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REVIEW

New Horizons on Non-invasive Brain Stimulation of the Social and Affective Cerebellum

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Abstract

The cerebellum is increasingly attracting scientists interested in basic and clinical research of neuromodulation. Here, we review available studies that used either transcranial magnetic stimulation (TMS) or transcranial direct current stimulation (tDCS) to examine the role of the posterior cerebellum in different aspects of social and affective cognition, from mood regulation to emotion discrimination, and from the ability to identify biological motion to higher-level social inferences (mentalizing). We discuss how at the functional level the role of the posterior cerebellum in these different processes may be explained by a generic prediction mechanism and how the posterior cerebellum may exert this function within different cortico-cerebellar and cerebellar limbic networks involved in social cognition. Furthermore, we suggest to deepen our understanding of the cerebro-cerebellar circuits involved in different aspects of social cognition by employing promising stimulation approaches that have so far been primarily used to study cortical functions and networks, such as paired-pulse TMS, frequency-tuned stimulation, state-dependent protocols, and chronometric TMS. The ability to modulate cerebro-cerebellar connectivity opens up possible clinical applications for improving impairments in social and affective skills associated with cerebellar abnormalities.

Keywords Cerebellum · Social cognition · Emotion · TMS · tDCS · Brain stimulation

Introduction

With more than 60% neurons of the brain, a highly organized structure and a cerebellar cortex accessible just below the skull, it may look obvious that the cerebellum is attracting scientists interested by neuromodulation. The works of early anatomists such as Vicq d'Azyr, Franz Joseph Gall, and Johann Kaspar Spurzheim already pointed out the highly regular arrangement of the cerebellum [1]. The functional localization of the cerebellum has evolved from a simple medio-lateral delineation to a complex polysynaptic topography, with the majority of the human cerebellum being mapped to association areas [2]. The discovery of the implication of the cerebellum in multiple segregated loops involving cerebral cortex, basal ganglia, brainstem, and spinal cord and the parcellation of the cerebellar circuitry into lobules immediately calls the question of which functions can be tuned by application of electric currents or magnetic stimuli over the cerebellar cortex, and whether the cognitive operations might become a subject of interest for cerebellar neuromodulation. These issues are particularly of interest when considering deficits in social and affective cognition that may be associated to cerebellar dysfunction (see Schmahmann's syndrome [3]).

The discovery of Schmahmann's syndrome (cerebellar cognitive affective syndrome [3]) is strongly impacting on clinical ataxiology [4]. The symptoms of Schmahmann's

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syndrome can be grouped in four main clusters: (1) executive functioning such as planning, set-shifting, verbal fluency, abstract reasoning, and working memory, (2) visuo-spatial cognition including memory and organization; (3) affective behavior resulting in blunting of affect or in disinhibited, inappropriate behavior; and (4) language disturbances including agrammatism and dysprosodia. The description of this syndrome has paved the way for research into the cerebellar involvement in several different types of neuropsychiatric disorders lying at the border between neurological sciences and psychiatry, including patients exhibiting difficulties in social interactions. Since the first report of the Schmahmann's syndrome in neuropsychological patients with acquired cerebellar lesions, growing evidence supports the view that the cerebellum exerts a critical role in mediating social cognition and affective functions (as well as other high-order processes, including language), beyond its well-known role as motor controller (e.g., [5, 6]). This evidence is mainly based on patients' and neuroimaging studies in healthy individuals, and corroborated by connectivity analyses showing that the posterior cerebellum is functionally connected to canonical social networks in the cerebral cortex [7]. New animal research also points to the role of the cerebellum in reward learning and anticipation, in addition to sensory feedback on movement errors [8, 9]. Consequently, success or failure to get an anticipated reward is also signaled by the cerebellum, supporting a cerebellar role in motivated social behavior and affective responses.

A cerebellar involvement in social cognition and affective functions is also suggested by studies employing non-invasive brain stimulation techniques, such as transcranial magnetic stimulation (TMS) and transcranial direct current stimulation (tDCS). These techniques allow to transiently perturb ongoing neural activity in the targeted area as well transsynaptically targeting distal connected sites allowing to study more direct links between brain and behavior [10, 11].

In the last 5 years, a growing number of studies have employed non-invasive brain stimulation to study high-level cerebellar functions in healthy individuals either offline or online [12–22]. In the next paragraphs, we first provide a short overview of principle of functioning of TMS and tDCS. We then review available recent studies *in healthy individuals* that have used TMS and tDCS to investigate the role of the posterior cerebellum in mediating critical processes involved in social cognition, such as mood regulation, recognition of others' emotional states, the capacity to discriminate biological from non-biological motion, and higher-level mentalizing (see Fig. 1). We propose that these processes may be possibly ascribed to a generic mechanism that seems to be (at least partially) mediated by the posterior cerebellum, that is, prediction. In the concluding part, we consider future research directions, from chronometric-approaches to protocols to increase functional resolution of cerebellar TMS and to assess and modify functional cerebro-cerebellar connectivity, also discussing critical implications for rehabilitation of impaired affective/social functions in patients.

Basic Principles of TMS and tDCS

TMS operates on Faraday's principle of electromagnetic induction: a rapidly changing magnetic field is generated when a high-voltage current is passed through a coil. If the coil is placed near the head, the magnetic field enters the brain unattenuated and induces an electric current in the underlying region of the cerebral cortex. This electric field in turn causes a transmembrane potential and, if intensity is sufficient, induces neuronal depolarization and an action potential. The propagation of this action potential along nerve structures and neuronal networks constitutes the neuronal basis for TMS effects [11]. TMS represents a powerful tool for investigating causal brain-behavior relations that complements correlative techniques such as functional neuroimaging. Indeed, if stimulating a cortical region significantly affects task performance relative to appropriate control conditions, this indicates that the targeted area is necessary to perform the task normally. The effects of TMS have traditionally been interpreted in the "virtual lesion" framework, where TMS is described as inducing a temporary, reversible lesion in the targeted region, with impairment as its default outcome [28, 29]. In this sense, TMS is more like traditional lesion-deficit analyses in patients with brain damage except that it is non-invasive and the effects are temporary and reversible. TMS also has several advantages over lesion studies: the effects of stimulation are generally more spatially precise than real lesions, and participants can be used as their own controls, thereby avoiding the issue of potential differences in pre-morbid abilities between patients and controls. Moreover, TMS-induced changes are limited to short time periods so that more long-term, uncontrolled-for, plastic changes that are possible in lesion studies are not an issue (for reviews, see [10, 28, 30]). Furthermore, by varying the duration and onset of the virtual lesion, and thanks to its high temporal resolution (in the order of milliseconds), TMS can also reveal the time course of normal processing (chronometry, e.g., [31]). It is worth noting though that the view of TMS as a "lesion" technique does not hold in a wide range of circumstances in which TMS leads to enhancement of cognitive performance (for a review, [32]). Indeed, factors such as stimulation intensity, task difficulty, and cognitive state can fundamentally change the nature of behavioral TMS effects [33–35].

In contrast to TMS, tDCS does not directly induce cerebral activity, but rather alters spontaneous brain activity and excitability by subthreshold modulation of the neural

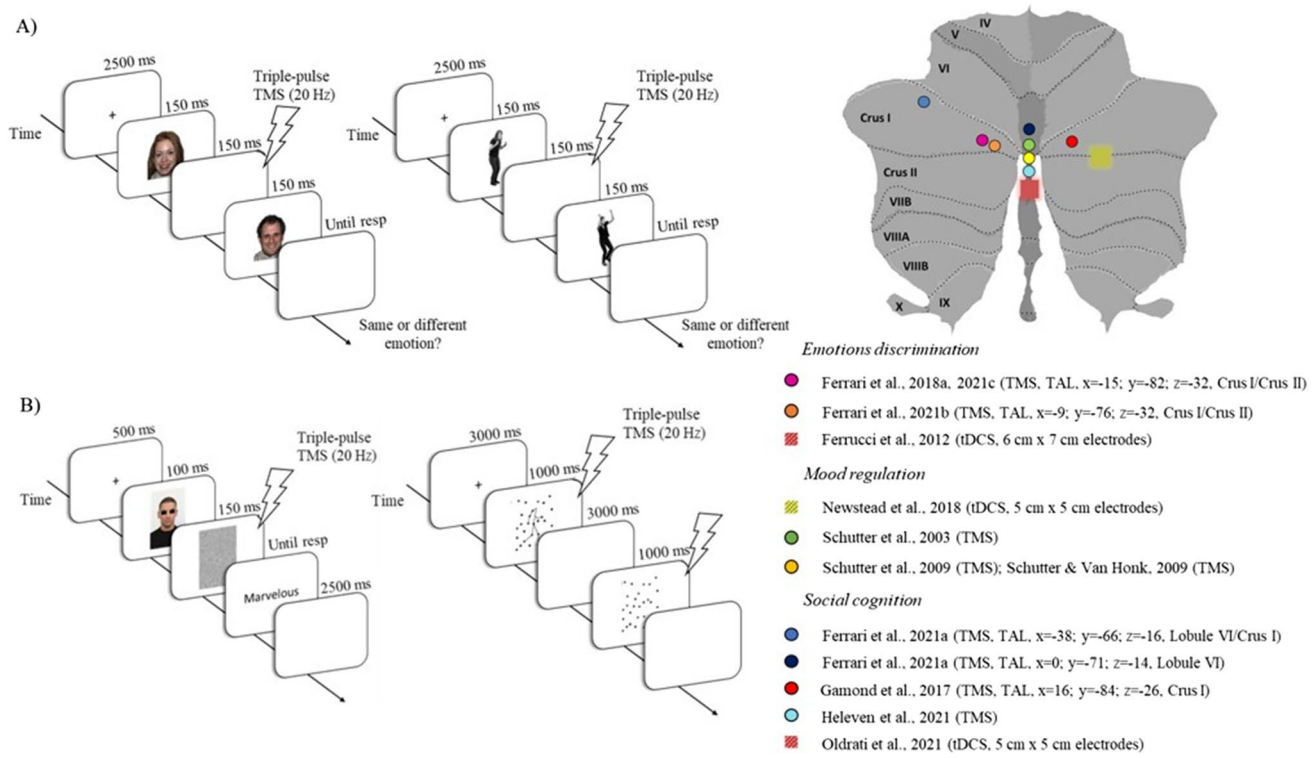

Fig. 1 Left panel: Examples of experimental paradigms (timeline of an experimental trial) used to investigate the role of the posterior cerebellum in (**A**) discrimination of facial and bodily emotional expressions [13, 15], and (**B**) other processes of social cognition, such as social stereotyping [23], left panel) and biological motion discrimination [14], right panel). Right panel: Schematic representation indicating the relative location of different cerebellar sectors targeted using non-invasive brain stimulation to assess social and affective functions in the studies reviewed here. When specific coordinates are not indicated, localization in the original study was based on craniometric points (i.e., distance from inion). For studies using neuronavigation, Talairach coordinates are reported and the corresponding sectors of the cerebellum according to Schmahmann's atlas [24] are indicated. For tDCS studies, the depicted locations correspond to the center of the active electrode,however, due to the size of the electrode (≥ 25 cm^2), the induced electric field is not as focal as represented here for graphical purposes. Note that Ferrari et al. [14–17] and Gamond et al. [23] used a 70-mm figure-of-eight coil Schutter et al. [25, 26] and Schutter and Van Honk [27] used an iron core coil, Heleven et al. [19] used a double cone coil

resting state potential [36]. Currently, tDCS devices apply a weak direct electrical current (0.5–2 mA) through two or more electrodes placed on the scalp, typically for a relatively long period of time (e.g., 20 min). Depending on the electrodes' polarity, the stimulation facilitates (anodal tDCS) or inhibits (cathodal tDCS) spontaneous neuronal activity putatively resulting in cortical excitability modulation and neuroplastic reorganization [36]. As for TMS, behavioral effects of tDCS depend on stimulation parameters and are not always consistent across studies (e.g., [37]). Traditionally, cathodal tDCS has been employed as a modality to create temporary cortical dysfunctions ("virtual lesions"). In turn, anodal tDCS has been used to examine whether the performance of a particular task that is linked to the stimulated brain region can be enhanced temporarily [36]. However, consistent evidence suggests that the physiological and behavioral effects of tDCS are nonlinear with regard to stimulation intensity or duration, critically depending on a complex interaction between stimulation parameters and endogenous neural activity at tDCS-delivery (e.g., [38]). Moreover, since the cerebellum has an entirely different cytoarchitecture than the neocortex, generalizations of the findings obtained in the studies based upon cerebral tDCS are hard to make [39]. Indeed, the cerebellar cell morphology and the complex cerebellar folding might have a great impact on the polarity-dependent excitability changes and on the effectiveness of the stimulation [40]. In line with this, a recent meta-analysis of studies employing cerebellar tDCS to modulate motor and non-motor cerebellar functions did not find the expected polarity-dependent effects of tDCS [41], calling for further research to clarify directionality of cerebellar tDCS effects.

Both TMS and tDCS may be applied either concurrently with the task (*online* protocols) or before (*offline* protocols) task performance. In online TMS protocols, either single pulses or short trains of pulses (typically delivered at 10 or 20 Hz) are delivered while subjects are engaged in a task (for review, [42]). In offline TMS paradigms,

task performance is assessed before and after repetitive TMS (rTMS), during which series of pulse trains are applied over a period typically lasting 10 to 20 min. The cumulative effect of rTMS is a temporary modulation of cortical excitability in the stimulated area and its associated circuits, which affects post-rTMS task performance as compared to that at pre-rTMS baseline [42]. rTMS-induced effects are frequency-dependent. Typically, low frequencies (≤ 1 Hz) are associated with decreased cortical excitability, while higher frequencies (≥ 5 Hz) generally lead to increased cortical excitability. Similarly, tDCS has been administered either online or offline (see [43]). As for TMS, 10 min or more of tDCS can lead to inhibitory (cathodal) or excitatory (anodal) effects on the cortex that outlast the period of stimulation by many minutes or hours (depending on stimulation parameters), with more robust behavioral effects being detectable immediately after the end of the stimulation (for reviews, [44]).

Critically, for both TMS and tDCS, the distribution of the electric field in the brain tissue needs to be carefully considered (for an in-depth discussion, see [45, 46]). The estimation of the current flow and the distribution of the electric field, which are primary determinants of the stimulation effects on the activity of the targeted region, depend not only on the position and geometry of the TMS coil [47, 48] or the placement and design of tDCS electrodes [49, 50], but also on the individual's anatomical features [51]. If this issue is relevant when targeting all cerebral regions, it is even more important for cerebellar stimulation, considering the convoluted structure of the cerebellar cortex. To improve effectiveness of the stimulation, several computational modellings of the electric field distribution of TMS and tDCS have been recently developed, some of these also including the cerebellum [51–54].

Finally, it is worth noting that whereas TMS and tDCS are capable of promoting functional recovery in treating neurological/neuropsychiatric conditions, none of these techniques can stimulate deep subcortical structures without influencing surrounding or intervening neural tissue. Recently, low-intensity focused ultrasound (LIFU)–mediated neuromodulation has been introduced as an alternative because of its bimodal capability (i.e., excitation and inhibition) and superior spatial resolution and penetrability (for a review, see [55]). Although we are not aware of any study using this technique to stimulate the human cerebellum, available animal evidence suggests that ultrasound stimulation may be successfully employed to entrain cerebellar Purkinje cell spiking activity [56] and that LIFU-induced cerebellar modulation could be an important strategy for poststroke recovery [57–59].

TMS and tDCS Studies Investigating the Role of the Posterior Cerebellum in Social Cognition

In order to understand and collaborate with others, human beings often attempt to infer the minds of others to anticipate future interactions with them. This dynamic ability to "read" others' mental states such as desires, intentions, and beliefs is termed social mentalizing [60–62]. In past research, neuroscientists focused primarily on the cerebral cortex, and in particular, the *mentalizing network* (see meta-analyses by [61–63]). This focus has only recently been extended to the cerebellum. A meta-analysis by Van Overwalle et al. [64] which included over 350 functional magnetic resonance imaging (fMRI) studies involving a large variety of social tasks revealed significant activation of the cerebellum in social mentalizing in over one-third of the studies included. Further studies on healthy participants, clinical patients, and animals identified the posterior cerebellar Crus II as a key area within this cerebellar mentalizing network [65–67]. Most recently, another meta-analyses identified the cerebellar Crus II as functionally specialized in social mentalizing and emotional self-experiences [67]. Further support comes from fMRI studies demonstrating that there was a distinct functional connectivity between the posterior cerebellar Crus II and cortical mentalizing areas during mentalizing tasks involving others' beliefs and traits [68, 69].

However, what is the function of the cerebellum in social cognition? The basic hypothesis in social mentalizing is that the cerebellum supports explicit or implicit learning of frequently executed sequences of actions and mental states [70–72]. It so contributes to identify and *predict* sequences of a person's actions which are only fully understood by inferring the underlying mental states of self or others, such as intentions and beliefs [6, 73]. More in general, the cerebellum would play a critical role in context-based prediction, where the available context (such as a particular place/situation, objects available in the scene) activates stored mental models of what can be expected in similar contexts [74] allowing to predict others' actions, emotions, or mental states and to control ongoing inter-actions necessary for successful social functions. This hypothesis originates from the well-known function of the cerebellum as a "predictive machine" in the sensorimotor domain [75, 76] and it is extended to different levels of social processing, such as understanding others' actions/intentions and emotions but also more abstract social inferential operations.

Processing of Actions' Sequences Which Involve Other Agents' Beliefs

The involvement of the cerebellum in understanding social action sequences is typically investigated using tasks where

social events have to be put in their correct chronological order, as in the picture sequencing task [77]. Cerebellar patients perform significantly worse than healthy matched controls on these tasks, especially when re-arranging photos or pictures of biological actions [78, 79], or when re-ordering actions requiring the identification of agents' beliefs [80], and less so for non-biological mechanical movements. Moreover, consistent fMRI evidence has shown that identifying sequences which involve other agents' beliefs led to consistent activations in Crus II [66].

But is this region *causally* involved in processing social sequences? To address this issue, Heleven et al. [19] have recently combined offline cerebellar TMS with the sequencing task. Participants were presented non-routine true and false belief stories (e.g., false beliefs: while being absent somebody eat the last cookie), routine social scripts (e.g., selecting items and paying in a shop), and mechanical control stories (e.g., a car accident). These stories were described in four images (pictorial version) or sentences (verbal version), presented in a random order. Participants had to put the events in the correct chronological order. Successful performance on this task requires sequencing capacities, explicit social information processing, and in the case of non-routine belief stories, mentalizing capacities. As noted above, both versions of the task, and especially non-routine belief stories, recruit the posterior cerebellar Crus II [66]. Half of 46 healthy participants received low frequency (1 Hz) repetitive TMS over the posterior cerebellum (the center of a double cone coil was placed 1–2 cm below the inion), while the other half received sham stimulation.

Effects on picture and verbal sequencing task performance were analyzed by comparing pre- and post-stimulation performance within participants, and by comparing TMS versus sham stimulation between participants. Group differences between the TMS and sham group were significant, but no other simple or interaction effects were significant. In order to further explore the differences between the TMS and sham group, separate analyses comparing pre- versus post-stimulation performance per group and per condition was performed. Learning improvements were observed on both picture and story sequencing tasks and for all types of sequence stories (i.e., true and false beliefs, social scripts, mechanical control) as reflected in significant faster reaction times from pre- to post-stimulation. Almost no effects were observed for the sham condition. These preliminary, but promising results indicate a potential beneficial role of cerebellar TMS on sequence learning, explicit social information processing, and mentalizing capacities. Especially this latter effect is crucial, as it demonstrates that the posterior cerebellum supports not only lower-level sequencing, but also higher-level social processing and in particular mentalizing. That is, the posterior cerebellum is causally involved in identifying the correct sequence of actions to understand true and false beliefs of other persons.

Context-Based Prediction

A recent tDCS study has shown that the posterior cerebellum is causally involved in using contextual information to predict others' actions [21]. Oldrati et al. [21] first familiarized participants with videos depicting a person acting in different ways upon an object, for examples, grasping an apple from a plate to perform either individual (i.e., eating) or interpersonal (i.e., giving the object to a peer) actions. Contextual elements (such as the color of the plate) were manipulated so to occur more often with (and hence being predictive of) one of the two actions. In the testing phase, videos were cut before the completion of the action and participants had to indicate (on the basis of available contextual information) whether the observed action was more likely to reflect an individual or interpersonal intention. During the task (anodal/cathodal/sham), tDCS was delivered over the medial cerebellum (localized as the point lying 2 cm below the inion) to modulate its excitability. Compared to the sham control condition, cathodal tDCS impaired participants' ability to predict the correct action, whereas anodal stimulation boosted it. Interestingly, these effects were also modulated by the strong versus moderate predictive potential of the provided contextual cues, resulting in state-dependent effects of stimulation (see [34, 35, 81]). Critically, tDCS did not affect a non-social control task requiring participants to predict the movements of physical shapes based on contextual priors. This finding is interesting because it seems to suggest a specific involvement of the posterior cerebellum (at least of its medial part) in forming expectations related to social events, possibly because action recognition may be directly rooted in more basic sensorimotor mechanisms (related to self-actions) implemented by the cerebellum (in line with a "grounded action cognition" framework, for a discussion see [82]).

Social stereotyping also somehow reflects prediction mechanisms [83], based on stereotypical associations that are prevalent in the social culture of that particular individual [84]. In this view, further support for the role of the cerebellum as a predictive device comes from a TMS study testing the neural bases of implicit social (stereotypical) associations [23]. Specifically, Gamond et al. [23] presented their participants with an in-group or out-group face followed by a trait adjective that participants had to evaluate. Normally, an in-group bias can be observed as reflected in faster categorizations of positive trait adjectives that follow in-group faces. However, this effect disappeared when triple-pulse 20 Hz TMS was delivered to the right cerebellum (Crus I) between the face presentation and trait evaluation as compared to stimulation of a control site (visual cortex). The

effect of cerebellar TMS on the in-group bias suggests that the right cerebellum processes emotional signals depending on the associated/learned social context [85, 86]. Moreover, in that study, stimulation of the dmPFC also affected the in-group bias, a finding consistent with a recent functional connectivity model [68, 69, 87] that showed that the mPFC and the right lateral cerebellum together with the temporal parietal cortex (TPJ) constitute a brain network dedicated to social cognition.

Biological Motion Discrimination

Studies employing TMS have also showed a causal role of the posterior cerebellum in mediating low-level social processing, such as body language reading [14]. Recognizing others' movements is a crucial ability for intention understanding and mentalizing functions (for a review see [88]). Neuroimaging findings suggest that this ability recruits the left posterior cerebellar hemisphere, specifically Crus I and lobule VIIB (e.g., [89]), as a node of a broader circuit that connects the cerebellum to the right superior temporal sulcus (STS, [90]), the core cerebral region dedicated to the processing of biological motion [91]. Based on this prior evidence, Ferrari et al. [14] applied 20 Hz TMS to interfere online with neural activity in the medial (vermal lobule VI) and lateral (left lobule VI/Crus I) sectors of the posterior cerebellar lobe while healthy participants had to discriminate biological from non-biological motion in point-light animations. Stimulation of both cerebellar sites significantly impaired performance compared to stimulation of a control site, although this depended on timing of stimulation. Indeed, TMS targeting the vermis impaired performance when delivered at onset of the stimuli, possibly affecting early movement identification. TMS of the left hemisphere selectively impaired performance at 300 ms from stimulus onset, likely reflecting interference with processing of feedback inputs from STS. Discrimination of biological motion may again reflect predictive mechanisms implemented by the posterior cerebellum. Indeed, predictions based on the representation of self-induced movements enable the discrimination between biological motion (that shares representation of the self-induced movement) and non-biological motion that deviates from these representations, [92]. As already mentioned by Oldrati et al. [21], mechanisms related to motor control and prediction of sensory consequence of one's own movements implemented by the sensorimotor (anterior) cerebellum may have expanded to the posterior cerebellum allowing these predictions to be used to identify others' movements as biological, and possibly to infer the intention of an action (see also [93]).

TMS and tDCS Studies Investigating the Role of the Posterior Cerebellum in Mood Regulation and Emotion Processing

Beyond deficits in mentalizing, cerebellar damage has been consistently associated to disorders in mood regulation and to difficulties to properly recognize and react to others' emotional states [94, 95]. With respect to high-level social processes, non-invasive brain stimulation has contributed (and may further add) to clarify the neuro-functional mechanisms via which the posterior cerebellum supports (both self-related and exogenous) affective processing.

Mood Regulation

Already in the late 1960s, it was shown that electrical (invasive) stimulation of the cerebellum in patients was associated with the experience of negative feelings, suggesting a possible connection between the cerebellum and emotion regulation (e.g., [96]). During the mid-1970s, administering subdural intracranial electric stimulation of the cerebellar vermis was found to markedly improve the ability of severe behaviorally disturbed patients to regulate their emotions and mood states [97]. Increased inhibitory tone of the Purkinje cells to the forebrain via the deep cerebellar nuclei was proposed to be among the possible working mechanisms. Direct evidence for the involvement of the cerebellum in emotion regulation assumption was recently provided by an optogenetic study in mice where increasing local activity of Purkinje cells in the vermis reduced the number of aggressive attacks towards intruders, while deactivation of the Purkinje cells in the vermis caused a notable increase of aggressive behavior [98]. In human research, non-invasive brain stimulation techniques are increasingly used to study the role of the cerebellum in emotion and mood regulation. Schutter and Van Honk [27], for instance, reported that 20 min of inhibitory slow-frequency (1 Hz) rTMS over the medial cerebellum in healthy volunteers increases self-reported negative mood after viewing aversive scenes as a result of impaired emotion regulation. Conversely, high-frequency rTMS (25 Hz) over the same cerebellar sector resulted into increased positive mood and alertness [26]. In agreement, in a double-blind, crossover study, 15 min of high-frequency rTMS (20 Hz) over the medial cerebellum as compared to occipital and sham rTMS increased pre-attentional biases to happy facial expressions [25]. The change in implicit processing of positive stimuli may reflect a transient alteration in the brain's motivational circuit and emotion regulation capacities. Interestingly, simultaneous stimulation of the right lateral cerebellum and left dorsolateral prefrontal cortex was found to result in mood elevation [20]. Although in the latter study [20], it is difficult to disentangle

the selective effect of cerebellar stimulation from the well-established effects of stimulation of the left prefrontal cortex on mood regulation [99],this result does seem to suggest that both medial and lateral sectors of the posterior cerebellum may be involved in these regulatory mechanisms.

What could possibly be the mechanisms by which stimulation of the posterior cerebellum affects mood regulation? Recent studies suggest that emotion regulation can be conceptualized as a component of a wider process of body energy regulation relying on predictive mechanisms that, by anticipating the body's needs and preparing to meet them, aims to maintain (body) energy balance, i.e., homeostasis [100–102]. From this perspective, stress-related disorders such as depression and anxiety are characterized by difficulties in emotion regulation associated with inefficient predictive coding [100, 103, 104]. Abnormal predictive coding leads to uncertainty and chronic elevated levels of distress and negative mood [101, 102]. The posterior cerebellum may participate to predictive mechanisms fundamental to autonomic activity and emotion regulation [101] as a node of broader subcortical and cortical anatomical and functional networks. One of these circuits is likely to be the cerebello-amygdaloid functional network in which the amygdala and clusters in the cerebellar lobule VI and VIII (in the posterior cerebellum, but mainly connected with sensorimotor cerebral networks) work together in order to prepare the more appropriate reaction to the emotional stimuli [105]. Furthermore, the monosynaptic reciprocal projections between the cerebellum and hypothalamus provide another important functional anatomical correlate of homeostatic regulation as part of the emotion-dedicated subcortical circuits [106]. Moreover, cerebellar sectors in the vermal and hemispheric lobule VI as well as the adjacent Crus I are functionally connected with the salience network involved in detecting, integrating, and filtering interoceptive, autonomic, and emotional information, relevant for energy and emotion regulation [2, 107–109], see also [110]. Finally, the hardwired connections between the posterior cerebellum and prefrontal cortex provide an additional neuro-anatomical argument for cerebellar involvement in the experience and regulation of emotions and mood (see [111]).

Emotion Discrimination

The posterior cerebellum does not only contribute to mood regulation, but also participates in processing of exogenous emotional stimuli, as evidenced by neuroimaging and patient studies (for recent meta-analyses, see [67, 112], for review, see [5]). Recent TMS studies have contributed to shed light on the topography of posterior cerebellar regions involved in the perception and recognition of emotional cues and in later integrative stages of emotional evaluation. In a first study, Ferrari and colleagues [17] showed that interfering via online triple-pulse TMS with neural activity in the posterior lateral cerebellum (in particular left Crus I/Crus II) affected processing of happy and angry facial expressions, both when these emotions needed to be explicitly discriminated and when they were irrelevant for the task at play (i.e., implicit). Using a similar protocol, Ferrari et al. [15] demonstrated that posterior lateral cerebellar sectors are also involved in discrimination of emotional body postures. More specifically, the targeted area here was the paravermal left cerebellar region close to Crus I that, in a previous study, was found to be activated during processing of bodily postures [113].

As a possible explanation by which stimulation of the posterior cerebellum affects emotion discrimination, an important lead comes from empirical evidence suggesting that the posterior cerebellum may be selectively involved in processing of negative emotional cues. Indeed, Ferrari et al. [15] showed that the detrimental effect of (left) cerebellar TMS on performance was limited to discrimination of negative body expressions (like anger or sadness), while cerebellar TMS did not affect discrimination of positive body expressions (i.e., happiness and surprise). Similarly, in an earlier study, tDCS over the medial cerebellum (localized as the site 2 cm below the inion) selectively affected processing of negative emotional facial expressions [18]. These findings support prior neuroimaging evidence that reported selective cerebellar activations in response to negative emotional cues [114–116]. Negative stimuli are known to trigger (motor) "fight or flight" response (e.g., [117]). The selective role of the posterior cerebellum in processing negative emotional cues may thus reflect fast preparation mechanisms to respond to a potential threat, again based on prediction mechanisms by which an agent expressing a negative emotion (e.g., anger or fear) may signal a potential danger (e.g., an angry person may be aggressive towards the perceiver, a scared person may signal an imminent threat in the surrounding) to the perceiver. Indeed, as already mentioned above for mechanisms of mood regulation, cerebellar lobule VI and lobule VIIIa seem to receive emotion-related information directly from the amygdala [2, 105], and based on this information, prepare the body for appropriate early (motor) re-action, such as withdrawal movements. A recent TMS study has showed that changes in motor cortical excitability (measured by MEP) in response to facial expressions of fear (versus neutral) are modulated by the *posterior* cerebellum [16]. Specifically, the study revealed that 15 min of 1 Hz TMS over Crus I/Crus II determined a reduction in amplitude of MEP recorded from the contralateral (but not ipsilateral) motor cortex during viewing of emotional faces. Inhibition of the motor cerebellum usually results into a generalized increase in MEP size due to a transiently reduced excitability of Purkinje cells and an increased excitability of spinal alpha-motor neurons [118]. In turn, the changes in MEP size

following TMS of the lateral posterior cerebellum reported by Ferrari et al. [16] were specific for emotional stimuli and possibly depended—as suggested by the authors—on cerebellar stimulation affecting activity in frontal and temporal cortices (e.g., [119]) involved in emotion discrimination thus only *indirectly* affecting corticospinal excitability.

Although evidence suggests that the main role of the posterior cerebellum in emotion processing may depend on prediction of (and need to react to) a potential threat, other mechanisms—possibly related to motivation appraisal and reward—may also be involved, considering that the posterior cerebellum is connected to the salience network and subcortical regions involved in reward processing (e.g., [2, 105, 108, 110]). Finally, the cerebellum also implements mirror-based mechanisms [60] that are known to be important in recognizing other agents' emotions. However, these mechanisms occur in the sensorimotor anterior cerebellum [95, 120, 121] that cannot be effectively reached by stimulation when using a standard figure of eight coil (see [48, 122]), as the one employed in the studies by Ferrari and colleagues [13–15, 17].

Future Directions

Define the Cerebro-Cerebellar Networks Involved in Social Prediction

While prediction seems to be the key mechanism by which the posterior cerebellum aids cognition (also beyond the social domain, e.g., [123, 124]), what remains to be assessed is whether there are specific areas or cerebro-cerebellar networks that are selectively involved in *social* prediction (for preliminary evidence, see [21, 67]). Moreover, within these networks, it should be investigated whether there are dedicated circuits for different social competences, such as emotion recognition, mood regulation, biological motion discrimination, and higher-level inferential processes (mentalizing), as well as for implicit and explicit social processing.

Owing to its high spatial resolution, TMS may greatly contribute to this investigation by allowing to selectively interfere with neural activity of different cerebellar sectors and test the effect of stimulation on different social (and non-social) tasks. Accordingly, prior studies have already reported clear dissociations (in within-subject designs) in TMS effects for medial/vermal versus hemispheric/lateral sectors of the posterior cerebellum in different perceptual tasks [12, 14, 125]. Future TMS studies may shed light on a possible representation of social functions along the medial–lateral axis of the posterior cerebellum. Indeed, prior evidence supported the existence of a medial-to-lateral functional gradient with sensorimotor processes being more medially located, and cognitive functions being primarily distributed in the lateral portion of the posterior cerebellum [126–128]. A similar gradient may apply to social and affective functions, with higher-level abstract social functions (mentalizing) possibly located more laterally as compared to lower-level social processes. There is some evidence that Crus II may be more involved in mentalizing [67], whereas Crus I may be more involved in body reading [6, 129, 130]. Whereas prior TMS studies targeted hemispheric regions that were somehow at the intersection of Crus I and II [13, 16], it would be certainly of interest to selectively test the role of Crus II and Crus I in different social processes. On a methodological note, neuronavigated-TMS on individual MRI scans would be needed in this case to ascertain selective stimulation of the two Crus.

TMS may also critically contribute to the investigation of possible lateralization of cerebro-cerebellar circuits involved in social cognition. It has been suggested that networks that are strongly lateralized within the cerebrum may also be lateralized within the cerebellum [131]. However, available evidence in the social domain points to a bilateral pattern of activation in the posterior cerebellum during tasks related to affective and social cognition (e.g., [68, 69, 132–134]). In the TMS studies reviewed above, researchers have selectively tested the role of either the left or right cerebellar hemisphere, guided by prior neuroimaging evidence suggesting that one of the two hemispheres may be more relevant for the investigated function (e.g., [14, 23]). Now that the causal role of the lateral posterior cerebellum in these tasks has been solidly established, we can move the investigation forward, and systematically assess via TMS whereas the cerebellar nodes of broader networks causally involved in different social processes are bilateral (as suggested by neuroimaging evidence).

Investigate the Functional Representations Implemented by the Posterior Cerebellum: State-Dependent Stimulation Approaches

Researchers can further enhance functional resolution of cerebellar TMS by using state-dependent TMS [34, 35, 135], see also [33]. Indeed, TMS effects are not "fixed" but they result from an interaction between stimulation parameters (e.g., intensity, frequency) and neural activity patterns at the time of stimulation. In state-dependent paradigms, behavioral adaptation or priming are used to selectively precondition a specific neuronal population. Adapted/primed neurons are differently susceptible to the effects of stimulation compared to non-preconditioned neurons: if the targeted area contains neural populations tuned to the adapted/primed features, TMS typically interacts with the effect of preconditioning (by canceling or even reversing the effect of adaptation/priming) [33]. Using this approach, and relevant for

clarification of the neuro-functional mechanisms involved in social prediction, Decroix et al. [136] have recently demonstrated the existence of specialized neuronal populations dedicated to grip/goal integration within the fronto-parietal network. Furthermore, using state-dependent TMS, Mazzoni et al. [137] have revealed that the anterior intraparietal sulcus contains an explicit representation of affective body movements. In a similar vein, state-dependent TMS may be employed to clarify the type of functional representations implemented by the posterior cerebellum: for instance, do they represent intentions in an abstract manner or are they related to the specific actions' kinematics? Are there distinct functional representations for different emotions? All these aspects can be assessed by combining cerebellar TMS with adaptation/priming behavioral paradigms.

Modulate Connectivity: Function-Tuning Paired-Associative Stimulation and Frequency-Tuned Stimulation

It is important to stress that TMS does not only affect the site underneath the coil but also distal sites that are anatomically and/or functionally connected with the targeted site (for a review, see [10]. Network effects of cerebellar stimulation have been investigated in studies combining cerebellar TMS with either fMRI (e.g., [138]) or EEG recording (e.g., [26, 139, 140]). Functional connectivity can be modulated by cortico-cortical-paired associative stimulation (ccPAS, e.g., [141, 142]). CcPAS with two TMS coils delivers TMS pulses to two cortical areas with millisecond-level asynchrony and may increase or decrease effective connectivity between the stimulated areas depending on the asynchrony (see [143] via synaptic plasticity mechanisms. Recent findings suggest that plasticity induction with ccPAS may even be function-specific: indeed, when applied concurrently with a task, ccPAS can selectively enhance the synaptic efficiency of *functionally* specific pathways [144], by acting only on neural populations that are activated by the task/stimuli. Function-related tuning using cerebello-cortical-paired associative stimulation may be a promising paradigm to deepen our understanding of feedback and feedforward cortico-cerebellar connections involved in different social processes, for instance Crus I-STS connectivity during biological motion perception [90], or TPJ-cerebellar Crus II during mentalizing tasks [68, 69].

Another pioneering way to toggle cerebellar participation in different networks/tasks is the use of frequency-tuned stimulation. This approach, for which both TMS and specific types of transcranial electrical stimulation (such as transcranial alternating current stimulation, tACS) can be used, consists in "entraining" specific frequencies in the endogenous brain oscillatory activity that are associated to a specific function (see [33, 145]). Previous studies showed frequency-tuned TMS effects on performance in perceptual and cognitive tasks [146–152], including the domain of social cognition. For instance, TMS-induced theta band entrainment of the right posterior TPJ improves (visuospatial) perspective taking while alpha band entrainment inhibits perspective taking [153]. This approach has also been recently applied to the cerebellum, showing that frequency-tuned stimulation can modulate cerebellar excitability in a time- and frequency-dependent manner (e.g., [154]). In this regard, in the cognitive domain, a recent study by Dave et al. [155] showed a double dissociation of cerebellar contribution to semantic prediction versus episodic memory based on stimulation rhythm (beta (~ 13–30 Hz), and theta (~ 3–8 Hz), respectively), suggesting that the cerebellum may be biased to support these distinct cognitive abilities at the command of network-specific rhythmic activity. Indeed, the cerebellar cortex harbors a variety of such local circuit rhythms, from those in the cerebellar cortex per se, to those dictated from important afferents (see [156]), and covering both the higher-frequency and the lower-frequency ranges [157]. For instance, the oscillating local field potentials that occur between 10 and 30 Hz (i.e., beta) have an important functional role in cerebellar-M1 communication during movement preparation and execution [158, 159]. In turn, cerebellar gamma oscillatory activity may have a specific role in implicit motor learning [160] but also in emotional processing [161]. Critically, the ability of the cerebellar cortex to generate population rhythms within the same frequency bands as neocortex suggests that they may act as a common spatiotemporal code within which corticocerebellar dialog may occur [162]. Indeed, there is converging evidence that motor and cognitive functions are accompanied by synchronized oscillatory activity at different frequencies proposing a mechanism of functional integration within brain networks [163]. Although non-invasive cerebellar electrophysiology has traditionally been assumed to be challenging because of the remote location of the cerebellum and its finely convoluted cortex, recent approaches have allowed a better understanding of spontaneous oscillatory cerebellar activity [157, 164]. Whereas this deserves further investigation, available evidence on cerebellar frequency-tuned stimulation (e.g., [154, 155, 160]) suggests encouraging implications for treatment of diseases manifesting with abnormal cerebellar oscillatory activity as well as for future behavioral studies.

Another technique that may prove to be effective in affecting cerebellar functions is transcranial random noise stimulation (tRNS). tRNS is a modification of tACS in which the stimulation waveform is a noise signal that is filtered to contain frequency components in the range of cortical oscillations and beyond. The mechanism of action is not completely understood, although phenomena such as stochastic resonance, a general principle by which adding noise to a subthreshold signal pushes the signal over the threshold and

thereby enhances it, have been proposed [165, 166]. tRNS has been showed to be effective in improving motor, cognitive, and affective functions in both healthy individuals (e.g., [167–170]) and patients (e.g., [171, 172]), however, so far, it has never been applied to the cerebellum.

Investigate the Time Course of Cerebellar Contribution to Social and Affective Processing

It is worth noting that the chronometry of cerebellar contribution to social processes is another aspect that so far has been almost completely neglected in the literature and to which TMS may greatly contribute. Indeed, while the anatomy of the cerebellum makes it difficult to apply traditional approaches of signal recording with techniques typically employed to investigate temporal aspects of brain processing (i.e., EEG and MEG) (but see [157]), chronometric-TMS approaches (see [31, 173]) appear feasible and promising. Chronometric-TMS protocols typically consist in delivering single pulses at different time points (separated by few tens of milliseconds) of stimulus processing, and allow to clarify at which stage of information processing the targeted area plays a causal role. Although Ferrari et al. [14] did not use a strict chronometric approach, their study—in which TMS was applied either at onset of following 300 ms from stimulus onset during biological motion discrimination—is still the first TMS study that examined the time course of the involvement of different posterior cerebellar sectors into social processing.

Clinical Applications and the Concept of Cerebellar Reserve

The brain stimulation approaches described in the previous sections are promising for their potential in the clinical setting (see [174], see also [175]). For instance, frequency-tuned stimulation of the cerebellum has been already consistently employed to improve motor functions [176–178] and may be similarly used to enhance high-level cerebellar functions. Functional connectivity of important networks involved in social cognition, such as the default network whose connectivity appears reduced in a number of psychiatric illnesses affecting social competences, such as schizophrenia and autism [179], may be strengthened via cerebellar TMS (see [138]). A promising avenue in rehabilitation is also the combination of functionally and/or frequency-tuned cerebellar stimulation with advanced behavioral interventions (including virtual reality, see [180, 181]).

A fruitful line of inquiry on intervention, close in line with the sequencing hypothesis in social cognition [73], could focus on the cerebellar role in identifying and automatizing action sequencing in understanding the mental states of others. Impairments in this critical cerebellar function may result in an outshoot of inflexible and dysfunctional thought-affective sequences which may have become overly automatic in many clinical pathologies (which may reflect critical reactions of others and thought about the self), such as rumination in depression and craving in addiction. This idea on inflexible and automatic social-affective though sequences may inspire alternative approaches to neurostimulation (i.e., during exposure of such though sequences) and neuro-guided treatment. In particular, these behavioral treatments, potentially combined with TMS, may focus on training to flexibly create alternative thought-affective sequences (e.g., narratives) which are less automatic, intrusive, and disturbing, contrary to traditional cognitive therapy which often attempts to take control over and abolish obsessive thoughts.

A key question is through which form(s) of plasticity in the cerebellum the changes occur. tDCS and rTMS are known to modulate neuronal activity in the DCN-thalamo-cortical pathway with a short-term or long-term time course and plasticity of the cerebellar cortex synapses is presumed to be the neural basis for the long-lasting modulation [182]. The cerebellar cortex is capable of various forms of synaptic plasticity, which allow compensation and restoration of function. This concept of cerebellar reserve designates the capacity of the cerebellum to compensate for tissue damage or loss of function resulting from many different etiologies [183]. Potentiation of cerebellar reserve may lead to compensation and restoration of function not only in the setting of pure cerebellar disorders, but also in disorders affecting primarily cerebral hemispheres and for which the cerebellum is part of the subcortical nodes. This can even be extended to disorders of basal ganglia. Therefore, the underlying plasticity of cerebellar microcircuitry appears to be of critical neurobiological importance to a wide range of neurological/neuropsychiatric conditions, including disorders impairing social life.

Conclusion

The cerebellum is increasingly attracting scientists interested in basic and clinical research of neuromodulation. We have shown how a growing number of studies in the last decade succeeded in significantly modulating affective and social behavior by targeting different sectors of the posterior cerebellum via TMS or tDCS. These findings pave the way for future research that should define the cerebro-cerebellar networks *causally* involved in affective and social cognition, as well as the specific functional representations and operations implemented by these circuits (also in comparison to other cognitive processes supported by cerebellar circuits). Finally, the possibility to modulate cerebro-cerebellar connectivity via non-invasive brain stimulation opens us

possible clinical applications for improvement of affective and social skills in patients with cerebellar dysfunctions.

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Declarations

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