

## Cerebellar anodal tDCS increases implicit remapping

1 **Cerebellar anodal tDCS increases implicit visuomotor remapping when strategic re-aiming is**  
2 **suppressed**

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17 rotation, cerebellum, transcranial direct current stimulation, sensorimotor adaptation

18

19 **Abstract**

20

21 The cerebellum is known to be critically involved in sensorimotor adaptation. Changes in cerebellar  
22 function alter behaviour when compensating for sensorimotor perturbations, as shown by non-invasive  
23 stimulation of the cerebellum and studies involving patients with cerebellar degeneration. It is known,  
24 however, that behavioural responses to sensorimotor perturbations reflect both explicit processes (such as  
25 volitional aiming to one side of a target to counteract a rotation of visual feedback) and implicit, error-  
26 driven updating of sensorimotor maps. The contribution of the cerebellum to these explicit and implicit  
27 processes remains unclear. Here, we examined the role of the cerebellum in sensorimotor adaptation to a  
28 30° rotation of visual feedback of hand position during target-reaching, when the capacity to use explicit  
29 processes was manipulated by controlling movement preparation times. Explicit re-aiming was  
30 suppressed in one condition by requiring subjects to initiate their movements within 300ms of target  
31 presentation, and permitted in another condition by requiring subjects to wait approximately 1050ms after  
32 target presentation before movement initiation. Similar to previous work, applying anodal transcranial  
33 direct current stimulation (tDCS; 1.5mA) to the right cerebellum during adaptation resulted in faster  
34 compensation for errors imposed by the rotation. After exposure to the rotation, we evaluated implicit  
35 remapping in no-feedback trials after providing participants with explicit knowledge that the rotation had  
36 been removed. Crucially, movements were more adapted in these no-feedback trials following cerebellar  
37 anodal tDCS than after sham stimulation in both long and short preparation groups. This suggests that  
38 cerebellar anodal tDCS increased implicit remapping during sensorimotor adaptation irrespective of  
39 preparation time constraints. This work shows that the cerebellum is critical in the formation of new  
40 visuomotor maps that correct perturbations in sensory feedback, both when explicit processes are  
41 suppressed and when allowed during sensorimotor adaptation.

42

43 **Cerebellar anodal tDCS increases implicit visuomotor remapping when strategic re-aiming is**  
44 **suppressed**

45 The cerebellum has long been known to play a crucial role in predicting the sensory consequences of  
46 motor commands [1]; a process that appears necessary both for rapid online responses to unexpected  
47 events, and for trial-by-trial compensation of systematic sensorimotor disturbances (for recent reviews,  
48 see [2, 3]). When a perturbation of sensory feedback (e.g., a rotation in visual feedback of a movement  
49 trajectory, or a force field that pushes the moving hand away from its intended direction) evokes a  
50 mismatch between the predicted sensory outcomes and the actual sensory outcomes, the internal mapping  
51 between motor commands and resulting changes in sensory state is thought to be updated, such that the  
52 prediction error is minimized in subsequent movements. The likely involvement of the cerebellum in this  
53 process is supported by a large body of computational, neurophysiological and neuropsychological work.  
54 For example, patients with selective degeneration of the cerebellum show substantially impaired capacity  
55 to correct for various different types of perturbations, including velocity-dependent force-fields [4-6],  
56 translated feedback of the entire visual field [7-9], rotated visual feedback of hand movement trajectories  
57 [10, 11], or adaptation of walking to differing speeds imposed on the left and right legs in split-belt  
58 treadmill adaptation [12, 13].

59 People compensate for systematic sensorimotor perturbations, either by using an explicit strategy to alter  
60 their movement characteristics (e.g., explicitly aiming in a different direction from the target), or through  
61 implicit learning of new sensory-motor mappings [14, 15]. It has been proposed that the cerebellum is not  
62 required to strategically modify movements, as patients with cerebellar degeneration can use re-aiming  
63 strategies when explicitly instructed how to do so [16]. Although this suggests that the cerebellum is not  
64 crucial in implementing strategic compensations to perturbations, the observation that patients typically  
65 do not spontaneously develop such strategies implies that the cerebellum may play a role in identifying or  
66 formulating strategies [16]. Importantly, it has been shown that the initial rapid rate of error reduction in  
67 sensorimotor adaptation tasks is dominated by the explicit component of sensorimotor adaptation [14, 17].  
68 Several studies have shown that increasing the excitability of the cerebellum via non-invasive brain  
69 stimulation increases the rate of the initial rapid error reduction in sensorimotor adaptation tasks [18-22],  
70 raising the possibility that faster error compensation with cerebellar anodal tDCS occurs in part by  
71 upregulating explicit processes.

72 No previous studies have assessed whether cerebellar anodal tDCS affects the rate or extent of  
73 sensorimotor adaptation when explicit compensatory processes are suppressed. One way to dissociate  
74 implicit and explicit mechanisms during adaptation is to reduce the amount of time available to prepare  
75 movement [23-25], because employing explicit re-aiming strategies is difficult under time pressure, and  
76 longer movement preparation time is associated with the employment of explicit re-aiming strategies [26,  
77 27]. Here, we examined whether cerebellar anodal tDCS affected adaptation to a 30° rotation of visual  
78 feedback of the movement trajectory when explicit processes were suppressed by enforcing short  
79 preparation times [24]. Crucially, we quantified the extent to which participants acquired new  
80 sensorimotor maps in trials where participants reached towards targets without visual feedback of  
81 movements, and with knowledge that the rotation had been removed. Cerebellar anodal tDCS increased  
82 the extent of *implicit* remapping resulting from exposure to the perturbation in both preparation time  
83 conditions. This suggests that the cerebellum contributes to implicit sensorimotor remapping regardless of  
84 whether explicit strategy use is suppressed or allowed during learning.

## 85 **Method**

### 86 **Participants**

87 Seventy-two right-handed individuals (mean age= 22.2, years SD=2.85) completed the study. We decided  
88 to collect a minimum of 14 datasets for each condition a-priori, based on our previous study which  
89 showed reliable effects of manipulating preparation time with 14 participants in short and long  
90 preparation time conditions [25]. For each participant group, half of the participants were randomly  
91 assigned to clockwise and counter-clockwise conditions. Data from four participants were excluded from  
92 the analysis: due to experimenter error for three participants (two received incorrect task instructions, one  
93 did not complete a baseline phase), and due to voluntary dropout in one participant. No other datasets  
94 were removed from the analyses. The final sample sizes for each experimental condition were as follows:  
95 Cerebellar Anodal Short Preparation time (n=15, 7 counterclockwise, 8 clockwise), Cerebellar Sham  
96 Short Preparation Time (n=14, 7 counterclockwise, 7 clockwise), Cerebellar Anodal Long Preparation  
97 Time (n=21, 10 counterclockwise, 11 clockwise), Cerebellar Sham Long Preparation Time (n=20, 9  
98 counterclockwise, 9 clockwise). All participants were naïve to visuomotor rotation and force-field  
99 adaptation tasks. Participants were reimbursed with course credits or with monetary reimbursement of  
100 \$10 per hour of participation. The experiments were approved by the Ethics Committee of the University  
101 of Queensland and are in accordance with The Declaration of Helsinki.

102 **tDCS**

103 Prior to behavioral testing, the scalp area overlying the right cerebellum was localized using the  
104 international electroencephalographic 10 – 20 system. For all groups, the anodal electrode was placed  
105 over the scalp area estimated to overlie the right cerebellar cortex (3 cm lateral to the inion), and the  
106 reference electrode was positioned on the skin area overlying the right buccinator muscle[28]. This  
107 method of localizing the right cerebellum has been found to be appropriate for tDCS of the right  
108 cerebellum. 4.5 x 4.5 cm carbon-rubber electrodes were encased in saline soaked sponge pads (4.5 cm x 6  
109 cm, Soterix Medical Inc. EasyPAD), and secured using Velcro straps, and stimulation was generated with  
110 a Soterix (Soterix Medical Inc., NY) (current density of approximately 0.08 mA/cm<sup>2</sup>). The current was  
111 gradually ramped up to 1.5 mA over 30 s starting from the last 10 baseline trials prior to the adaptation  
112 block, before the initial block of adaptation trials. The stimulation lasted the entire adaptation block, or a  
113 maximum of 40 minutes, whichever came sooner, and then was gradually ramped down over 30s. For the  
114 sham tDCS conditions, the current was ramped down over a 30 s period immediately after achieving the  
115 maximum of 1.5mA.

116 **Apparatus**

117 Participants completed the task using the VBOT planar robotic manipulandum, a custom-built planar  
118 robotic interface with a low-mass, two-link carbon fibre arm which measures position with optical  
119 encoders sampled at 1,000 Hz. For more details of the experimental setup, see Howard, Ingram (29).  
120 Participants made centre-out horizontal reaching movements by moving the handle of the manipulandum  
121 to move an on-screen circular cursor (radius 0.25cm) from a start circle (radius 0.5cm) to a target circle  
122 (radius 0.5cm), projected on a computer monitor (ASUS, VG278H, Taiwan) running at 60Hz mounted  
123 above the vBOT via a mirror in a darkened room. Participants observed the monitor via its reflection onto  
124 a horizontal mirror which prevented direct vision of their arm, and gave the illusion that the cursor and  
125 targets were located in the plane of hand motion. Participants were seated on a chair height-adjusted to  
126 allow optimal viewing of the screen for the duration of the experiment. The right forearm was supported  
127 by an air-sled which rested on a glass table. Compressed air was forced out of small holes in the air-sled  
128 runners, which allowed low friction in the plane of movement. Targets appeared randomly in one of eight  
129 locations (0°, 45°, 90°, 135°, 180°, 225°, 270° and 315° relative to the start circle located centrally on-  
130 screen). The distance from the center of the start circle to the center of the targets was 9cm.

## 131 **General Trial Structure**

132 Participants were instructed that their goal was to move the cursor (radius 0.25cm) as accurately as  
133 possible from the start circle (radius 0.5 cm) to the target circle (radius 0.5cm). Participants were  
134 instructed not to stop on the target, but to slice through the target. Across all conditions, a sequence of  
135 three tones spaced 500 ms apart were presented at a clearly audible volume via external speakers.  
136 Participants were instructed to time the onset of their movements with the onset of the third tone. This  
137 timed-response paradigm has previously been shown to be effective in encouraging adherence to stringent  
138 response time requirements [30-33]). Movement initiation was defined online as when hand speed  
139 exceeded 2cm/s. Targets appeared at 1000ms (long preparation time condition) or 250 ms minus a display  
140 latency ( $27.6 \pm 1.8$  ms), prior to the third tone. Thus target direction information became available 972.4  
141 or 222.4ms before the desired initiation time. When movements were initiated 50 ms later than the third  
142 tone, the trial was aborted: the screen was blanked and a “Too Late” on-screen error signal appeared.  
143 Similarly, when movements were initiated more than 100 ms before the desired initiation time, the trial  
144 was aborted: the screen was blanked and a “Too Soon” on-screen error signal appeared. No visual  
145 feedback about movements was available when trials were aborted. Thus, all movements recorded and  
146 analysed were made according to the following “hard cut-off” times: within 1022.4 ms after target  
147 presentation for the long preparation time condition, and within 272.4 ms after target presentation for the  
148 short preparation time condition.

149 Participants in all conditions first completed a **baseline** pre-rotation block of 6 cycles (48 trials) with  
150 veridical feedback of their movement trajectories via on-screen cursor position to familiarize them with  
151 the task. The baseline block was followed by an adaptation block (60 cycles, i.e., 480 trials) with either a  
152 30° clockwise or counterclockwise rotation of visual feedback relative to the center of the start circle. The  
153 **adaptation** block was followed by a **no-feedback** block of 6 cycles (i.e., 48 trials), where visual feedback  
154 of cursor position was hidden immediately after the cursor left the start circle. Crucially, before  
155 commencing this block, participants were explicitly instructed that there was no longer any disturbance of  
156 visual feedback, and that they should aim straight towards the target [14, 34]. The residual learning that  
157 remained after removing the influence of explicit learning is therefore assumed to be implicit in nature--  
158 this no-feedback block is therefore thought to assay implicit acquisition of new sensorimotor maps  
159 (thereafter termed **implicit remapping**). Finally, participants completed a **washout** block of 6 cycles (48  
160 trials) where unrotated visual feedback of cursor position was available to enable participants to return

161 movements to the unadapted state. The same preparation time constraints were maintained throughout  
162 the entire experiment for each group.

### 163 **Data analysis**

164 Movement onset time was taken as the time at which hand speed first exceeded 2 cm/s. Movement  
165 direction was quantified at 20 percent of the movement distance. This procedure ensured that movement  
166 direction was quantified at less than 200ms into the movement, at which time the size of online  
167 corrections in hand position is small [35].

168 Intrinsic biases in reaching direction can affect adaptation behaviour [36-38]. Intrinsic biases were  
169 estimated by averaging movements from the last baseline cycle that were within 90° of the target (i.e., 45°  
170 clockwise or counterclockwise of the target). Then, this (estimated) bias was subtracted from movement  
171 direction for each trial. Trials were averaged in cycles of 8 trials (one cycle for each of the 8 target angles)  
172 for analysis. In the adaptation, no-feedback, and washout blocks, data for participants who experienced  
173 counterclockwise rotations (-30°) were sign-transformed and collapsed for analysis with data for  
174 participants who experienced clockwise (+30°) rotations. We did not apply any outlier removal procedure  
175 for the adaptation phase, the no-feedback phase, and the washout phase.

176 For the adaptation phase, we defined adaptation into an early phase and a late phase by splitting the 60-  
177 cycle adaptation block into two phases: the early phase (Cycles 1-30), and the late phase (Cycles 31-60).  
178 Separate ANOVAs with between-subjects factors Stimulation (cerebellar anodal tDCS, cerebellar sham  
179 tDCS) and Preparation Time (short preparation time, long preparation time) and within-subjects factors  
180 Cycle were run for the early and the late phase. To evaluate implicit remapping after attaining explicit  
181 knowledge that the rotation had been removed, we ran Stimulation (cerebellar anodal tDCS, cerebellar  
182 sham tDCS) x Preparation Time (short preparation time, long preparation time) x Cycle ANOVAs, and a  
183 separate stimulation (Sham, Stim) x Preparation Time (Short, Long) ANOVA on the No Feedback block.  
184 For these mixed-ANOVAs, rotation direction was included as a variable of no interest in our ANOVAs,  
185 as rotation direction was not part of our hypotheses, and multi-way mixed ANOVAs with a large number  
186 of factors have an increased likelihood of generating spurious results (Cramer et al. 2016).

187 In addition, to examine the rate of adaptation without the possible confound of intrinsic bias in movement  
188 direction, we also fit cycle-averaged movement directions for each dataset to a single-rate exponential  
189 function [39], as follows:

$$y = y_0 e^{-kx} + a$$

190 where  $y$  is the movement direction,  $x$  is the trial number,  $k$  is the rate constant that indicates the rate with  
191 which movement direction changes,  $a$  is the movement direction at which performance reaches  
192 asymptote, and  $y_0 + a$  is the hypothetical  $y$  value when  $x$  is zero.

193 We also examined the rate of de-adaptation in the washout block by fitting cycle-averaged movement  
194 directions for the washout block to a straight line, as follows:

$$195 \quad y = YIntercept + slope * x$$

196 where  $y$  is the movement direction,  $x$  is the trial number, slope is the rate constant that indicates the rate  
197 with which movement direction changes, and  $YIntercept$  is the hypothetical  $y$  value when  $x$  is zero.

198 GraphPad 7.0 least squares non-linear regression was used to fit data to both functions. Non-linear  
199 regression failed to converge to the exponential function for one cerebellar sham tDCS long preparation  
200 time dataset.

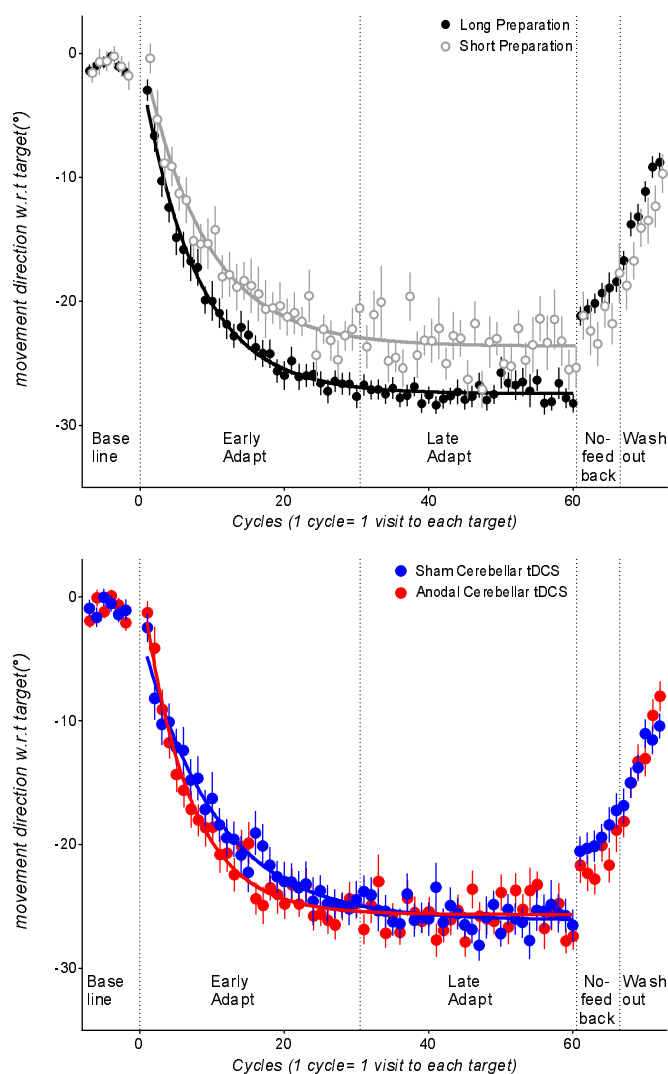
201 Stimulation (cerebellar anodal tDCS, cerebellar sham tDCS) x Preparation Time (short preparation time,  
202 long preparation time) x Rotation Direction (clockwise, counterclockwise) ANOVAs were run on rate  
203 constants. For all ANOVAs, when Mauchly's test of sphericity was significant, the Greenhouse-Geisser  
204 correction was used to adjust degrees of freedom. Partial  $\eta$ -squares were used to report ANOVA effect  
205 sizes, with values of 0.01 or less considered small, values between 0.01 and 0.09 considered medium; and  
206 values in excess of 0.25 considered large. Sidak corrections were used for post-hoc tests where necessary.

## 207 **Results**

208 Figure 1 plots movement directions for all experimental blocks, collapsed across the long and the short  
209 preparation time conditions (Figure 1 top panel) and collapsed across the cerebellar anodal tDCS and the  
210 cerebellar sham tDCS conditions (Figure 1 bottom panel). Figure 2 plots movement directions for all  
211 experimental blocks separately for each preparation time condition (short preparation time condition  
212 shown in Figure 2 top panel, long preparation time condition shown in Figure 2 bottom panel).

213 insert Figure 1 about here—



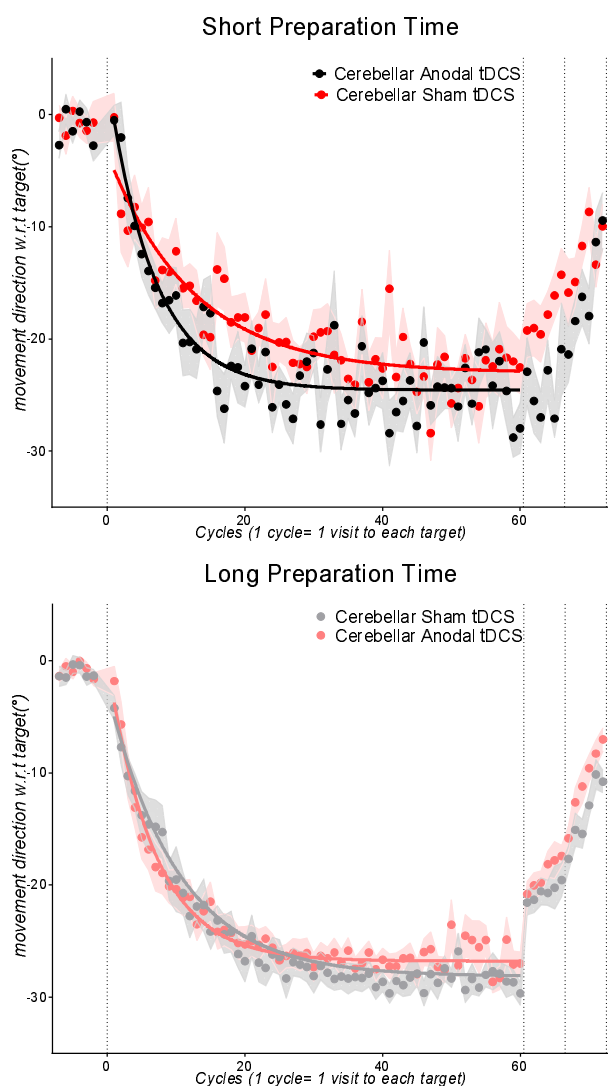


214

215 *Figure 1. Top panel: cycle by cycle movement directions relative to the target, averaged across the short preparation time*  
216 *groups (clear circles), and the long preparation time groups (grey circles) (i.e., pooled across the cerebellar tDCS anodal and*  
217 *sham conditions). Bottom panel: cycle by cycle movement direction relative to the target, averaged across all participant groups*  
218 *who received cerebellar sham tDCS and cerebellar anodal tDCS (i.e., pooled across long and short preparation time groups).*  
219 *Data from the counterclockwise rotation groups were sign-transformed to allow statistical comparisons between clockwise and*  
220 *counterclockwise groups. In the adaptation block, values closer to -30° indicate more complete error compensation. In the no-*  
221 *feedback block, values closer to -30° indicate more implicit remapping, as participants were instructed that the rotation was*  
222 *removed, and that they were to aim straight towards the target without visual feedback of their movement. Error bars indicate*  
223 *standard errors of the mean. Lines indicate group mean data fit to the single-rate exponential function for the adaptation phase.*

224

Insert Figure 2 about here.



225

226 *Figure 2. Top: Cycle by cycle movement directions with respect to the target for the short preparation time participants who*  
227 *received cerebellar anodal tDCS (red symbols) and cerebellar sham tDCS (black symbols). Bottom: cycle by cycle movement*  
228 *directions with respect to the target for the long preparation time participants who received cerebellar anodal tDCS (pink*  
229 *circles) and cerebellar sham tDCS (grey circles). Solid lines indicate group mean data fit to the single-rate exponential function*  
230 *for the adaptation phase.*

231 Before the rotation was imposed, participants completed 48 baseline trials (i.e., 6 cycles; 6 visits to each  
232 target). Participants tended to show a clockwise bias in this baseline phase (see Figure 1 top and bottom  
233 panels). To evaluate whether participant groups differed in accuracy of movement direction before the  
234 rotation was imposed, we ran a cycle (baseline cycle4, baseline cycle 5, baseline cycle 6) x Preparation  
235 Time (Short, Long) x Stim (Sham, Stim) ANOVA. Importantly, groups receiving anodal or sham

236 cerebellar tDCS did not differ reliably in directional accuracy, as there was no significant main effect of  
237 stimulation. Movement directions also did not differ reliably between the long and the short preparation  
238 time conditions (non-significant main effect of Preparation Time, no significant interactions with  
239 preparation time, all  $p > 0.2$ ).

240 **Early adaptation:** After the 30° rotation was imposed, participants compensated for the error  
241 imposed by the rotation by moving in the opposite direction to the rotation (see Figure 1, where  
242 more compensation for a 30° clockwise rotation would be indicated by movements closer to 30°:  
243 data from the counterclockwise rotation conditions were sign transformed to allow collapsing  
244 with data from the clockwise rotation condition). To evaluate the effect of the tDCS and  
245 preparation time manipulations on the early phase of error compensation, a Stimulation  
246 (cerebellar anodal tDCS, cerebellar sham tDCS) x Preparation Time (short preparation time, long  
247 preparation time) x Cycle (Adaptation Cycle 1...Cycle 30) ANOVA was run. Movement  
248 directions became progressively closer to the adapted movement direction with increasing cycles,  
249 as shown by a significant main effect of Cycles,  $F(12,721.6) = 69.09$ ,  $p = 0$ , partial  $\eta$ -squared =  
250 0.53. Constraining preparation time resulted in less error compensation (see Figure 1 top panel,  
251 where better compensation for the rotation is indicated by movements closer to -30°), as shown  
252 by a significant main effect of Preparation Time,  $F(1,60) = 6.71$ ,  $p = 0.012$ , partial  $\eta$ -squared =  
253 0.1. Hence, shortening preparation time resulted in less error compensation in the early phase of  
254 adaptation, corroborating our previous results which showed that shortening preparation time can  
255 provide a sufficient assay of implicit learning [25]. We previously showed that shortening  
256 preparation time in this way resulted in similar rates and extents of error compensation to  
257 estimates of implicit learning obtained by subtracting aiming directions[14].

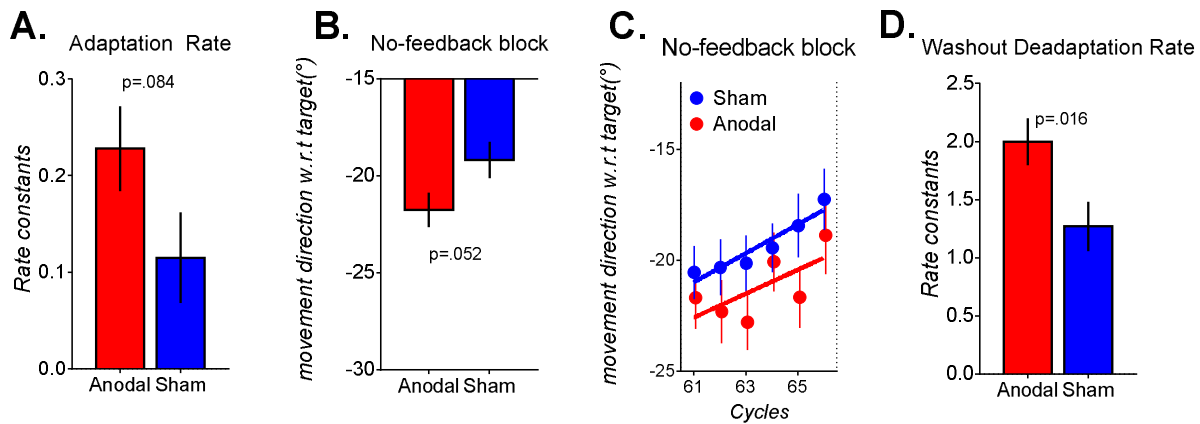
258 Similar to previous research [19, 21, 40], error compensation for the visuomotor rotation tended  
259 to be faster for cerebellar anodal tDCS than for sham tDCS (see Figure 1 bottom panel),  
260 (significant Cycles x Stim interaction,  $F(12,721.6) = 2.18$ ,  $p = 0.011$ , partial  $\eta$ -squared = 0.03).  
261 Note however that this was only a moderate effect size, appeared considerably weaker than that  
262 found in previous studies[19, 21, 40].

263 **Late adaptation:** Stimulation (cerebellar anodal tDCS, cerebellar sham tDCS) x Preparation  
264 Time (short preparation time, long preparation time) x Cycle ANOVA was run on the late phase  
265 (cycles 31...60) of the adaptation block. Similar to our previous results [25], restricting  
266 preparation time resulted in less error compensation in the late adaptation phase (see top panel  
267 Figure 1), as shown by a significant main effect of Preparation Time,  $F(1,60) = 12.02$ ,  $p = 0.001$ ,  
268 partial  $\eta$ -squared = 0.16. There was a significant Cycles x Stim interaction,  $F(13.8,829.4) = 2$ ,  $p$   
269 = 0.016, partial  $\eta$ -squared = 0.03.

### 270 **Rate of adaptation quantified by rate constants**

271 To guard against the possibility that results from analyses of mean movement directions resulted from  
272 individual differences in intrinsic directional biases in reaching movements, we additionally quantified  
273 error compensation in terms of rate constants obtained from fitting adaptation phase single subject data to  
274 a single-rate exponential model [19]. Preparation Time x Stimulation ANOVAs on rate constants showed  
275 a marginal main effect of stimulation,  $F(1,59) = 3.09$ ,  $p = 0.084$ , partial  $\eta$ -squared = 0.05. This reflected a  
276 trend for larger mean rate constants (i.e., faster adaptation) with cerebellar anodal tDCS than with sham  
277 (see Figure 3A). Rate constants for the groups receiving anodal tDCS tended to be larger than rate  
278 constants for the groups receiving sham tDCS (see Figure 3A). The main effect of preparation time was  
279 not reliable. There were no other reliable main effects or interactions.

280           insert Figure 3 about here.



281

282 Figure 3. Group mean (error bars are SEM) for data from the cerebellar anodal tDCS condition (Stim,  
283 red) and the cerebellar sham tDCS condition (Sham, blue). **A:** rate constants from fitting a single-rate  
284 exponential function to cycle-averaged movement directions from the adaptation block—larger values  
285 indicate faster adaptation to the rotation. **B & C.** Group mean movement direction from the no-feedback  
286 block, averaged across cycles (B) or cycle-by-cycle (C)—values closer to  $-30^\circ$  represent more adapted  
287 movements. **D.** Slopes from fitting a straight line to individual cycle-averaged movement directions in the  
288 washout block-- larger values indicate faster de-adaptation to the unadapted state.

### 289 Cerebellar anodal tDCS increased implicit remapping

290 After exposure to the perturbation in the adaptation block, participants were explicitly told the rotation  
291 was removed, and they should aim straight to the targets in the subsequent post-adaptation no-feedback  
292 block, following protocols from Taylor, Krakauer (14). These instructions were crucial to properly  
293 quantify *implicit* acquisition of sensorimotor maps resulting from adaptation to the rotation (thereafter  
294 termed *implicit remapping*), as movements that remained adapted despite explicit instructions that the  
295 rotation was no longer present are likely to reflect residual implicit learning after removing the influence  
296 of explicit learning. Explicit knowledge that the rotation has been removed results in an abrupt drop-off of  
297 adaptation from the last adaptation cycle to the first no-feedback cycle, as previously documented [25].

298 A Preparation Time (Long, Short) x Stimulation (anodal, sham) x Cycle (No Feedback Cycle 1... Cycle  
299 6) ANOVA showed a significant main effect of Cycles,  $F(3.3,201.2) = 3.48$ ,  $p = 0.013$ , partial  $\eta$ -squared  
300 = 0.05, as movements decayed slowly across cycles in the absence of visual feedback, corroborating  
301 previous results [14, 21, 41]. There was a marginal main effect of Stim,  $F(1,60) = 3.94$ ,  $p = 0.052$ , partial  
302  $\eta$ -squared = 0.06 (moderate effect size), as movements were overall more adapted with anodal tDCS than  
303 with sham (see Figure 3B, cycle averaged movement directions across the no-feedback block: anodal

304 tDCS:  $-21.7 \pm 0.9^\circ$ , sham tDCS:  $-19.1 \pm 0.9^\circ$ ). There was a significant Preparation Time x Stim  
305 interaction,  $F(1,60) = 10.39$ ,  $p = 0.002$ , partial  $\eta$ -squared = 0.14. Follow-up ANOVAs were run separately  
306 for the Short and the Long preparation time datasets. For short preparation time, there was a significant  
307 main effect of stimulation,  $F(1,25) = 7.65$ ,  $p = 0.01$ , partial  $\eta$ -squared = 0.23, as movements were more  
308 adapted in this no-feedback block with anodal stimulation than with sham stimulation (group mean of no-  
309 feedback cycles: sham tDCS =  $17.7 \pm 1.8^\circ$ , anodal tDCS =  $24.5 \pm 1.7^\circ$ ,  $p = .010$ , sidak-corrected,  $d = 1.04$ ,  
310 large effect size). For the long preparation time group, the main effect of stimulation and the cycle x  
311 stimulation interaction failed to reach significance.

312 **Washout:** Here, cursor feedback of movements was returned, and the error incurred by removal of the  
313 rotation became visible to participants. Participants thus rapidly returned movements to the un-adapted  
314 state (see Figure 1 washout phase). Preparation Time (Short, Long) x Stim (Anodal, Sham) x Cycles  
315 (Washout 1...Washout 6) ANOVA showed a significant Preparation Time x Stim interaction,  $F(1,60) =$   
316  $6.85$ ,  $p = 0.011$ , partial  $\eta$ -squared = 0.1 a significant Cycles x Stim interaction,  $F(4,245.6) = 2.4$ ,  $p =$   
317  $0.049$ , partial  $\eta$ -squared = 0.03, and a significant Cycles x Preparation Time x Stim interaction,  $F(4,245.6)$   
318  $= 2.76$ ,  $p = 0.027$ , partial  $\eta$ -squared = 0.04. Follow-up ANOVAs were run separately for the short and  
319 long preparation time conditions. For the short Preparation Time groups, there was a significant Cycles x  
320 Stim interaction,  $F(4.4,114.9) = 2.49$ ,  $p = 0.041$ , partial  $\eta$ -squared = 0.08, as participants in the anodal  
321 tDCS condition showed slower washout of adapted movements to the un-adapted state compared to sham  
322 tDCS. For the long preparation time condition, there was main effect of stimulation,  $F(1,35) = 5.61$ ,  $p =$   
323  $0.023$ , partial  $\eta$ -squared = 0.13, as movements in the anodal tDCS condition tended to be *less* adapted  
324 compared to sham (mean of washout cycles 1-6: sham tDCS:  $-13.6 \pm 0.9^\circ$ , anodal tDCS  $-10.8 \pm 0.8^\circ$ ).  
325 These results corroborate that of Galea et al. (2011) who found a trend for faster washout with cerebellar  
326 anodal tDCS in their Experiment 1.

327 **Rate of deadaptation quantified by rate constants:** We fit individual cycle-averaged washout phase  
328 movement directions to a straight line to obtain slopes—this provides an assay of the rate of washout  
329 which is less influenced by differences in the intrinsic biases in reaching direction, as well as movement  
330 direction at the start of the washout phase. We ran a Preparation Time x Stim x Rotation Direction  
331 ANOVA on the slopes. There was a significant main effect of Stim  $F(1,60) = 6.16$ ,  $p = .016$ , partial  $\eta$ -  
332 squared = .09, as the rate of washout was faster with anodal tDCS than with sham (see Figure 3D).

333

## 334 **Discussion**

335 The cerebellum has long been known to play a crucial role in adapting movements to perturbations of  
336 sensory feedback [7-9]. Previous work showed that increasing cerebellar excitability via non-invasive  
337 stimulation of the cerebellum speeds up error compensation during adaptation to perturbations such as  
338 rotated visual feedback [19, 21, 40], force-field perturbations of movement trajectories [22], as well as  
339 locomotor adaptation to split-belt treadmill walking [20]. However, to the best of our knowledge, none of  
340 these previous studies controlled for the use of explicit processes, such as volitionally applied  
341 compensatory strategies. Previous studies demonstrating the effects of cerebellar tDCS tended to be  
342 clearest in the initial stage of error compensation [21], which is now known to be dominated by explicit  
343 processes [14]. Given accumulating evidence for the cerebellum's role in predicting sensory events and  
344 fine-tuning of behavioral responses in many higher-order cognitive tasks [42], it was unclear whether  
345 previous findings of faster error compensation with cerebellar stimulation were due to the effects of  
346 cerebellar stimulation on explicit processes, implicit processes, or both. The current data show that  
347 despite reducing the amount of time available for movement preparation to suppress explicit strategy use,  
348 cerebellar anodal tDCS still increased the rate of adaptation. Furthermore, after perturbation removal and  
349 despite explicit knowledge that the rotation had already been removed, movements remained more  
350 adapted with cerebellar anodal tDCS than with sham tDCS. These results provide evidence of cerebellar  
351 involvement in implicit learning processes in adaptation to visuomotor rotations in healthy adults.

352 These current findings that increasing cerebellar excitability increased post-adaptation implicit remapping  
353 corroborates a large body of work in humans and non-human primates [3]. Previous studies have shown  
354 smaller aftereffects in patients with cerebellar degeneration [4, 7, 43, 44], however, these findings of  
355 smaller aftereffects might not reflect deficits in implicit error-based learning alone, as it is unclear  
356 whether patients and healthy controls had equivalent explicit knowledge of perturbation removal in those  
357 studies.

358 We also found that increasing cerebellar excitability with anodal tDCS increased the rate at which  
359 participants altered movements to (1) reduce errors resulting from a rotation in the adaptation phase, and  
360 (2) reduce errors resulting from sudden removal of a rotation after adapting movements to the rotation.  
361 This result corroborates that of previous work, although the effect of cerebellar anodal tDCS on error  
362 compensation here was substantially weaker in comparison to previous studies which did not control  
363 movement preparation time [45]. This might be due to differences in our experimental procedure, for

364 example the stimulation intensity employed here (1.5mA) was weaker than that of previous studies (2mA)  
365 [18, 19, 21, 40]. Note however that a recent study that used a 2.0mA stimulation intensity found non-  
366 significant effect of cerebellar tDCS on sensorimotor adaptation [46], and recent evidence suggests that  
367 anodal tDCS intensities of 1.0 mA, 1.5mA and 2.0mA cause in similar effects on cortical excitability, at  
368 least in the motor cortex [47]. However, this comprehensive review by Jamil et al. (2016) shows that there  
369 are typically large individual differences in stimulation sensitivity, which might have contributed to the  
370 weak effect of cerebellar tDCS on error compensation in our results.

### 371 **Possible cerebellar involvement in explicit and implicit learning**

372 Explicit and implicit processes are thought to work in tandem to compensate for errors resulting from  
373 perturbed sensory feedback [48-51]. It is possible that previously reported improvements in error  
374 compensation with cerebellar anodal tDCS might be partly driven by augmentation of explicit processes  
375 that result in the rapid error compensation early in sensorimotor adaptation [14]. The proposal that  
376 cerebellar anodal tDCS might alter explicit processes is consistent with reports of faster error  
377 compensation with cerebellar anodal tDCS in older adults [19], who have been widely documented to  
378 show slower error compensation as a result of poorer explicit learning [34, 52-55]. Poorer cerebellar  
379 function in older adults has also been linked to poorer explicit learning [56, 57]. There is evidence  
380 supporting cerebellar involvement in explicit learning: although cerebellar degeneration patients can  
381 employ an strategy when explicitly instructed to do so, they appear unable to spontaneously generate an  
382 explicit strategy [16], unlike healthy controls. Explicit learning is likely to be sensitive to reinforcement-  
383 based processes that influence movement selection[58]. The employment of reinforcement-based explicit  
384 processes is affected by cerebellar function, as recent studies show that although cerebellar degeneration  
385 patients can sometimes show residual ability to use compensatory mechanisms (e.g., online feedback  
386 and/or reinforcement mechanisms) to adapt movements to perturbed feedback that has been imposed  
387 gradually [59-63], they are poorer at learning from reinforcement [64, 65], possibly because of increased  
388 motor noise. The possibility that explicit processes are supported by cerebellar function is consistent with  
389 a growing body of work demonstrating the role of the cerebellum in predicting sensory events and fine-  
390 tuning of behavioral responses in many “non-motor” cognitive processes (for reviews, see [66, 67]. Thus,  
391 it seems likely that the cerebellum contributes to both explicit and implicit processes in sensorimotor  
392 adaptation[68].



393 There is evidence supporting the suggestion that distinct regions of the cerebellum support explicit and  
394 implicit processes in sensorimotor adaptation. For example, patients with posterior cerebellar lesions  
395 show deficits in the early part of error compensation thought to be primarily driven by explicit strategic  
396 processes, but not deficits in aftereffects thought to be driven by implicit processes [11]. In contrast,  
397 patients with superior cerebellar lesions showed more severe deficits in both the rate and extent of error  
398 compensation, as well as aftereffects, suggesting involvement of the superior cerebellum in implicit  
399 processes in sensorimotor adaptation [11]. Neuroimaging work in prism adaptation [69-71] also support  
400 the idea that distinct sub-regions of the cerebellum sub-serve implicit and explicit processes. In prism  
401 adaptation, the early phase of error compensation dominated by explicit processes is thought to be sub-  
402 served by a network encompassing the ventro-caudal dentate nucleus to the posterior parietal cortex [72,  
403 73]. This proposal is supported by neuroimaging evidence showing greater activation of the ventro-caudal  
404 dentate nucleus and the posterior cortex of the cerebellum in the early phase of error compensation than in  
405 the late phase of error compensation [74]. Implicit processes are associated with greater cerebellar  
406 activation in the right anterior lobules IV/V in prism adaptation [75] and in lobule V and VI in adaptation  
407 to visuomotor rotations [76]. Our current findings do not allow us to speculate on which area of the  
408 cerebellum is affected by our cerebellar stimulation protocol, as tDCS effects are not focal. Employing  
409 concurrent cerebellar tDCS with fMRI whilst experimentally manipulating the use of explicit strategies  
410 might help illuminate how the cerebellum contributes to explicit processes during sensorimotor adaptation.

#### 411 **Summary**

412 Previous work using non-invasive brain stimulation demonstrated that the cerebellum plays a role in  
413 sensorimotor adaptation, however, because these studies did not dissociate explicit and implicit processes  
414 that occur during adaptation, it was unclear whether the cerebellum plays a role in implicit or explicit  
415 processes, or both. Here, we show that when explicit re-aiming processes is suppressed, increasing  
416 cerebellar excitability via anodal tDCS increases implicit remapping after adaptation to a 30° rotation.  
417 Thus, the cerebellum contributes to implicit sensorimotor remapping when people learn to compensate a  
418 visuomotor rotation.

419

420

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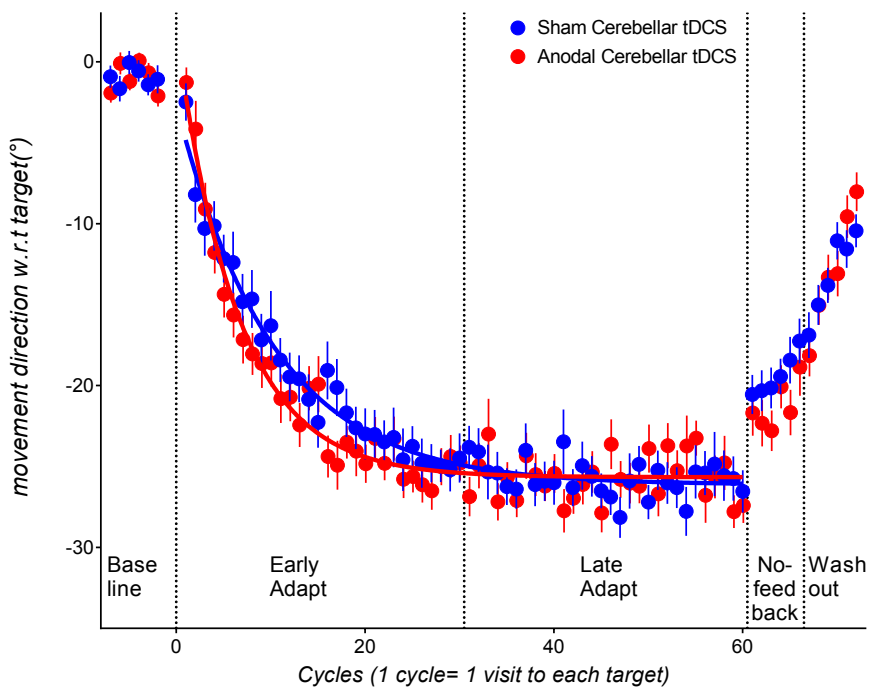
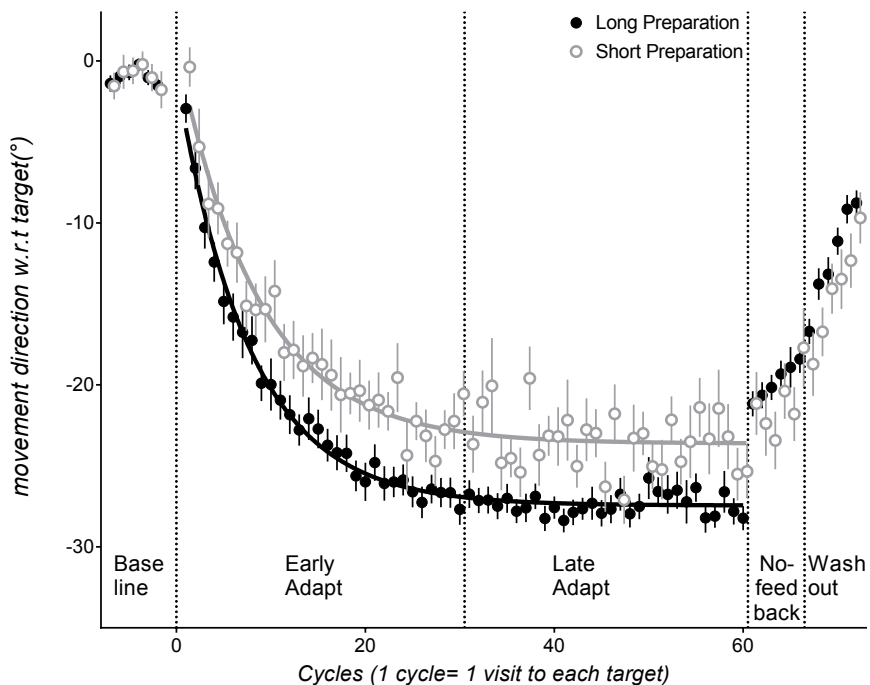
652 *Figure Legends*

653 *Figure 1. Top panel: cycle by cycle movement directions relative to the target, averaged across the short*  
654 *preparation time groups (clear circles), and the long preparation time groups (grey circles) (i.e., pooled*  
655 *across the cerebellar tDCS anodal and sham conditions). Bottom panel: cycle by cycle movement*  
656 *direction relative to the target, averaged across all participant groups who received cerebellar sham*  
657 *tDCS and cerebellar anodal tDCS (i.e., pooled across long and short preparation time groups). Data*  
658 *from the counterclockwise rotation groups were sign-transformed to allow statistical comparisons*  
659 *between clockwise and counterclockwise groups. In the adaptation block, values closer to -30° indicate*  
660 *more complete error compensation. In the no-feedback block, values closer to -30° indicate more implicit*  
661 *remapping, as participants were instructed that the rotation was removed, and that they were to aim*  
662 *straight towards the target without visual feedback of their movement. Error bars indicate standard*  
663 *errors of the mean. Lines indicate group mean data fit to the single-rate exponential function for the*  
664 *adaptation phase.*

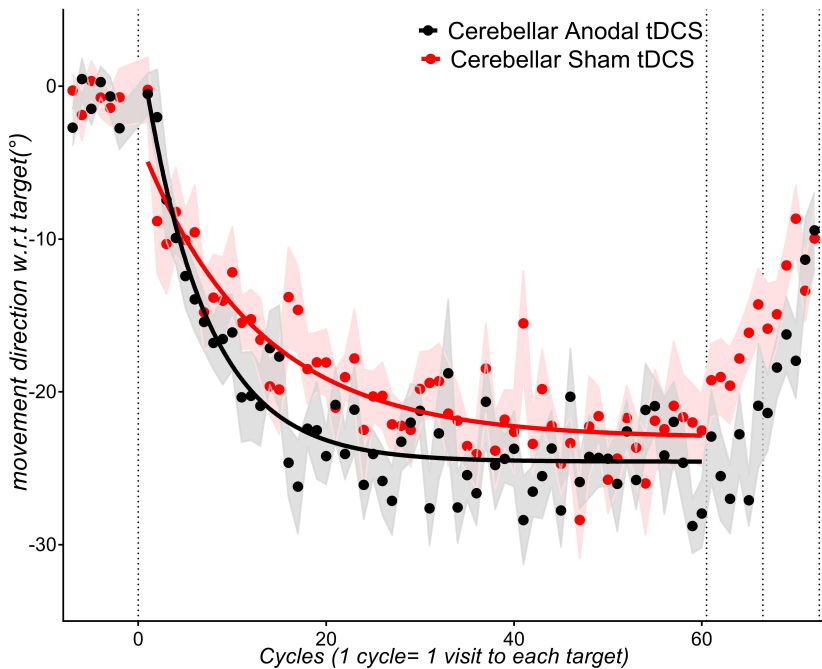
665  
666 *Figure 2. Top: Cycle by cycle movement directions with respect to the target for the short preparation*  
667 *time participants who received cerebellar anodal tDCS (red symbols) and cerebellar sham tDCS (black*

668 *symbols). Bottom: cycle by cycle movement directions with respect to the target for the long preparation*  
669 *time participants who received cerebellar anodal tDCS (pink circles) and cerebellar sham tDCS (grey*  
670 *circles). Solid lines indicate group mean data fit to the single-rate exponential function for the*  
671 *adaptation phase.*

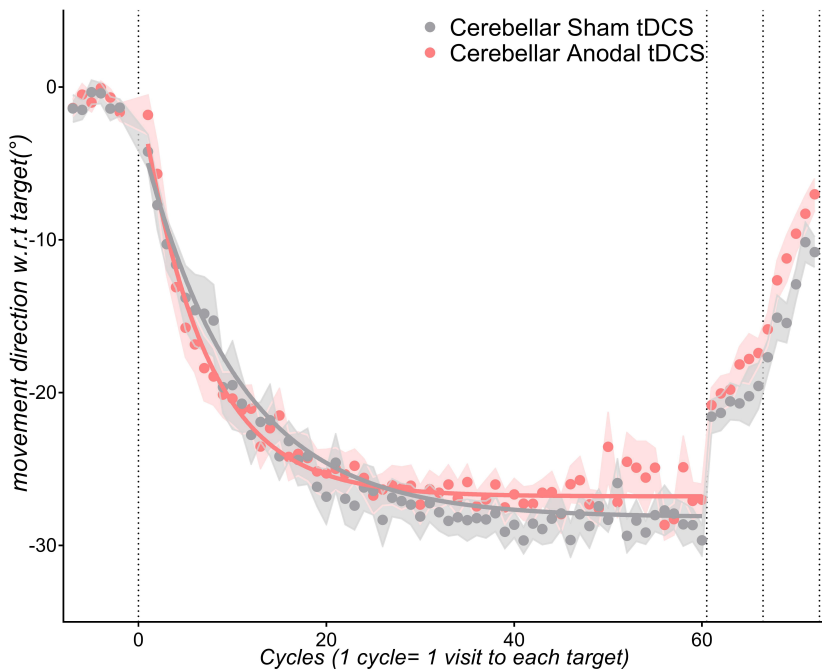
672  
673 *Figure 3. Group mean (error bars are SEM) for data from the cerebellar anodal tDCS condition (Stim,*  
674 *red) and the cerebellar sham tDCS condition (Sham, blue). A: rate constants from fitting a single-rate*  
675 *exponential function to cycle-averaged movement directions from the adaptation block—larger values*  
676 *indicate faster adaptation to the rotation. B & C. Group mean movement direction from the no-feedback*  
677 *block, averaged across cycles (B) or cycle-by-cycle (C)—values closer to  $-30^\circ$  represent more adapted*  
678 *movements. D. Slopes from fitting a straight line to individual cycle-averaged movement directions in the*  
679 *washout block-- larger values indicate faster de-adaptation to the unadapted state.*

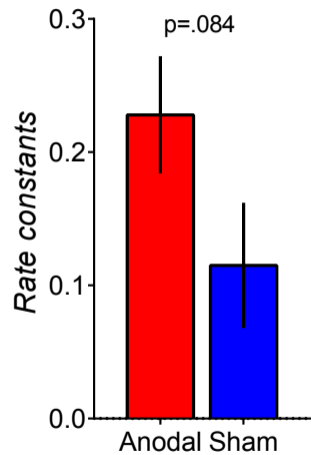
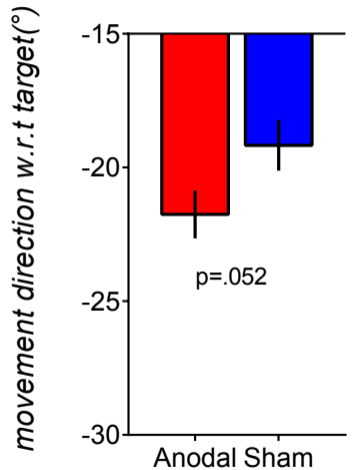
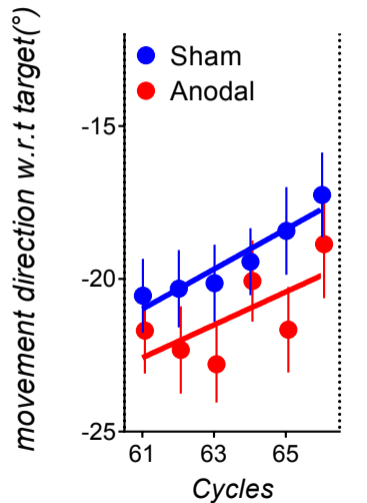


## Short Preparation Time



## Long Preparation Time



**A.** Adaptation Rate**B.** No-feedback block**C.** No-feedback block**D.** Washout Deadadaptation Rate