The role of the cerebellum in explicit and incidental processing of facial emotional expressions: a study with transcranial magnetic stimulation

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Abstract

Growing evidence suggests that the cerebellum plays a critical role in non-motor functions, contributing to cognitive and affective processing. In particular, the cerebellum might represent an important node of the "limbic" network, underlying not only emotion regulation but also emotion perception and recognition. Here, we used transcranial magnetic stimulation (TMS) to shed further light on the role of the cerebellum in emotional perception by specifically testing cerebellar contribution to explicit and incidental emotional processing. In particular, in three different experiments, we found that TMS over the (left) cerebellum impaired participants' ability to categorize facial emotional expressions (explicit task) and to classify the gender of emotional faces (incidental emotional processing task), but not the gender of neutral faces. Overall, our results indicate that the cerebellum is involved in perceiving the emotional content of facial stimuli, even when this is task irrelevant.

Introduction

Consistent neuroimaging evidence suggests that the cerebellum represents a key node of the network underpinning the ability to process emotional stimuli. In particular, different meta-analyses of neuroimaging studies have shown robust activations of the vermis and Crus I (bilaterally) during emotional perception (Fusar-Poli, Placentino, Carletti, Landi, & Abbamonte, 2009; Keren-Happuch, Chen, Ho, & Desmond, 2014; Stoodley & Schmahmann, 2009). A recent consensus paper on the role of the cerebellum in the emotional domain (Adamaszek et al., 2017) suggests that the cerebellum is an integral part of the limbic network and points to the vermis, Crus I and Crus II (in the cerebellar hemispheres) as relevant in mediating different stages of emotion perception and recognition.

Lesions studies also converge in identifying the cerebellum as crucial in both regulating own emotions (e.g., Lupo et al., 2015; Schmahmann, 2010; Schmahmann & Sherman, 1998) and in allowing recognition of others' emotions (Adamaszek et al., 2014; D'Agata et al., 2011; Hoche, Guell, Sherman, Vangel, & Schmahmann , 2015; Sokolovsky, Cook, Hunt, Giunti, & Cipolotti, 2010). In fact, cerebellar patients may show dysregulated emotional experience characterized by dysphoria and depression, and dysregulated emotional behaviors, such as exaggerated anxiety and aggressive conducts (e.g., Schmahmann, Weilburg, & Sherman, 2007). Moreover, cerebellar lesions may affect recognition of both facial basic emotions (Adamaszek et al., 2015) and social emotions, such as arrogance and guilt (D'Agata et al., 2011), without though affecting processing of non-emotional facial features (such as identity) (Adamaszek et al., 2015). Finally, cerebellar dysfunctions have been reported in psychiatric syndromes characterized by emotional and social deficits, such as schizophrenia and autism (for reviews, see Phillips, Hewedi, Eissa, & Moustafa, 2015; Shakiba, 2014).

In recent years, non invasive brain stimulation/modulation techniques have contributed to shed light on the role of cerebellar structures in emotional processing (for reviews, Ferrucci & Priori, 2014; van Dun, Bodranghien, Manto, & Mariën, 2017). Using transcranial direct current stimulation (*t*DCS), Ferrucci et al. (2012) showed that both anodal and cathodal *t*DCS significantly fastened recognition of negative facial emotions leaving perception of positive and neutral facial expressions unchanged. Using transcranial magnetic stimulation (TMS), Schutter and colleagues (Schutter & van Honk, 2009; Schutter, Enter, & Hoppenbrouwers, 2009) found that inhibiting cerebellar activity by means of low-frequency TMS induced negative mood in healthy participants, whereas enhancing cerebellar activity via high-frequency TMS selectively affected implicit processing of positive emotional stimuli. Moreover, electrophysiological studies have found that cerebellar TMS modulates theta and gamma frontal activity (Schutter, van Honk, d'Alfonso, Peper, & Panksepp, 2003; Van Honk & Schutter, 2006), oscillatory activity in theta and gamma frequency being also related to emotional processing (for a review see Symons, El-Deredy, Schwartze, & Kotz, 2016).

If it is now well accepted that the cerebellum plays a role in emotional processing, several questions remain to be addressed, as for instance at which level of emotional information processing the cerebellum is involved. Indeed, neuroimaging and lesion evidence suggest that partially dissociable neural networks underpin explicit and implicit emotional processing in the cerebrum (Bowler, 1992; Critchley et al., 2000; Gorno-Tempini et al., 2001; Saver & Damasio, 1991; Wright et al., 2008). Whether the cerebellum contributes to a different extent to implicit and explicit emotional processing is still debated. On one hand, previous studies suggest that the cerebellum may be more involved when explicit compared to implicit emotional processing is required. For instance, Scheuerecker et al. (2007) reported cerebellar activations when participants matched emotional faces as a function of their emotional expression but not as a function of their gender (see also Critchley et al., 2000). Accordingly, Wright et al. (2008) found cerebellar responses during explicit evaluation of pleasant and unpleasant images but not during frequency estimation (i.e., How frequently do images with similar content appear on television?) of the same images. Moreover, cerebellar patients have shown deficits in reporting their own emotional state but not in implicit measures of emotional behaviour (Clausi et al., 2015). On the other hand, Habel et al. (2007) found significant cerebellar activations both during explicit emotion discrimination and implicit emotion processing (see also Schutter et al., 2009).

In this study, we used TMS to interfere with the neural activity of the cerebellum while participants were presented with facial emotional expressions that had to be explicitly discriminated or that were incidental for the task at play (i.e., face gender discrimination). In three different experiments, we selectively stimulated the left cerebellar hemisphere in light of prior evidence specifically pointing to this region as crucial in emotional processing (for a meta-analysis, see Stoodley & Schmahmann, 2009). Overall, our results indicate that interfering with cerebellar activity affects both explicit and implicit emotional processing, whereas it is not detrimental for judging neutral face features (ruling out unspecific effects of stimulation on visual discrimination).

Experiment 1

Method

Participants

Thirty-six Italian volunteers (9 males, mean age=22.5 years, SD=2.2) took part in the experiment. Another group of 20 participants was recruited in a pilot study (Supplementary Materials). All participants were right-handed and had normal or corrected-to-normal vision. Prior to the TMS experiment, each participant filled in a questionnaire to evaluate compatibility with TMS (translated from Rossi, Hallett, Rossini, & Pascual-Leone, 2011). The protocol was approved by the local ethical committee and participants were treated in accordance with the Declaration of Helsinki.

Stimuli

Stimuli were images selected from the NimStim database (Tottenham et al., 2009) depicting 14 male and 14 female different young faces (each covering approximately 23×14 degrees of visual angle) showing happy or angry expressions.

Procedure

Participants seated in front of a 19’ screen at an approximate distance of 80 cm. Figure 1 shows an example of the experimental trial. Each trial started with a black fixation cross (2500 ms), followed by a first face (visible for 150 ms), a blank screen (150 ms), and a second face (150 ms). The second face was followed by a blank screen until participants’ response. Participants were randomly assigned to two different task conditions. In the Emotion Discrimination task, participants indicated whether the two faces expressed the same or a different emotion; in the Gender Discrimination task participants indicated whether the two faces belonged to the same gender. Participants had to respond by left/right key pressing using their right hand as fast as possible. Response key assignment was counterbalanced across participants. In both tasks, the same face pairs were used. In particular, 28 face pairs were created for each of the four possible gender/emotion combinations (i.e., same emotion/same gender; same emotion/different gender; different emotion/same gender; different emotion/different gender), for a total of 112 trials in each experimental block. After a short training session consisting of 8 trials, participants performed three experimental blocks, one for each TMS site (see below). Order of site stimulation was counterbalanced across participants. The software E-prime 2.0 (Psychology Software Tools, Pittsburgh, PA) was used for stimulus presentation, data collection and TMS triggering.

[Insert Figure 1 about here]

TMS

Online neuronavigated TMS was performed with a Magstim Rapid^2 stimulator (Magstim Co., Ltd, Whitland, UK) connected to a 70-mm butterfly coil. At the beginning of each session, single pulse TMS was applied over the left M1 at increasing intensities to determine each individual motor threshold (MT). MT was defined as the lowest TMS intensity capable of evoking a muscle twitch in the controlateral hand in 5 out of 10 consecutive trials (Koch et al., 2007; see also Hanajima et al., 2007, for methodological details on this standard procedure). During the experiment participants were stimulated at 100% of their MT (mean stimulation intensity=53.2% of the maximum stimulator output, *SD*=3.9), in line with prior TMS studies targeting the cerebellum (e.g., Demirtas-Tatlidede, Freitas, Pascual-Leone, & Schmahmann, 2011; Desmond, Chen, & Shieh, 2005; Koch et al., 2007; Schutter et al., 2003). Intensity of stimulation was kept constant for the stimulation of all the three target sites. Triple-pulse 20 Hz TMS was delivered 150 ms before the presentation of the second face. 20 Hz rTMS has been found to effectively modulate behavioral responses in previous TMS studies, also targeting the cerebellum (e.g., Bestmann, Thilo, Sauner, Siebner, & Rothwell, 2002; Cattaneo et al., 2014; Gamond, Ferrari, La Rocca, & Cattaneo, 2017; Koch et al., 2007; Wagner, Rihs, Mosimann, Fisch, & Schlaepfer, 2006). TMS was delivered over the left cerebellum, early visual cortex and the vertex (control site). Early visual cortex was chosen as additional control area since prior evidence suggests that cerebellar stimulation may spread to primary visual cortex (Renzi, Vecchi, D’Angelo, Silvanto, & Cattaneo, 2014); it is thus important to rule out the possibility that cerebellar TMS effects depend on indirect stimulation of visual cortex. TMS focality is typically around 0.5-1 cm (Sliwinska, Vitello, & Devlin, 2014). This is likely to be the case also of cerebellar stimulation, as suggested by prior studies observing different behavioral and neural connectivity effects following stimulation of nearby cerebellar sectors within the same participants (e.g., Koch et al., 2007; Halko, Farzan, Eldaief, Schmahmann, & Pascual-Leone, 2014; Théoret, Haque, Pascual-Leone, 2001). The timing of stimulation was chosen so not to affect the processing of face information by the early visual cortex, information about facial features already reaching face-selective regions in extra-striate visual cortex 60-100 ms from face onset (see Pitcher, Walsh, Yovel, & Duchaine, 2007; for recent ERP evidence, see Colombatto & McCarthy, 2017). The left cerebellum and the early visual cortex were localized by means of stereotaxic navigation on individual estimated magnetic resonance images (MRI) obtained through a 3D warping procedure fitting a high-resolution MRI template with the participant's scalp model and craniometric points (Softaxic 2.0, EMS, Bologna, Italy). This procedure has been proven to ensure a global localization accuracy of about 5 mm, a level of precision close to that obtained using individual MRI scans (Carducci & Brusco, 2012), and it has been successfully used in many prior studies (e.g., Cattaneo et al., 2011, 2015; Ferrari et al., 2016**;** Mattavelli, Cattaneo, & Papagno, 2011). The anatomical Talairach coordinates (Talairach & Tournoux, 1998) of the left cerebellum were x=−15, y=-82, z=-32 (corresponding to cerebellar loci of activation during emotional processing reported in prior neuroimaging work, see Schraa-Tam et al., 2012), and Talairach coordinates of early visual cortex were x=-2, y=-75, z=32 (Anderson, Ferguson, Lopez-Larson, & Yurgelun-Todd, 2011). The coil was placed tangentially to the scalp and held parallel to the midsagittal line (see Figure 2), according with consistent evidence suggesting that this is an effective coil orientation to successfully modulate activity in cerebellar structures (e.g., Bijsterbosch, Barker, Lee, & Woodruff, 2012; Halko et al., 2014; Jayasekeran, Rothwell, & Hamdy, 2011; Théoret, Haque, & Pascual-Leone, 2001; van Dun et al., 2017). The handle pointed backward in the vertex stimulation condition, and superiorly in the cerebellum and early visual cortex stimulation conditions. Since repetitive TMS over sites close to the neck may induce muscular neck contractions, prior to the experiment participants were given few magnetic pulses over the cerebellar hemisphere to familiarize with the induced sensation. Participants were reassured that possible experienced neck contractions were expected superficial side-effects. Furthermore, in order to minimize neck tension during the whole experiment, participants' head was stabilized using a chinrest and few minutes breaks were given after each block.

[Insert Figure 2 about here]

Statistical Analyses

The dependent variables were accuracy rates and correct response latencies (RT). Trials in which participants' RT were ±3 SD compared to their block mean were excluded from the analyses (following this criterion 1.4% of trials were excluded). A mixed logistic model has been estimated for accuracy rates with TMS (cerebellum, visual cortex and vertex) and Task (emotion discrimination vs. gender discrimination) and their interaction as fixed effects, and intercepts and TMS effects as random coefficients across participants. In this way, maximal random component has been obtained for all the estimated models (Barr, Levy, Scheepers, & Tily, 2013). Statistical significance was obtained by a Type III Wald chi-square test. RT have been log-transformed and a mixed linear model has been estimated with the experimental factors (TMS, Task, and their interaction) as fixed effects, and intercepts and TMS effects as random coefficients across participants. Statistical significance was obtained with the F-test with Sattherwaite approximation of degrees of freedom. All the models were estimated using R (version 3.3.1) and lme4 R package (version 1.1).

Results

The analysis on accuracy rates (Figure 3) revealed a significant main effect of TMS, $\chi^2(2)=8.99$, $p=.011$. Contrast analysis showed that when TMS was delivered over the cerebellum participants' accuracy rates were lower (Prop. correct=.88) compared to TMS over the vertex (Prop. correct=.90), z=2.06, $p=.04$, and TMS over the visual cortex (Prop. correct=.91), z=2.97, $p=.003$. The main effect of Task was significant, $\chi^2(1)=9.00$, $p=.003$, with higher accuracy rates in the gender discrimination task (Prop. correct=.93) compared to the emotion discrimination task (Prop. correct=.87). The interaction effect TMS by Task did not reach significance, $\chi^2(2)=.09$, $p=.954$.

[Insert Figure 3 about here]

Mean RT for correct responses in the emotion discrimination task were 536 ms (*SD*=143) for cerebellar TMS, 510 ms (*SD*=144) for early visual cortex TMS, and 528 ms (*SD*= 122) for vertex TMS. For the gender discrimination task, correct mean RT were 472 ms (*SD*=170) for cerebellar TMS, 474 ms (*SD*=171) for early visual cortex TMS and 465 ms (*SD*=162) for vertex TMS.

RT were not effectively modulated by any of the experimental conditions: main effect of TMS, $F(2,33.80)=1.09$, $p=.348$; main effect of Task, $F(1,34.00)=2.03$, $p=.163$; interaction effect TMS by Task, $F(2,33.80)=1.38$, $p=.266$.

Experiment 2

In Experiment 1 we found that applying TMS over the left cerebellum affected participants' performance when explicitly discriminating between facial emotional expressions (note that a similar pattern was also reported in a preliminary pilot investigation, see Supplementary Materials) and when classifying the gender of emotional faces. These results suggest that the cerebellum is involved in perceiving the emotional content of facial stimuli, even when this is task irrelevant. Given the importance of replicability when testing new hypotheses, we carried out Experiment 2 to ensure that the findings of Experiment 1 could be replicated within-subjects in a new sample of participants (within-subjects designs also allowing for more powerful tests of effects than between-subjects designs, reducing variability due to individual differences among subjects, see Pollatsek & Well, 1995). Procedure was identical to Experiment 1 but face stimuli and their duration were slightly modified in order to increase the complexity of gender discrimination so to make the two tasks equally difficult. This because in Experiment 1 participants performed overall better in gender discrimination than in emotion discrimination, possibly due to the use of natural faces with also hair visible (for similar effects, see Gorno-Tempini et al., 2001). Previous fMRI studies indicated that cerebellar responses may vary as a function of task complexity (e.g., Boecker et al., 2002; Schubotz & von Cramon, 2002) and response uncertainty (Volz, Schubotz, & von Cramon, 2003). Although in Experiment 1 cerebellar stimulation affected both tasks, regardless their different baseline accuracy, we considered it as important to balance task difficulty when repeating the experiment to better control for possible confounding effects.

Method

Participants

Twenty Italian volunteers (7 males, mean age= 23.7 years, SD=3.2) took part in the experiment. All participants were right-handed and had normal or corrected-to-normal vision. None of them had participated in Experiment 1. Inclusion criteria were the same as for Experiment 1.

Stimuli and procedure

Stimuli and procedure were similar to Experiment 1, but this time the same participants performed both the emotion discrimination and the gender discrimination task (in two different blocks). Moreover, to make gender discrimination harder (so to reach a similar level of accuracy in the two tasks), face images used in both tasks were cropped so that hair was not visible. With the same purpose, faces in the gender discrimination block were presented for 100 ms (rather than for 150 ms as in the emotion discrimination task). TMS parameters were similar to Experiment 1, but only two sites were targeted (to ensure a proper duration of the experiment, within safety-limits guidelines): the left cerebellum and the early visual cortex (control site). Mean stimulation intensity was set for each participant as in the previous experiment and corresponded to 53.1% of the maximum stimulator output (*SD* =2.6).

Statistical Analysis and Results

Data were analyzed similarly to Experiment 1. Trials in which participants' RT were ±3 SD compared to their block mean were excluded from the analyses (following this criterion 1.4% of trials were excluded). For accuracy rates (Figure 4), a mixed logistic model has been estimated with TMS (cerebellum vs. early visual cortex) and Task (emotion discrimination vs. gender discrimination) and their interaction as fixed effects; intercepts, TMS, and Task effects were the random coefficients across participants. Log-transformed correct RT were analyzed with a mixed linear model with TMS and Task and their interaction as fixed effects; intercepts, TMS and Task effects were the random coefficients across participants.

The analysis on accuracy rates (Figure 4) revealed a significant main effect of TMS, $\chi^2(1)=9.34$, $p=.002$, indicating lower performances during TMS over the cerebellum (Prop. correct=.82) compared to the early visual cortex (Prop. correct=.84). Neither the main effect of Task, $\chi^2(1)=.15$, $p=.703$, nor the interaction effect TMS by Task, $\chi^2(1)=.50$, $p=.479$, were significant.

[Insert Figure 4 about here]

Mean RT for correct responses in the emotion discrimination task were 527 ms (*SD*=192) for cerebellar TMS and 599 ms (*SD*=185) for early visual cortex TMS. For the gender discrimination task, mean correct RT were 546 ms (*SD*=186) for cerebellar TMS and 575 ms (*SD*=151) for early visual cortex TMS.

The analysis on RT revealed a non-significant main effect of TMS, $F(1,19.00)=.06$, $p=.81$. In turn, the main effect of Task was significant, $F(1,19.03)=16.60$, $p=.001$, indicating that overall participants were slower in the gender discrimination task compared to the emotional discrimination task. Note that the Task effect we reported here shows that cropping the face stimuli and reducing their presentation duration in the gender task were effective manipulations in making gender discrimination harder compared to Experiment 1. The interaction TMS by Task, $F(1,18.82)=7.75$, $p=.012$, reached significance. Nonetheless, simple effects analysis failed to reveal any significant difference between RT during TMS over the cerebellum and TMS over the early visual cortex, either when participants discriminated emotions, $t(18.82)=-1.29$, $p=.213$, or gender, $t(19.00)=1.30$, $p=.208$.

Experiment 3

Experiment 2 replicated the results of Experiment 1 by showing (in a within-subjects design) that interfering with activity in the left cerebellum impaired participants' ability to process emotional facial expressions both when these had to be explicitly discriminated and when they were incidental for the task. However, the observed impairment following cerebellar stimulation in Experiment 1 and Experiment 2 may have depended on unspecific effects of cerebellar TMS in evaluating facial characteristics or, more in general, in decision making *per se* (regardless of the stimuli used). In order to rule out this possibility, in Experiment 3 we tested a new group of participants with the same paradigm used in Experiment 2 but in which neutral faces, rather than emotional faces, were presented in the gender discrimination task. If the effects we reported in Experiment 1 and Experiment 2 reflect the specific contribution of the cerebellum in processing emotional cues, cerebellar TMS should not affect gender discrimination when neutral faces are used.

Methods

Participants

Twenty Italian volunteers (4 males, mean age=23.7 years, *SD*=2.6) took part in the experiment. All participants were right-handed and had normal or corrected-to-normal vision. None of them had participated in either Experiment 1 or 2. Inclusion criteria were the same as for the previous experiments.

Stimuli and procedure

As in Experiment 2, participants performed both the emotion discrimination task and the gender discrimination task. Stimuli of the emotion discrimination task were the same of Experiment 2. In the gender discrimination task though, the emotional faces used in the prior experiments were replaced by corresponding male and female faces showing a neutral expression (from the Radboud database, Langner et al., 2010). Neutral faces were cropped so that hair was not visible (in order to make gender classification less obvious), but duration of face presentation in the gender task was set back to 150 ms (as in Experiment 1). Each experimental block consisted of 36 trials, repeated twice for a total of 72 trials. TMS sites and parameters were identical to Experiment 2. Mean stimulation intensity was set for each participant as in the previous experiments and was 53.5% of the maximum stimulator output (*SD*=3.0). Order of Task and TMS targeted sites was counterbalanced among participants.

Statistical Analysis and Results

Data were analyzed similarly to previous experiments. Trials in which participants' RT were ±3 SD compared to their block mean were excluded from the analyses (following this criterion 1.3% of trials were excluded). A mixed logistic model has been estimated for accuracy rates (Figure 5) with TMS (cerebellum vs. early visual cortex) and Task (emotion discrimination vs. gender discrimination of neutral faces) and their interaction as fixed effects, and intercepts, TMS and Task effects as random coefficients across participants. Log-transformed correct RT were analyzed by means of a mixed linear model with TMS and Task as fixed effects, and intercepts, TMS and Task effects as random coefficients across participants.

The analysis on accuracy rates (Figure 5) revealed a nonsignificant main effect of TMS, $\chi^2(1)=.98$, $p=.321$. In turn, the main effect of Task, $\chi^2(1)=4.37$, $p=.036$, and the interaction TMS by Task, $\chi^2(1)=4.23$, $p=.04$, were significant. Simple effect analysis showed that TMS over the cerebellum lowered accuracy rates (Proportion correct=.87) compared to TMS over the early visual cortex (Proportion correct =.89) in the emotion discrimination task, $\chi^2(1)=4.13$, $p=.042$, but not in the gender discrimination task, $\chi^2(1)=.49$, $p=.485$ (Proportion correct=.85 for cerebellar TMS; Proportion correct=.84 for early visual cortex TMS).

[Insert Figure 5 about here]

Mean RT for correct responses in the emotion discrimination task were 550 ms (*SD*=164) for cerebellar TMS and 478 ms (*SD*=139) for early visual cortex TMS. For the gender discrimination task, mean correct RT were 558 ms (*SD*=179) for cerebellar TMS and 498 ms (*SD*=143) for early visual cortex TMS.

The analysis on RT revealed a significant main effect of Task, $F(1,19.01)=5.22$, $p=.034$, indicating that overall participants performed slightly faster in the gender discrimination task compared to the emotional discrimination task. Neither the main effect of TMS, $F(1,19.00)=.77$, $p=.39$, nor the interaction effect TMS by Task, $F(1,18.37)=1.56$, $p=.227$, reached significance.

Discussion

In a series of experiments, we found that interfering with activity in the (left) cerebellum via online TMS impaired participants' accuracy in processing facial emotional expressions. Although the reported effects were overall of small size, the disruptive effect of cerebellar TMS was evident across different experiments (Experiments 1 and 2, see also Supplementary Materials). TMS effects were selective for emotional faces, ruling out unspecific effects of stimulation on visual discrimination or decision making *per se* (Experiment 3). Critically, our data show that the (left) cerebellum is implicated in emotional processing both when emotions have to be explicitly classified and when they are irrelevant for the task at play (i.e., gender discrimination).

While it is already well known that the cerebellum takes part in affective processing (for meta-analyses see Fusar-Poli et al., 2009; Keren-Happuch et al., 2014; Stoodley & Schmahmann, 2009), our study is the first online TMS study to reveal such an effect and to suggest that the (left) cerebellar hemisphere is likely to process emotional expressions even when the emotional content is task irrelevant. Indeed, available neuroimaging findings are controversial on this point, some showing that the cerebellum preferentially activates when explicit discrimination of emotions is required (Fusar-Poli et al., 2009; Scheuerecker et al., 2007; Wright et al., 2008), and others reporting activity in cerebellum (specifically in the left hemisphere) also when emotion is task-incidental (Habel et al., 2007). Our results support the latter view, suggesting a general role of the cerebellum (specifically of Crus I and Crus II) in emotional appraisal, in line with the hypothesis that neurons of lobule VII (in which the Crus I and II are located) contribute to both emotional perception and evaluation (Adamaszek et al., 2017).

The mechanisms through which the cerebellum contributes to emotional processing remain to be clarified. It is possible that the cerebellum affects emotional processing by modulating responses in other cortical regions, such as the medial prefrontal cortex (involved in higher-order regulation and evaluative aspects of emotions, see Etkin, Egner, & Kalisch, 2011), with which Crus I is functionally connected (Krienen & Buckner, 2009). Accordingly, Cho et al. (2012) showed that 1Hz inhibitory repetitive TMS over the left lateral cerebellum decreased glucose metabolism in areas mediating emotions, such as orbitofrontal, medial frontal and anterior cingulate gyri (see also Halko et al., 2014). Similarly, Schutter et al. (2003) found that cerebellar TMS induced shifts in asymmetry in gamma frequency band in prefrontal cortices. Also, cerebellar lesions are associated to functional changes in neural activity in frontal areas during the perception of emotional stimuli (Adamaszek et al., 2015). The cerebellum seems also to be connected with the ventral premotor cortex (e.g., Dum & Strick, 2003), the inferior parietal lobule (e.g., Clower, West, Lynch, & Strick, 2001; Schmahmann & Pandya, 1989, 1991), and the inferior frontal gyrus (e.g., Tamada, Miyauchi, Imamizu, Yoshioka, & Kawato, 1999), all these areas representing crucial nodes of the mirror neuron systems (Iacoboni & Dapretto, 2006; Rizzolatti & Craighero, 2004; Urgesi, Candidi, & Avenanti, 2014). Mirrors mechanisms are relevant for the understanding of others' emotional states, as demonstrated by the finding that viewing facial expressions that convey emotions activates regions involved in experiencing similar emotions (e.g., Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Leslie, Johnson-Frey, & Grafton, 2004). Accordingly, altered cerebellar feedback projections to the inferior parietal lobule have been found in individuals with Asperger syndrome (Catani et al., 2008), in which deficits in mirroring ability are key features of the syndrome.

Nonetheless, the cerebellum may also directly mediate mechanisms important in emotion processing. For instance, Likowski et al. (2012) showed that activity in the lateral cerebellum correlated with activity in facial muscles (assessed by electromyography) in response to the observation of others' emotional facial expressions. Accordingly, mirror neurons (i.e., active during action observation and execution) have been identified in the cerebellum (Gazzola & Keysers, 2009; for a meta-analysis see Molenberghs, Cunnington, & Mattingley, 2012), with cerebellar regions specifically responding to observation and imitation of emotional expressions (Leslie et al., 2004; Schraa-Tam et al., 2012). Studies in the motor and cognitive domain suggest that the cerebellum mainly operates by generating simulations of events (i.e., actions) in the form of internal feedforward models (e.g., Courchesne & Allen, 1997; Ito, 2008; Leggio & Molinari, 2015; Peterburs et al., 2015; Schmahmann, 2010; for reviews see Bellebaum, Daum, & Suchan, 2012; D'Angelo & Casali, 2013). These internal models allow to predict the sensory consequences of a motor command but also, inversely, to transform a desired sensory end-state into a suitable motor pattern. In this view, observation of other agents' actions (but also others' emotional expressions) can be considered an instance of the inverse model (Gazzola & Keysers, 2009) in which the visual input is transformed into a simulated motor pattern able to facilitate action/emotion comprehension. Interfering by means of TMS with cerebellar activity might affect these (automatic) sensory-motor integration mechanisms, impairing emotional processing in our tasks, even when the emotional cues were task-irrelevant.

The impairment in emotion discrimination we observed is unlikely to depend on unspecific effects of cerebellar stimulation on face evaluation or decision making. Indeed, in Experiment 3 cerebellar TMS did not affect participants' capacity to classify gender of neutral faces. Accordingly, cerebellar patients are impaired in emotion discrimination but perform similarly to controls when non-emotional features (such as identity of neutral faces) need to be processed (Adamaszek et al., 2015). These findings are in line with previous evidence suggesting that the cerebellum is not part of the distributed brain network involved in face perception (e.g., Haxby, Hoffman, & Gobbini, 2000), but it rather plays a specific role in extracting the emotional content of facial expressions (Fusar-Poli et al., 2009). Also, our findings are unlikely to reflect unspecific interference on eye movements control exerted by the cerebellum (e.g., Lynch & Tian, 2006; Ramat, Leigh, Zee, & Optican, 2007): if that were the case, TMS should have affected gender discrimination of neutral faces as well. Furthermore, we set the timing of stimulation in our experiment so not to affect the processing of face information by the early visual cortex, information about facial features already reaching face-selective regions in extra-striate visual cortex 60-100 ms from face onset (see Pitcher et al., 2007). Therefore, the lack of TMS effects on the visual cortex in our experiment represents an important control to claim for cerebellar-selective stimulation effects (see Renzi et al., 2014), given the proximity of the cerebellum to early visual cortex.

Prior evidence suggests that the vermis and the right cerebellar hemisphere (that we did not stimulate in our experiments) are also important in emotional processing (e.g., Adamaszek et al., 2017; Fusar-Poli et al., 2009; Keren-Happuch et al., 2014). The vermis and paravermis regions have been found to be involved in experiencing and regulating emotions (Schmahmann et al., 2007; see also Schutter & von Honk; Schutter et al., 2009 for TMS evidence) and in emotional learning (e.g., Sacchetti, Scelfo, & Strata, 2009). In turn, the role of more posterior and lateral sections of the cerebellum in emotional processing has been less investigated. Moreover, although in our study we focused on visual discrimination, the role of the cerebellum in emotional processing is likely to extend beyond the visual domain. Indeed, the cerebellum seems to contribute to speech prosody comprehension (e.g., Wildgruber, Ackermann, Kreifelts, & Ethofer, 2006), and specifically to emotional prosody (e.g., Kotz et al., 2003; Sokolovsky et al., 2010). Future studies may investigate cerebellar contribution to emotion recognition across sensory modalities, considering different basic emotions (such as disgust) but also more sophisticated “social” emotions. Indeed, prior studies showed cerebellar involvement in the recognition of guilt and arrogance (D’Agata et al., 2011) and in moral evaluation (from the experience of moral emotion as compassion to the perception of moral violations, e.g., Han, Chen, Jeong, & Glover, 2016; Reniers et al., 2012). Moreover, recent views consider the cerebellum as a crucial neural node of the mentalizing network (e.g., Van Overwalle, Baetens, Mariën, & Vandekerckhove, 2014; Van Overwalle & Mariën, 2016).

In our study, cerebellar TMS affected accuracy without delaying response times. Cerebellar TMS may enhance excitability in *contralateral* motor cortex (Oliveri, Koch, Torriero, & Caltagirone, 2005), thus priming motor responses and possibly counteracting effects of cognitive interference. To avoid this though in our study participants responded with the cerebellar contralateral hand. A more likely explanation for our pattern of results is that in this paradigm error rate is more prone than response latencies to be modulated by TMS, as suggested by prior studies using a similar task (e.g., Pitcher, Garrido, Walsh, & Duchaine, 2008; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009) and also reporting selective effects of TMS on accuracy measures.

In interpreting our results, a few limitations need to be acknowledged. Our targeted sites were localized on *estimated* MRIs, a procedure widely used in TMS research (see Carducci & Brusco, 2012). Nonetheless, the use of *real* MRIs of each participant would have better controlled for intra- and inter-subjects anatomical variability enhancing localization precision (Parkin, Ekhtiari, & Walsh, 2015; Rusjan et al., 2010; Sack et al., 2009) and guiding coil orientation to obtain most effective stimulation (Kammer, Beck, Erb, & Grodd, 2001; Fox et al., 2004; Krieg, Salinas, Narayana, Fox, & Mogul, 2013; Sommer et al., 2012). Furthermore, we could not adjust for scalp-cortex distance in setting intensity of stimulation (e.g., Fox, Liu, & Pascual-Leone, 2013; Salinas, Lancaster, & Fox, 2007; Stokes et al., 2007), this possibly resulting into suboptimal stimulation of the cerebellar regions. Note though that TMS over the cerebellar hemispheres at 90%-100% of the motor threshold effectively modulated activity of cerebellar neurons and functional connectivity between the cerebellum and the cerebrum in prior studies (Cho et al., 2012; Halko et al., 2014). Finally, it is important to note that the effects we observed were overall small in size (also possibly due to the methodological limitations discussed above, see Sack et al., 2009), deserving further investigation.

In conclusion, our study using an online TMS paradigm shows that the (left) cerebellum is involved in perceiving the emotional content of facial stimuli, even when this is task irrelevant. Clarifying the role of the cerebellum in emotional processing and recognition may have critical clinical implications. Indeed, cerebellar dysfunctions have been associated to psychiatric disorders (such as schizophrenia and autism, e.g., Phillips et al., 2015; Shakiba, 2014), and cerebellar TMS has already been successfully tested as a therapeutic tool for psychiatric syndromes (Demirtas-Tatlidede et al., 2010).

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Figure legends

Figure 1. The timeline of an experimental trial in Experiment 1. Each trial started with a fixation cross (2500 ms), followed by the first face (150 ms), a blank screen (150 ms), and then by the second face (150 ms). Depending on the task they were assigned to (between-group design), participants had to indicate either 1) whether the two faces expressed the same or a different emotion (Emotion discrimination task); or 2) whether the two faces belonged to the same gender (Gender discrimination task). Triple-pulse TMS (20 Hz) was delivered between the offset of the first face and the onset of the second face.

Figure 2. Targeted sites on the scalp of one representative participant as shown by the neuronavigation system (Softaxic 2.0, EMS, Bologna, Italy): A) Left cerebellar hemisphere (x=−15, y=-82, z=-32, TAL), B) Early visual cortex (x=-2, y=-75, z=32, TAL). The blue line represents the magnetic field generated by the stimulator and the white and green segments represent the longitudinal and lateral orientation of the coil, respectively.

Figure 3. Bar chart displaying estimated marginal mean accuracy rates (A) and **box plots displaying accuracy rates** (B) as a function of TMS condition (Left cerebellum, Early visual cortex and Vertex) and Task (Emotion discrimination vs. Gender discrimination) in Experiment 1. **The error bars in the bar chart represent 95% CI. The boxes represent the middle 50% of the data in each experimental condition. The horizontal line within each box represents the median score and data points represent individual values.** TMS over the cerebellum impaired participants' accuracy in discriminating both facial emotional expressions and gender of emotional faces, compared to the other two stimulation conditions.

Figure 4. Bar chart displaying estimated marginal mean accuracy rates (A) and **box plots displaying accuracy rates** (B) as a function of TMS condition (Cerebellum vs. Early visual cortex) and Task (Emotion discrimination task vs. Gender discrimination) in Experiment 2.
The error bars in the bar chart represent 95% CI. The boxes represent the middle 50% of the data in each experimental condition. The horizontal line within each box represents the median score and data points represent individual values. TMS over the cerebellum impaired participants' accuracy in both tasks, compared to control stimulation**.**

Figure 5. Bar chart displaying estimated marginal mean accuracy rates (A) and **box plots displaying accuracy rates** (B) as a function of TMS condition (Cerebellum vs. Early visual cortex) and Task (Emotion discrimination task vs. Gender discrimination of neutral faces) in Experiment 3. **The error bars in the bar chart represent 95% CI. The boxes represent the middle 50% of the data in each experimental condition. The horizontal line within each box represents the median score and data points represent individual values.** TMS over the cerebellum selectively impaired participants' accuracy in discriminating facial emotional expressions, leaving gender discrimination of neutral faces unaffected. The asterisk denotes a significant difference between TMS conditions**.**

Figure 1

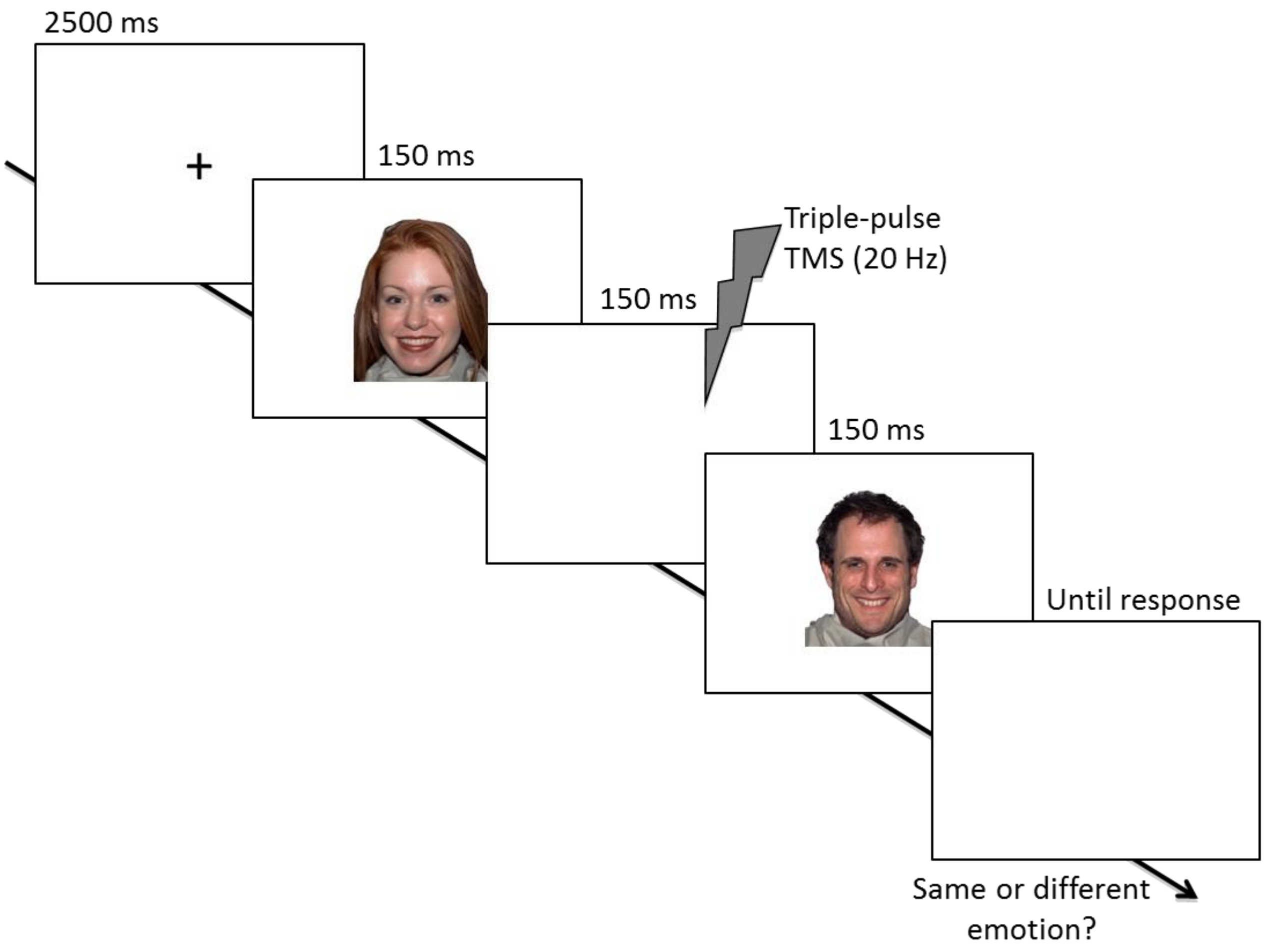


Figure 2

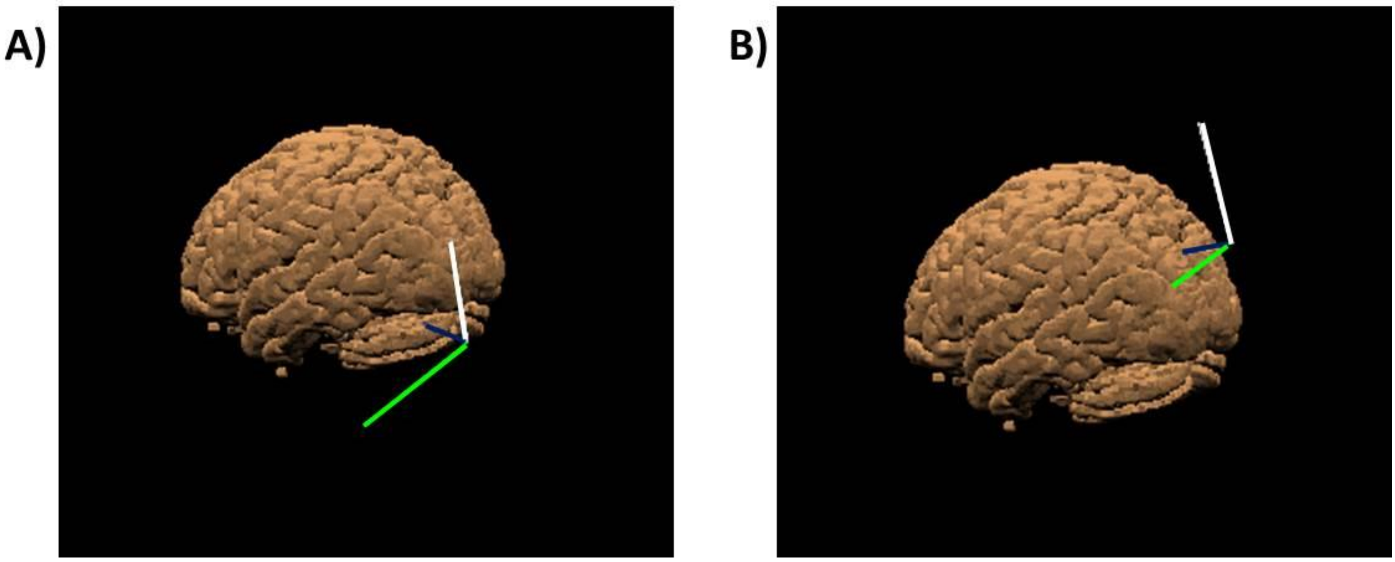
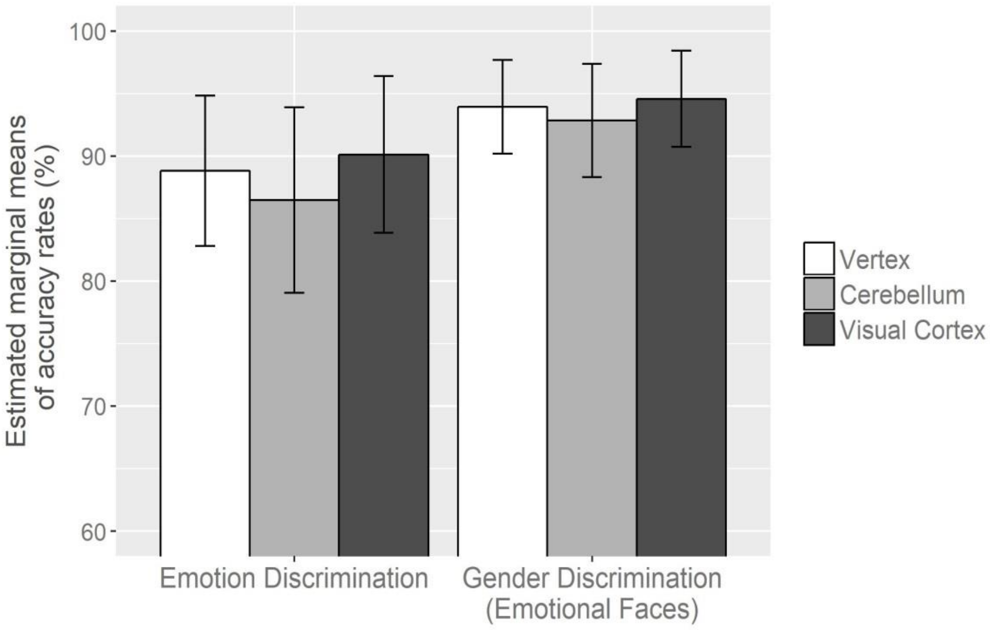


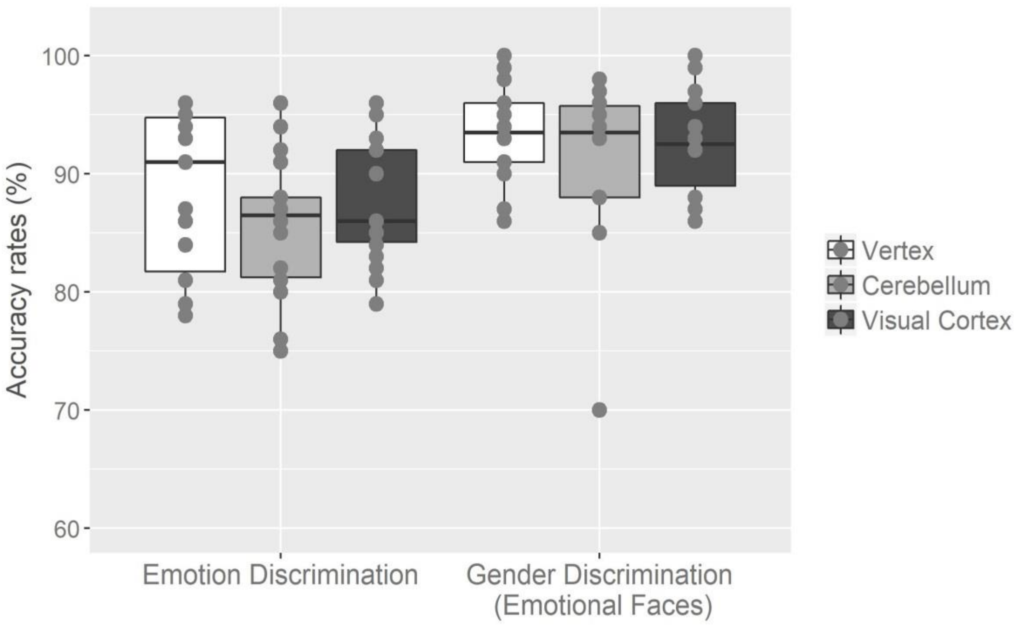
Figure 3

A)



Estimated marginal means of accuracy rates (%)
100
90
80
70
60
Emotion Discrimination
Gender Discrimination (Emotional Faces)
Vertex
Cerebellum
Visual Cortex

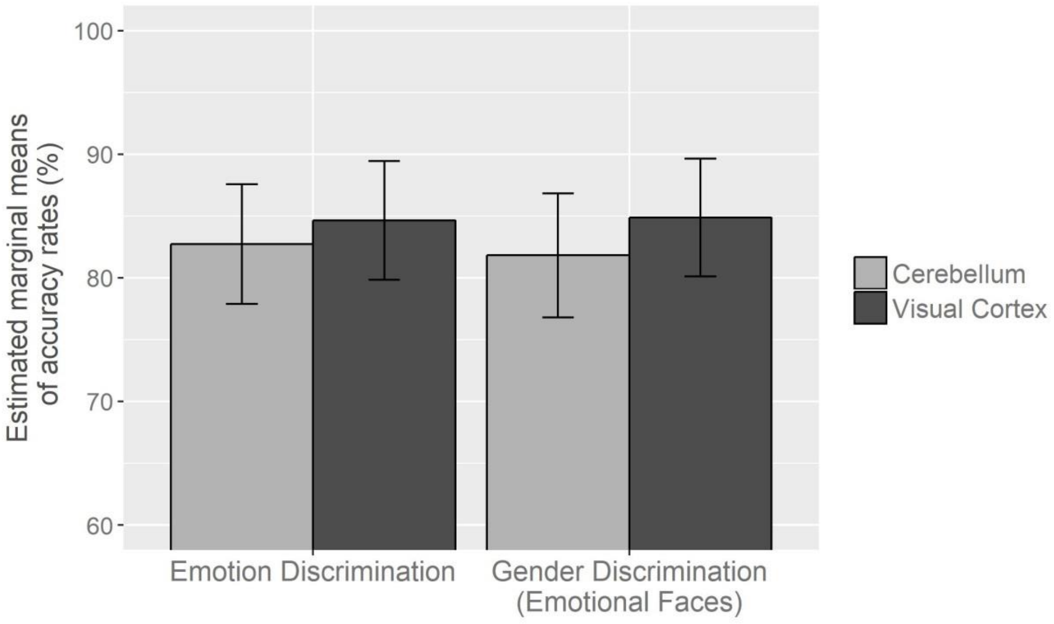
B)



Accuracy rates (%)
100
90
80
70
60
Emotion Discrimination
Gender Discrimination (Emotional Faces)
Vertex
Cerebellum
Visual Cortex

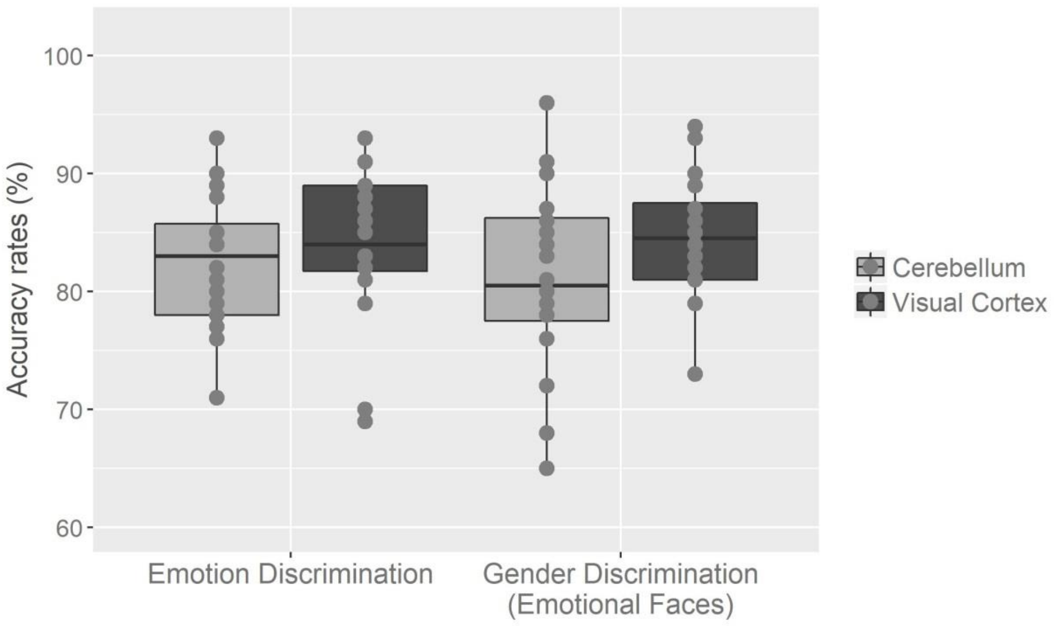
Figure 4

A)



100
90
80
70
60
Estimated marginal means of accuracy rates (%)
Emotion Discrimination
Gender Discrimination (Emotional Faces)
Cerebellum
Visual Cortex

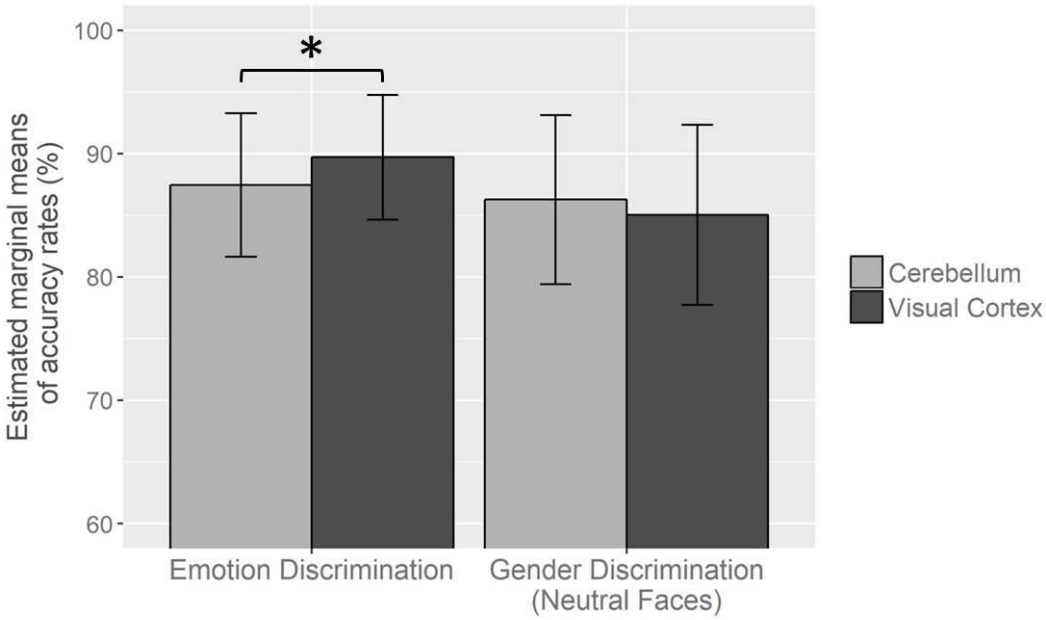
B)



100
90
80
70
60
Accuracy rates (%)
Emotion Discrimination
Gender Discrimination (Emotional Faces)
Cerebellum
Visual Cortex

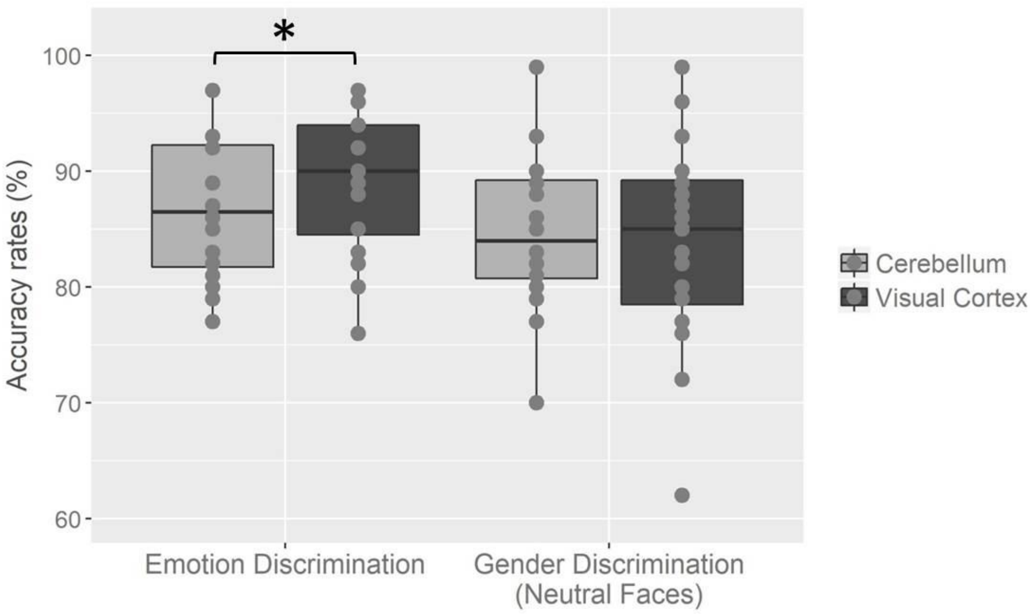
Figure 5

A)



100
90
80
70
60
*
Estimated marginal means of accuracy rates (%)
Emotion Discrimination
Gender Discrimination (Neutral Faces)
Cerebellum
Visual Cortex

B)



100
90
80
70
60
*
Accuracy rates (%)
Emotion Discrimination
Gender Discrimination (Neutral Faces)
Cerebellum
Visual Cortex