.C. and C.F..; data curation, A.C. and C.F.; writing—original draft preparation, A.C., C.F., L.B. and Z.C.; writing—review and editing, A.C., C.F., L.B., and Z.C.; funding acquisition, CF and Z.C. The authors A.C. and C.F. equally contributed to the manuscript and shared first co-authorship.

Declaration of interest

The authors declare no competing interests**.**

Figure legends

Figure 1. Experimental design and localization of the targeted regions. **A)** Example trial of the emotion discrimination task used across all the three experiments. Each trial started with a fixation cross (2500 ms), followed by the first face (500 ms), a blank screen (1000 ms), and the probe face (500 ms). Participants had to indicate whether the two faces expressed the same or a different emotion (by left/right key pressing). **B)** Timeline of an experimental session of Experiment 3. Participants received 15 minutes of 1 Hz (offline) conditioning rTMS over the posterior left paravermal cerebellum and the vertex (in a counterbalanced order in two experimental sessions performed on separate days). Following conditioning rTMS, participants performed the facial emotion discrimination task while receiving perturbing (online) rTMS over the pSTS and the vertex (in a counterbalanced order). **C)** Coronal, sagittal and axial views (from upper left in clockwise order) of a representative participant showing the localization of the posterior left paravermal cerebellum (left panel: TAL; x=-15, y=-82, z=-32), V1/V2 (middle panel: functionally localized using visual phosphenes) and the right pSTS (right panel: TAL: x=52, y=-48, z=8). **D)** Representation of the estimated electric field obtained using SimNIBS[28-29] in the posterior left paravermal cerebellum, V1/V2 (control site) and right pSTS induced by TMS using a Magstim Rapid2 stimulator and a 70-mm figure-of-eight coil.

Figure 2. rTMS over the posterior left paravermal cerebellum disrupts discrimination of facial emotions when delivered at 120 ms from probe face onset. Mean accuracy rates (%) as a function of TMS site (Vertex, V1/V2, left paravermal cerebellum) and triple-pulse 20 Hz TMS timing (20ms, 120 ms, 220ms, 320 ms from probe face onset). Error bars indicate ±1 SEM. Asterisks indicate significant differences ($p<.05$, Bonferroni-Holm corrected; note the difference between TMS over V1/V2 and the cerebellum when the first pulse was delivered at 20 ms only approached significance, $p=.056$ uncorrected) across conditions.

Figure 3. Double-pulse TMS over the posterior left paravermal cerebellum and over the pSTS disrupts discrimination of facial emotions at a similar timing. Mean accuracy rates (%) as a function of TMS site (Vertex, pSTS, left paravermal cerebellum) and TMS timing (first pulse at 100ms, 130ms, 170ms). Error bars indicate ±1 SEM. Asterisks indicate significant differences ($p<.05$, Bonferroni-Holm corrected) across conditions.

Figure 4. Inhibition of the left paravermal cerebellum modulates the effects of perturbing TMS over the right pSTS during facial emotion discrimination. Mean accuracy rates (%) as a function of conditioning TMS (vertex, left paravermal cerebellum) and perturbing TMS (vertex, pSTS). Error bars indicate ±1 SEM. Asterisks indicate significant differences ($p<.05$, Bonferroni-Holm corrected) across conditions.

STAR Methods

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and data should be directed to and will be fulfilled by the lead contact, Z.C. (zaira.cattaneo@unibg.it).

Materials availability

This study did not generate new unique reagents.

Data and code availability

The original datasets of this study have been deposited to the Zenodo.org repository and accession numbers are listed in the key resources table.

This paper does not report original code.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Human participants

Male and female healthy Italian human volunteers participated in this study. Twenty-five (7 males, mean age = 23.9 years, SD = 2.9) participated in Experiment 1, twenty-four (9 males, mean age = 22.30 years, SD = 2.35) in Experiment 2, and thirty-eight (10 males, mean age = 23.19 years, SD = 3.08) in Experiment 3. Each participant took part in only one experiment. All participants had normal or corrected-to-normal vision and none of them had a history of medical, neurological, or psychiatric disease. Before the experiment, all participants were screened to assess their compatibility with TMS (translated from Rossi et al[63]) and gave written informed consent before taking part in the study, which had been approved by the Local Ethics Committee in accordance with the Declaration of Helsinki.

METHOD DETAILS

Experimental task

The same facial emotion discrimination task was used across the three experiments. Stimuli consisted of images selected from the NimStim database[64] depicting eight male and eight female Caucasian faces (each covering approximately 23 × 14 degrees of visual angle) expressing the six

basic emotions (happiness, sadness, surprise, fear, disgust, and anger). Stimuli were displayed on a 19" screen and were viewed from a distance of 57 cm. Participants were presented with pairs of emotional faces (presented sequentially and belonging to two different individuals of different gender) and had to indicate whether the two faces expressed the same emotion (two-alternative forced choice task) (see Figure 1A). Each trial began with a fixation cross appearing in the center of the screen (2500 ms), followed by the presentation of the first face (500 ms), a blank screen (1000 ms), and the probe face (500 ms). This was followed by a blank screen until participants responded. In half of the trials, the two faces had the same emotional expression; in the other half, the two faces expressed different emotions. In each experimental block, the six emotional expressions appeared the same number of times. Participants were instructed to respond as quickly as possible by pressing the left or right arrow key with their right hand (response key assignment was counterbalanced across participants). The experimental blocks were preceded by a short practice block (10 trials) without TMS. The software E-prime 2.0 (Psychology Software Tools, Pittsburgh, PA) was used for stimulus presentation, data collection, and TMS delivery. Each session lasted on average 1 hour and 30 min (including instructions, completion of the TMS questionnaire and informed consent, neuronavigation to identify the target regions, and debriefing). Note that although we did not employ a control task, prior studies have already demonstrated that TMS over the posterior left paravermal cerebellum and the right pSTS selectively affected discrimination of emotional faces, and not processing of non-emotional face features (e.g., gender and identity[1, 31]).

TMS

In all the three experiments, TMS was applied using a Magstim Rapid^2 stimulator (Magstim Co, Ltd, Whitland, UK) connected to a 70-mm butterfly coil.

Recording of the individual motor threshold: Prior to each experiment, single-pulse TMS was applied over the left motor cortex (M1) at increasing intensities to determine each participant's resting motor threshold (rMT). Individual rMT was defined as the minimum intensity of the stimulator output that produced motor-evoked potentials (the motor response measured by electrodes placed on the hand muscles) with an amplitude of at least 50 mV in the first dorsal interosseous with a 50% probability[65] (see also Hanajima et al[66] for methodological details of this standard procedure).

Localization of targeted sites: To localize the cerebellar and pSTS targets for each individual we used a stereotaxic navigation system and the magnetic resonance images (MRIs) obtained by a 3D warping procedure that fitted a high-resolution MRI template with the participant's scalp model and craniometric points (Softaxic 3.0, EMS, obtained using individual estimated MRI scans[67]). Anatomical Talairach coordinates[68] of the targeted posterior left paravermal cerebellum (x=-15, y=-

82, z=-32) were taken from a previous neuroimaging study of facial emotional processing[69] and correspond to the left medial sector of lobule VI/VII (see Figure 1C). In previous studies, we demonstrated that targeting this region with TMS significantly impairs facial emotional processing[1, 18, 54]. Talairach coordinates for the right pSTS (x=52, y=- 48, z=8) were taken from a previous fMRI study that reported stronger activation of the right pSTS when individuals viewed emotional faces compared to neutral faces[70] (see also Ferrari et al[71] for a TMS study using the same coordinates). The early visual cortex (V1/V2) was functionally localized in each participant using visual phosphenes[72]. Specifically, the coil was initially positioned 2 cm above the inion and its position was subsequently adjusted until foveal phosphenes were induced. Phosphenes were searched for each participant after dark adaptation using a modified binary search algorithm that defines the phosphenes threshold (PT)[73-74]. The mean PT was 65.26% (SD = 13.65). For participants who could not perceive phosphenes (N = 6), the early visual cortex was localized as the point lying 1.5 cm superior to the inion on the midline connecting the inion to the nasion (e.g., Cattaneo et al[75]) and further confirmed by neuronavigation. V1/V2 was also targeted to rule out the possibility that cerebellar TMS effects may depend on spread of activation to nearby early visual cortex[30]. The vertex was localized as the point halfway between the nasion and the inion on the same midline.

During stimulation, for cerebellar and V1/V2 stimulation, the coil was placed tangential to the scalp and held parallel to the midsagittal line with the handle pointing superiorly, consistent with evidence that this is an effective coil orientation for modulating activity in cerebellar and visual structures[76-77]. For the pSTS stimulation, the coil was held parallel to the midsagittal line. For the vertex stimulation, the coil was placed tangentially to the scalp and held parallel to the midsagittal line with the handle pointing backwards.

No participant reported any discomfort or adverse effects during TMS, nor perception of phosphenes.

Experiment 1. Participants performed three blocks of the emotion discrimination task, one for each TMS site (the left paravermal cerebellum, V1/V2, and the vertex), in a counterbalanced order. Each block consisted of 72 trials (18 for each TMS interval). We delivered triple-pulse 20 Hz TMS (i.e., one pulse every 50 ms, for a total duration of 100 ms) at four different latencies after the onset of the second probe face: 20 ms, 120 ms, 220 ms, and 320 ms. These timings were meant to cover approximately the first 500 ms of emotional face processing, since previous studies observed brain responses to emotional faces up to 500 ms from face onset[78-79]. The first pulse was given 20 ms after onset as in Pitcher[31]. Stimulation intensity was set for all stimulation sites at 100% of participants' rMT, as in previous TMS studies[80]. Note that recent meta-analytic evidence indicates

that rMT and phosphene threshold (PT) are correlated and that both indexes may be used as global measures of cortical excitability[81]; with the PT being though usually higher than the rMT. The average stimulation intensity was 49.80% of the maximum stimulator output (SD=2.58). .

Experiment 2. As in Experiment 1, participants performed three blocks of the emotion discrimination task, one for each TMS site (the left paravermal cerebellum, the pSTS, and the vertex), in a counterbalanced order. We focused on the relevant time-window identified in Experiment 1, and we delivered double-pule TMS at narrower timings as in prior TMS work[25, 31]. Specifically, we delivered double-pulse TMS (with 40 ms between pulses, resulting into a TMS frequency of 25 Hz) over the left paravermal cerebellum, the vertex, and pSTS at three different latencies after the onset of the second probe face: 100 ms, 130 ms, and 170 ms. The stimulation intensity was set at 100% of rMT (mean rMT was 49.30%, SD = 2.95) and it was kept constant for the stimulation of all the target sites.

Experiment 3. Participants completed two experimental sessions on separate days (session duration was kept constant for each participant; mean interval between sessions = 8 days; minimum interval = 5 days). Participant's rMT was determined at the beginning of each session. Mean rMT was 49.6% (SD = 2.9) and 49.5% (SD = 2.6) for the first and second sessions, respectively. A paired-sample t-test revealed no difference in rMT between the two sessions ($t(35)<1$, $p=.52$). Participants were administered 15 minutes of conditioning (offline) 1 Hz TMS over the posterior left paravermal cerebellum or the vertex (control conditioning condition) and then performed two blocks of the emotion discrimination task while receiving online TMS over the right pSTS or the vertex (control perturbation condition) (see Figure 1B). Specifically, the conditioning rTMS consisted of 900 pulses at 1 Hz delivered offline (i.e., before the task) at 100% of participants' rMT. 1 Hz rTMS is thought to reduce the neural excitability of the targeted region and to subsequently disrupt its associated functions for at least half of the stimulation duration[72]. Following conditioning TMS, participants performed two blocks of the emotion discrimination task (each composed of 40 trials), one for each TMS site (pSTS and vertex). During the task, at the onset of the probe face, participants received trains of five 10 Hz TMS pulses (i.e., one pulse every 100 ms, for a total duration of 500 ms) at 120% of rMT. These stimulation parameters were chosen to maximize the disruptive effect of TMS, consistent with previous studies targeting pSTS[31, 37, 82]. Each block lasted approximately 3.5 min ensuring that the task was performed within a time window in which offline TMS is effective[83-84]. The order of stimulation sites for both conditioning and perturbing TMS was counterbalanced across subjects.

QUANTIFICATION AND STATISTICAL ANALYSIS

Sample size calculation. Sample size of Experiments 1 and 2 was calculated using an a priori power analysis (conducted using G-Power 3.1 software[85]) indicating that a sample size of at least 18 subjects was required to achieve 80% of power at a significance threshold alpha of 0.05, with an expected large effect size (f(U) = 0.33, η_p^2=0.10) based on our previous data[25]. For Experiment 3, the a priori power analysis indicated that 38 individuals were necessary to achieve 80% of power at a significance threshold alpha of 0.05, with an expected large effect size of f(U) = 0.48 (η_p^2 = 0.19) based on previous data[37].

Statistical analyses. Mean accuracy rates and mean correct reaction times (RTs, recorded from the *onset* of the probe face) were computed for each participant in each experimental condition and were analyzed separately. A significance threshold of p=0.05 is set for all analyses; Bonferroni-Holm correction for multiple comparisons is reported. In Experiment 1, accuracy scores and RTs were analyzed using a repeated measures ANOVA, with TMS site (vertex, V1/V2, left paravermal cerebellum) and TMS timing (20, 120, 220, 320ms from the onset of the probe face) as within-subjects variables. The same dependent variables were analyzed using repeated measures ANOVAs, with TMS site (vertex, left paravermal cerebellum, pSTS) and TMS timing (100, 130, 170 ms from the onset of the probe face) as within-subject variables in Experiment 2. In Experiment 3, repeated measures ANOVAs were conducted with conditioning TMS (left paravermal cerebellum and vertex) and perturbing TMS (pSTS and vertex) as within-subject variables.

References

1. Ferrari, C., Oldrati, V., Gallucci, M., Vecchi, T., and Cattaneo, Z. (2018). The role of the cerebellum in explicit and incidental processing of facial emotional expressions: a study with transcranial magnetic stimulation. NeuroImage. 169, 256-264.
2. Ferrari, C., Ciricugno, A., Urgesi, C., and Cattaneo, Z. (2022). Cerebellar contribution to emotional body language perception: a TMS study. SCAN. 17(1), 81-90.
3. Ferrucci, R., Giannicola, G., Rosa, M., Fumagalli, M., Boggio, P. S., Hallett, M., Zago, S. and Priori, A. (2012). Cerebellum and processing of negative facial emotions: cerebellar transcranial DC stimulation specifically enhances the emotional recognition of facial anger and sadness. Cognition Emotion. 26(5), 786-799.
4. Metoki, A., Wang, Y., and Olson, I. R. (2022). The social cerebellum: a large-scale investigation of functional and structural specificity and connectivity. Cereb. Cortex. 32(5), 987-1003.
5. Clausi, S., Lupo, M., Funghi, G., Mammone, A., and Leggio, M. (2022). Modulating mental state recognition by anodal tDCS over the cerebellum. Sci Rep. 12(1), 22616.
6. Heleven, E., Van Dun, K., De Witte, S., Baeken, C., and Van Overwalle, F. (2021). The role of the cerebellum in social and non-social action sequences: a preliminary LF-rTMS study. Front Hum Neurosci. 15, 593821.
7. Ferrari, C., Ciricugno, A., Battelli, L., Grossman, E. D., & Cattaneo, Z. (2022). Distinct cerebellar regions for body motion discrimination. SCAN. 17(1), 72-80.
8. Sokolov, A. A., Erb, M., Gharabaghi, A., Grodd, W., Tatagiba, M. S., and Pavlova, M. A. (2012). Biological motion processing: the left cerebellum communicates with the right superior temporal sulcus. Neuroimage. 59(3), 2824-2830.
9. Sokolov, A. A., Erb, M., Grodd, W., and Pavlova, M. A. (2014). Structural loop between the cerebellum and the superior temporal sulcus: evidence from diffusion tensor imaging. Cereb Cortex. 24(3), 626-632.
10. Oldrati, V., Ferrari, E., Butti, N., Cattaneo, Z., Borgatti, R., Urgesi, C., and Finisguerra, A. (2021). How social is the cerebellum? Exploring the effects of cerebellar transcranial direct current stimulation on the prediction of social and physical events. Brain Struct Funct. 226(3), 671-684.
11. Oldrati, V., Butti, N., Ferrari, E., Cattaneo, Z., Urgesi, c. and Finisguerra, A. (2024). Excitatory cerebellar transcranial direct current stimulation boost the leverage of prior knowledge for predicting action. SCAN. 19(1), nsae019
12. Gamond, L., Ferrari, C., La Rocca, S., and Cattaneo, Z. (2017). Dorsomedial prefrontal cortex and cerebellar contribution to in-group attitudes: a transcranial magnetic stimulation study. Eur J Neurosci. 45(7), 932-939.
13. Ciricugno, A., Oldrati, V., Cattaneo, Z., Leggio, M., Urgesi, C., and Olivito, G. (2024). Cerebellar Neurostimulation for Boosting Social and Affective Functions: Implications for the Rehabilitation of Hereditary Ataxia Patients. Cerebellum. 1-27.
14. Pezzetta, R., Gambarota, F., Tarantino, V., Devita, M., Cattaneo, Z., Arcara, G., Mapelli, D. and Masina, F. (2023). A meta-analysis of non-invasive brain stimulation (NIBS) effects on cerebellar-associated cognitive processes. Neurosci Biobehav R, 105509.
15. Van Overwalle, F., Manto, M., Cattaneo, Z., Clausi, S., Ferrari, C., Gabrieli, J. D., Guell, X., Heleven, E., Lupo, M., Ma, Q. et al. (2020). Consensus paper: cerebellum and social cognition. Cerebellum. 19, 833-868.
16. Guell, X. (2022). Functional gradients of the cerebellum: a review of practical applications. Cerebellum. 21(6), 1061-1072.
17. Guell, X., Schmahmann, J. D., Gabrieli, J. D., and Ghosh, S. S. (2018). Functional gradients of the cerebellum. Elife. 7, e36652.
18. Ferrari, C., Ciricugno, A., Arioli, M., and Cattaneo, Z. (2023). Functional segregation of the human cerebellum in social cognitive tasks revealed by TMS. J Neurosci. 43(20), 3708-3717.
19. Andersen, L. M., Jerbi, K., and Dalal, S. S. (2020). Can EEG and MEG detect signals from the human cerebellum?. NeuroImage. 215, 116817.

20. Ito, M. (2008). Control of mental activities by internal models in the cerebellum. Nat Rev Neurosci. 9(4), 304-313.
21. Hull, C. (2020). Prediction signals in the cerebellum: beyond supervised motor learning. Elife. 9, e54073.
22. Leggio, M., and Molinari, M. (2015). Cerebellar sequencing: a trick for predicting the future. Cerebellum. 14, 35-38.
23. Van Overwalle, F., Manto, M., Leggio, M., and Delgado-García, J. M. (2019). The sequencing process generated by the cerebellum crucially contributes to social interactions. Med Hypotheses. 128, 33-42.
24. Sliwinska, M. W., Vitello, S., and Devlin, J. T. (2014). Transcranial magnetic stimulation for investigating causal brain-behavioral relationships and their time course. JoVE. 89, e51735.
25. Cattaneo, Z., Bona, S., Ciricugno, A., and Silvanto, J. (2022). The chronometry of symmetry detection in the lateral occipital (LO) cortex. Neuropsychologia. 167, 108160.
26. Van Overwalle, F., Van de Steen, F., and Mariën, P. (2019). Dynamic causal modeling of the effective connectivity between the cerebrum and cerebellum in social mentalizing across five studies. Cogn Affect Behav Ne. 19, 211-223.
27. Silvanto, J., Muggleton, N., and Walsh, V. (2008). State-dependency in brain stimulation studies of perception and cognition. Trends Cogn Sci. 12(12), 447-454.
28. Thielscher, A., Antunes, A., and Saturnino, G. B. (2015). Field modeling for transcranial magnetic stimulation: a useful tool to understand the physiological effects of TMS?. Annu Int Conf IEEE Eng Med Biol Soc. 222-225.
29. Weise, K., Numssen, O., Thielscher, A., Hartwigsen, G., and Knösche, T. R. (2020). A novel approach to localize cortical TMS effects. Neuroimage. 209, 116486.
30. Renzi, C., Vecchi, T., D'Angelo, E., Silvanto, J., and Cattaneo, Z. (2014). Phosphene induction by cerebellar transcranial magnetic stimulation. Clin Neurophysiol. 125(10), 2132-2133.
31. Pitcher, D. (2014). Facial expression recognition takes longer in the posterior superior temporal sulcus than in the occipital face area. J Neurosci. 34(27), 9173-9177.
32. Numssen, O., van der Burght, C. L., and Hartwigsen, G. (2023). Revisiting the focality of non-invasive brain stimulation-implications for studies of human cognition. Neurosci Biobehav R. 105154.
33. de Graaf, T. A., Koivisto, M., Jacobs, C., and Sack, A. T. (2014). The chronometry of visual perception: review of occipital TMS masking studies. Neurosci Biobehav R. 45, 295-304.
34. Seitz, R. J., Schäfer, R., Scherfeld, D., Friederichs, S., Popp, K., Wittsack, H. J., Azari, N.P. and Franz, M. (2008). Valuating other people's emotional face expression: a combined functional magnetic resonance imaging and electroencephalography study. Neuroscience. 152(3), 713-722.
35. Streit, M., Dammers, J., Simsek-Kraues, S., Brinkmeyer, J., Wölwer, W., and Ioannides, A. (2003). Time course of regional brain activations during facial emotion recognition in humans. Neurosci Lett. 342(1-2), 101-104.
36. Habas, C., Guillevin, R., and Abanou, A. (2011). Functional connectivity of the superior human temporal sulcus in the brain resting state at 3T. Neuroradiology. 53, 129-140.
37. Sliwinska, M. W., Elson, R., and Pitcher, D. (2020). Dual-site TMS demonstrates causal functional connectivity between the left and right posterior temporal sulci during facial expression recognition. Brain Stimul. 13(4), 1008-1013.
38. Silvanto, J., Bona, S., and Cattaneo, Z. (2017). Initial activation state, stimulation intensity and timing of stimulation interact in producing behavioral effects of TMS. Neuroscience. 363, 134-141.
39. Silvanto, J., Bona, S., Marelli, M., and Cattaneo, Z. (2018). On the mechanisms of transcranial magnetic stimulation (TMS): how brain state and baseline performance level determine behavioral effects of TMS. Front Psychol. 9, 741.
40. Silvanto, J., Cattaneo, Z., Battelli, L., and Pascual-Leone, A. (2008). Baseline cortical excitability determines whether TMS disrupts or facilitates behavior. J Neurophysiol. 99(5), 2725-2730.
41. Ethofer, T., Bretscher, J., Wiethoff, S., Bisch, J., Schlipf, S., Wildgruber, D., and Kreifelts, B. (2013). Functional responses and structural connections of cortical areas for processing faces and voices in the superior temporal sulcus. Neuroimage. 76, 45-56.

42. Borgomaneri, S., Zanon, M., Di Luzio, P., Cataneo, A., Arcara, G., Romei, V., Tamietto, M. and Avenanti, A. (2023). Increasing associative plasticity in temporo-occipital back-projections improves visual perception of emotions. Nat Commun. 14(1), 5720.
43. Pitcher, D., and Ungerleider, L. G. (2021). Evidence for a third visual pathway specialized for social perception. Trends Cogn Sci. 25(2), 100-110.
44. Walbrin, J., Downing, P., and Koldewyn, K. (2018). Neural responses to visually observed social interactions. Neuropsychologia. 112, 31-39.
45. Patel, G. H., Sestieri, C., and Corbetta, M. (2019). The evolution of the temporoparietal junction and posterior superior temporal sulcus. Cortex. 118, 38-50.
46. Santavirta, S., Karjalainen, T., Nazari-Farsani, S., Hudson, M., Putkinen, V., Seppälä, K., Sun, L., Glerean, E., Hirvonen, J., Karlsson, H.K. et al. (2023). Functional organization of social perception networks in the human brain. NeuroImage. 272, 120025.
47. Zhu, X., Woo, S. E., Porter, C., and Brzezinski, M. (2013). Pathways to happiness: From personality to social networks and perceived support. Soc Networks. 35(3), 382-393.
48. Sokolov, A. A., Miall, R. C., and Ivry, R. B. (2017). The cerebellum: adaptive prediction for movement and cognition. Trends Cogn Sci. 21(5), 313-332.
49. Ma, Q., Pu, M., Haihambo, N. P., Baetens, K., Heleven, E., Deroost, N., Baeken, C., and Van Overwalle, F. (2022). The posterior cerebellum and temporoparietal junction support explicit learning of social belief sequences. Cogn Affect Behav Neurosci. 1-25.
50. Van Overwalle, F., Ma, Q., and Heleven, E. (2020). The posterior crus II cerebellum is specialized for social mentalizing and emotional self-experiences: a meta-analysis. SCAN. 15(9), 905-928.
51. Palesi, F., Lorenzi, R. M., Casellato, C., Ritter, P., Jirsa, V., Gandini Wheeler-Kingshott, C. A., and D'angelo, E. (2020). The importance of cerebellar connectivity on simulated brain dynamics. Front Cell Neurosci. 14, 240.
52. Rastogi, A., Cash, R., Dunlop, K., Vesia, M., Kucyi, A., Ghahremani, A., Downar, J., Chen, J., Chen, R. (2017). Modulation of cognitive cerebello-cerebral functional connectivity by lateral cerebellar continuous theta burst stimulation. Neuroimage. 158, 48-57.
53. Fernandez, L., Major, B.P., Teo, W.P., Byrne, L.K., and Enticott, P.G. (2018). The impact of stimulation intensity and coil type on reliability and tolerability of cerebellar brain inhibition (CBI) via dual-coil TMS. Cerebellum. 17(5), 540–9.
54. Ferrari, C., Fiori, F., Suchan, B., Plow, E. B., and Cattaneo, Z. (2021). TMS over the posterior cerebellum modulates motor cortical excitability in response to facial emotional expressions. Eur J Neurosci. 53(4), 1029-1039.
55. Cho, S.S., Yoon, E.J., Bang, S.A., Park, H.S., Kim, Y.K., Strafella, A.P., and Kim, s.E. (2012). Metabolic changes of cerebrum by repetitive transcranial magnetic stimulation over lateral cerebellum: a study with FDG PET. Cerebellum. 11(3), 739–48.
56. Romei, V., Chiappini, E., Hibbard, P. B., and Avenanti, A. (2016). Empowering reentrant projections from V5 to V1 boosts sensitivity to motion. Curr Biol. 26(16), 2155-2160.
57. Sato, W., Kochiyama, T., Uono, S., Sawada, R., Kubota, Y., Yoshimura, S., and Toichi, M. (2019). Widespread and lateralized social brain activity for processing dynamic facial expressions. Hum Brain Mapp. 40(13), 3753-3768.
58. Rice, L. C., D'Mello, A. M., and Stoodley, C. J. (2021). Differential behavioral and neural effects of regional cerebellar tDCS. Neuroscience. 462, 288-302.
59. Yuan, Q., Li, H., Du, B., Dang, Q., Chang, Q., Zhang, Z., Zhang, M., Ding, G., Lu, C. and Guo, T. (2023). The cerebellum and cognition: further evidence for its role in language control. Cereb Cortex. 33(1), 35-49.
60. Bongaerts, F. L., Schutter, D. J., and Klaus, J. (2022). Cerebellar tDCS does not modulate language processing performance in healthy individuals. Neuropsychologia. 169, 108206.
61. Klaus, J., and Schutter, D. J. (2021). Functional topography of anger and aggression in the human cerebellum. NeuroImage. 226, 117582
62. Pierce, J. E., Thomasson, M., Voruz, P., Selosse, G., and Péron, J. (2023). Explicit and implicit emotion processing in the cerebellum: a meta-analysis and systematic review. Cerebellum. 22(5), 852-864.

63. Rossi, S., Hallett, M., Rossini, P.M., and Pascual-Leone, A. (2011). Screening questionnaire before TMS: an update. Clin Neurophysiol. 122, 1686–6.
64. Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., Marcus, D.J., Westerlund, A., Casey, B.J. and Nelson, C. (2009). The NimStim set of facial expressions: Judgments from untrained research participants. Psychiatry Res. 168(3), 242-249.
65. Rossini, P.M., Barker, A.T., Berardelli, A., Caramia, M.D., Caruso, G., Cracco, R.Q., Dimitrijević, M.R., Hallett, M., Katayama, Y., Lücking C.H. et al. (1994). Non-invasive electrical and magnetic stimulation of the brain, spinal cord and roots: basic principles and procedures for routine clinical application. Report of an IFCN committee. Electroencephalogr Clin Neurophysiol. 91(2), 79–92.
66. Hanajima, R., Wang, R., Nakatani-Enomoto, S., Hamada, M., Terao, Y., Furubayashi, T., Okabe, S., Inomata-Terada, S., Yugeda, A., Rothwell, J.C., et al. (2007). Comparison of different methods for estimating motor threshold with transcranial magnetic stimulation. Clin Neurophysiol. 118, 2120–2.
67. Carducci, F., and Brusco, R. (2012). Accuracy of an individualized MR-based head model for navigated brain stimulation. Psychiat Res-Neuroim. 203(1), 105–8.
68. Talairach, J., and Tournoux, P. (1998). Co-planar Stereotaxic Atlas of the Human Brain, New York: Thieme Medical.
69. Schraa-Tam, C. K., Rietdijk, W. J., Verbeke, W. J., Dietvorst, R. C., van den Berg, W. E., Bagozzi, R. P., and De Zeeuw, C. I. (2012). fMRI activities in the emotional cerebellum: a preference for negative stimuli and goal-directed behavior. Cerebellum. 11, 233-245.
70. Engell, A. D., and Haxby, J. V. (2007). Facial expression and gaze-direction in human superior temporal sulcus. Neuropsychologia., *45*(14), 3234-3241.
71. Ferrari, C., Schiavi, S., and Cattaneo, Z. (2018b). TMS over the superior temporal sulcus affects expressivity evaluation of portraits. Cogn Affect Behav Ne. *18*, 1188-1197.
72. Walsh, V., and Pascual-Leone, A. (2003). Transcranial magnetic stimulation: a neurochronometrics of mind. MIT press.
73. Tyrrell, R. A., and Owens, D. A. (1988). A rapid technique to assess the resting states of the eyes and other threshold phenomena: the modified binary search (MOBS). Behav Res Meth Ins C, *20*(2), 137-141.
74. Thilo, K. V., Santoro, L., Walsh, V., & Blakemore, C. (2004). The site of saccadic suppression. Nat Neurosci, 7(1), 13-14.
75. Cattaneo, Z., Renzi, C., Casali, S., Silvanto, J., Vecchi, T., Papagno, C., D'Angelo, E. (2014). Cerebellar vermis plays a causal role in visual motion discrimination. Cortex. *58*, 272–80.
76. Bijsterbosch, J.D., Barker, A.T., Lee, K.H., and Woodruff, P.W. (2012). Where does transcranial magnetic stimulation (TMS) stimulate? Modelling of induced field maps for some common cortical and cerebellar targets. Med Biol Eng Comput, *50*(7), 671–81.
77. van Dun, K., Bodranghien, F., Manto, M., and Mariën, P. (2017). Targeting the cerebellum by noninvasive neurostimulation: a review. Cerebellum. *16*(3), 695–741.
78. Dima, D. C., Perry, G., Messaritaki, E., Zhang, J., and Singh, K. D. (2018). Spatiotemporal dynamics in human visual cortex rapidly encode the emotional content of faces. Hum Brain Map, 39(10), 3993-4006.
79. Sabbagh, M. A., Moulson, M. C., and Harkness, K. L. (2004). Neural correlates of mental state decoding in human adults: An event-related potential study. J Cog Neurosci. 16(3), 415-426.
80. Demirtas-Tatlidede, A., Freitas, C., Pascual-Leone, A., and Schmahmann, J.D. (2011). Modulatory effects of theta burst stimulation on cerebellar nonsomatic functions. Cerebellum. 10(3), 495–503.
81. Phylactou, P., Pham, T., Nasrkhani, N., Diya, N., Seminowicz, D. A., and Schabrun, S. M. (2023). Phosphene and Motor Transcranial Magnetic Stimulation Thresholds Are Correlated: A Meta-Analytic Investigation. bioRxiv, 2023-12.
82. Sliwinska, M. W., and Pitcher, D. (2018). TMS demonstrates that both right and left superior temporal sulci are important for facial expression recognition. NeuroImage. *183*, 394-400.
83. Battelli, L., Grossman, E. D., and Plow, E. B. (2017). Local immediate versus long-range delayed changes in functional connectivity following rTMS on the visual attention network. Brain stimulation, 10(2), 263-269.

84. Plow, E. B., Cattaneo, Z., Carlson, T. A., Alvarez, G. A., Pascual-Leone, A., & Battelli, L. (2014). The compensatory dynamic of inter-hemispheric interactions in visuospatial attention revealed using rTMS and fMRI. Front Hum Neurosci. 8, 226.
85. Faul, F., Erdfelder, E., Lang, A.-G., and Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. Behav Res Methods. 39, 175-191